

TEMPORAL AND SPATIAL DYNAMICS OF PARASITE RICHNESS IN A *DAPHNIA* METAPOPULATION

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Abstract. Several models have been suggested to explain variation in parasite richness among populations. Most of these models are based on epidemiological factors (population size, number of host species), biological factors (patch quality, interspecific competition) and the spatial and temporal structure of the host metapopulation. We studied the parasites of 137 rock pool populations of the planktonic crustacean *Daphnia magna* to determine the factors that account for total parasite richness, richness of endoparasites and epibionts, and the presence/absence patterns of individual parasite species. The rock pools of 86 of these populations have been studied since 1982, and it is known how long these pools have been continuously inhabited by *Daphnia*. By far the best predictor of total parasite richness was host population age, which explained ~50% of the variance. While endoparasite richness increased linearly with age over 16 yr, epibiont richness saturated ~3 yr after pool colonization, which may be explained by the higher dispersal rate of epibionts. After we corrected for host population age, endoparasite richness was positively correlated with the water volume of the rock pool (an estimator for host population size), and epibiont richness was correlated with water conductivity. Pools with lower water conductivity (less influenced by the brackish water of the Baltic Sea) had more epibiont species. The local network size of the host metapopulation (local pool density and number of pools per island) hardly influenced parasite richness. There was also no strong indication of spatial effects (isolation by distance and island effects) on the parasite community. The factors that were correlated with species richness were, however, not the same as those related to the presence of single parasite species. At least for certain epibionts, it appears that presence/absence patterns were influenced by interspecific competition. In conclusion, our analysis shows that predictions derived from epidemiological and temporal models, but not from spatial models, can explain parasite richness patterns, despite apparent conflicting patterns found for individual parasite species. Our analysis extends the scope of these models, which were previously supported mainly with helminths, to bacteria and protozoa.

Key words: bacteria; competition; interspecific; colonization; *Daphnia magna*; endoparasite; epibiont; metapopulation; parasite richness; protozoa; rock pools; spatial patterns; temporal patterns.

INTRODUCTION

There is hardly any multicellular organism that is not parasitized during some stage of its life. But not every host population harbors every potential parasite species. Most host populations coexist with only a small set of their potential parasites. A number of factors have been suggested to explain why in a given population some parasites are present, while other are not (Price 1980, Anderson and May 1991, Hanski and Simberloff 1997, Poulin 1998). It is the aim of this study to find correlational evidence to support some of the predicted relationships.

The factors proposed to explain parasite community

richness can be roughly grouped into four partially overlapping categories (Table 1). The first category is here called epidemiological factors and concerns factors related to host population size. Larger populations (often described by a larger geographic range) have been predicted and shown to harbor more parasite species than smaller populations (Anderson and May 1978, 1979, 1991, Price and Clancy 1983, Gregory 1990, Dobson and Pacala 1992). This may be because larger populations have higher absolute encounter rates with parasites, are less likely to pass through population bottlenecks (which may cause parasite extinction), are more likely to be above the parasite specific population threshold size (above which parasite $R_0 > 1$ [Anderson and May 1991]), and may also be more dense on average. Linked to the population size argument is a prediction concerning the number of host species that a parasite can attack besides the host species of interest (focal host species). With more hosts occurring in sym-

Manuscript received 27 October 1999; revised 26 June 2000; accepted 30 November 2000; final version received 22 January 2001.

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TABLE 1. Categories of ecological factors that were predicted to influence parasite species richness on *Daphnia* in Baltic seacoast rock pools off southern Finland.

Category	Factor	Sign of predicted association	Variable studied or test employed	Sign of predicted association
1) Epidemiological factors	population size	+	rock pool volume	+
	no. host species	+	no. <i>Daphnia</i> species	+
2) Network size and density	local density of patches	+	host populations within 10-m radius	+
	Spatial factors	distance to neighbor	short distance is correlated with high similarity	test for spatial autocorrelation
3) Temporal factors	age of patch	+	time since <i>D. magna</i> colonized pool	+
			time since <i>Daphnia</i> colonized pool	+
4) Patch quality	impact of the sea	-	water conductivity	-
			water color	+
			relative distance to sea	+
				+

patry, the total host population size (and possibly total host density) is likely to become larger. Thus, more parasites may be found on the focal species because of a lower likelihood that a parasite goes extinct during a population crash of one of these host species (Table 1). The contention that parasite richness is affected by the size of the host population is analogous to a version of the species-area relationships (Simberloff and Moore 1996).

The second category concerning parasite presence and absence in particular populations takes the spatial dynamics of extinction and colonization into account (Kuris et al. 1980, Simberloff and Moore 1996) (Table 1). Patches with host populations can be viewed as islands (MacArthur and Wilson 1967) or as parts of a metapopulation (Hanski and Simberloff 1997, Hanski 1999), and the theories for spatially subdivided populations can be used to derive predictions for parasite presence and absence. With increasing isolation, colonization becomes less likely. Therefore, it has been predicted that spatial isolation of host populations reduces parasite richness (Kennedy and Bush 1994, Simberloff and Moore 1996). Further, in subdivided habitats connected by dispersal, species may be able to persist that would not be able to persist in a single population. From this, one can predict that host populations in close proximity to each other and populations within larger and denser networks are likely to have more parasites than isolated populations. These effects of metapopulation network size and density are analogous to the host population size effect in epidemiology (see Table 1, category 2).

Category 3 in Table 1 concerns the temporal dynamics of host population turnover. Recently founded host populations are likely to have fewer parasite species than older populations, because in young host populations the parasite community is not yet saturated (Dobson and Pacala 1992). This is consistent with the observation that introduced host species have fewer parasite species than resident hosts (Guégan and Ken-

nedy 1993). There may be an evolutionary and an ecological explanation for this. The evolutionary hypothesis states that young populations have less parasites because it takes time for parasites present in the habitat to extend their host range to the new host species. Of more importance for the issues addressed in this study is the ecological hypothesis, which states that young host populations have not yet encountered all parasites for which they are potential hosts. This isolation by encounter probability hypothesis is analogous to the observation that older host individuals often have more parasites than younger individuals (Doigel 1964). However, whereas body size increases with age, and thus confounds the age-richness relationship with a size-richness relationship (Simberloff and Moore 1996), the age of the host population is usually not confounded by population size (except over short time scales).

Parasite richness patterns can be further influenced by habitat characteristics (category 4, Table 1). Ectoparasites in particular may be influenced by their physicochemical environment (e.g., temperature, toxins, and salinity). However, as the criteria for assessing habitat quality may differ among parasite species, it is usually not possible to make general predictions about parasite richness in relation to environmental variables. Nevertheless, for *Daphnia* parasites in the rock pools along the Baltic sea coast we derived a prediction based on the observation that species richness of free living organisms in rock pools (e.g., algae, water beetles, rotifers) generally declines with increasing salinity (Järnefelt 1940, Lindberg 1944, Ghilarov 1967, Ranta 1982). It has been argued (references as before) that this is because rock pools are essentially freshwater habitats and that increased salinity represents a strong environmental stress for most species inhabiting rock pools. We speculate therefore that parasite richness, and in particular ectoparasite richness, will decline with increasing salinity as well.

Here we present a study that aims to find correla-

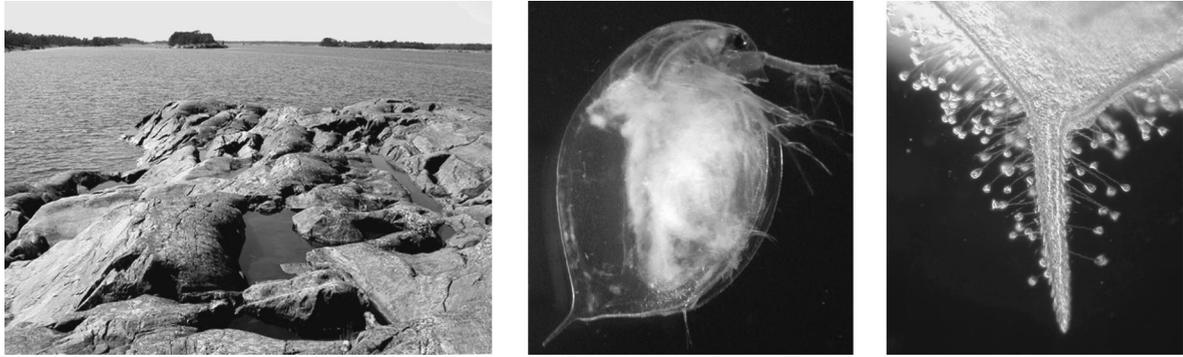


PLATE 1. (Left) A typical island shoreline with several small pools among the rocks, in the Tvaerminne Archipelago of the Baltic Sea. In the background, the island of Furusjar (in the upper left) and other islands are visible. (Middle) An adult *Daphnia magna* infected with the microsporidian parasite *Octosporea bayeri*. The infection is visible as the white diffuse mass filling much of the host's body cavity. (Right) Spina of an adult *Daphnia magna* covered with the peritrich ciliate *Vorticella octava*. This epibiont attaches to the host with the help of a contractible stalk. All photographs are by Dieter Ebert.

tional support for the predictions listed in Table 1. We tried to avoid a number of problems known to deflate the proportion of unexplained variance in the data. First, the number of parasite species recorded is usually strongly correlated with the number of host individuals sampled and the time and effort spent by the investigators (Guegan and Kennedy 1996). To avoid these problems, we sampled the same number of individuals per site and all samples were analyzed in a standardized way by the same investigator. Second, much of the evidence cited in support of the predictions listed above are based on studies of macro-ecological patterns, which include several host species. While some of the predictions are robust against phylogenetic correction of host relatedness (e.g., Arneberg et al. 1998), others are not (Poulin 1995, 1998). We avoided this problem by focusing only on one host species. Third, for many parasites, host gender-specific effects have been reported. We avoid this by including only female hosts. With this design for our study, we were able to use multiple regressions to disentangle the effects of explanatory variables. Using bacteria and protozoa, we aim to underline the generality of concepts that have so far mainly been tested with helminths.

THE STUDY SYSTEM

We studied the parasite community of the aquatic crustacean *Daphnia magna* Strauss in a rock pool metapopulation. *D. magna* is a cyclical parthenogen that typically inhabits small to medium sized ponds. It is the largest European species with an adult size ≤ 5 mm (length at maturity about 2–2.5 mm, generation time 7–15 d at 20°C).

In many places along the Baltic Sea, one can find rock pools, small water filled depressions in the bare rocks (see Plate 1, left). Besides their patchy distribution, rock pools are characterized by an inherent instability caused by frequent drying up followed by sudden invasion of brackish water from the Baltic Sea or

of rainwater. The flora and fauna of most rock pools is characterized by freshwater communities rather than by marine organisms (Levander 1900, Lindberg 1944). Many rock pools are inhabited by a number of freshwater invertebrates. Among the more prominent inhabitants are three species of the genus *Daphnia*: *D. magna*, *D. pulex*, and *D. longispina*. *Daphnia* reproduce asexually during most parts of the warmer season and produce resting stages to endure the harsh winter conditions. The resting stages also serve for short and long distance dispersal. The metapopulation dynamics of *Daphnia* have been studied intensively and much is known about the factors that influence extinction and colonization patterns (Lagerspetz 1955, Ranta 1982, Hanski and Ranta 1983, Pajunen 1986, Bengtsson 1993). Among the factors that influence metapopulation dynamics are competition among *Daphnia* species and clones, isolation in space, and a number of factors that characterize the rock pools, such as salinity, pH, rock pool volume, predation and parasitism (Ranta 1979, 1982, Korpelainen 1986, Pajunen 1986, Weider and Hebert 1987, Wilson and Hebert 1992, 1993, Bengtsson 1993, Bengtsson and Milbrink 1995, Bengtsson and Ebert 1998). Rock pools along the southern coast of Finland are mainly found on small islands, which adds an additional level of complexity to the system, as pools on islands might form a metapopulation by themselves and are at the same time part of a metapopulation that includes different islands (Ranta 1982, Hanski and Ranta 1983, Pajunen 1986). The study presented here was conducted in such a hierarchical *Daphnia* metapopulation in southern Finland. In our study area ~ 10 –20% of all rock pool *Daphnia* populations go extinct every year and roughly the same percentage are recolonized, producing a metapopulation with an approximately constant proportion of occupied rock pools over the last 16 yr (Pajunen 1986; V. I. Pajunen, *unpublished manuscript*).

Daphnia species in rock pools are often parasitized

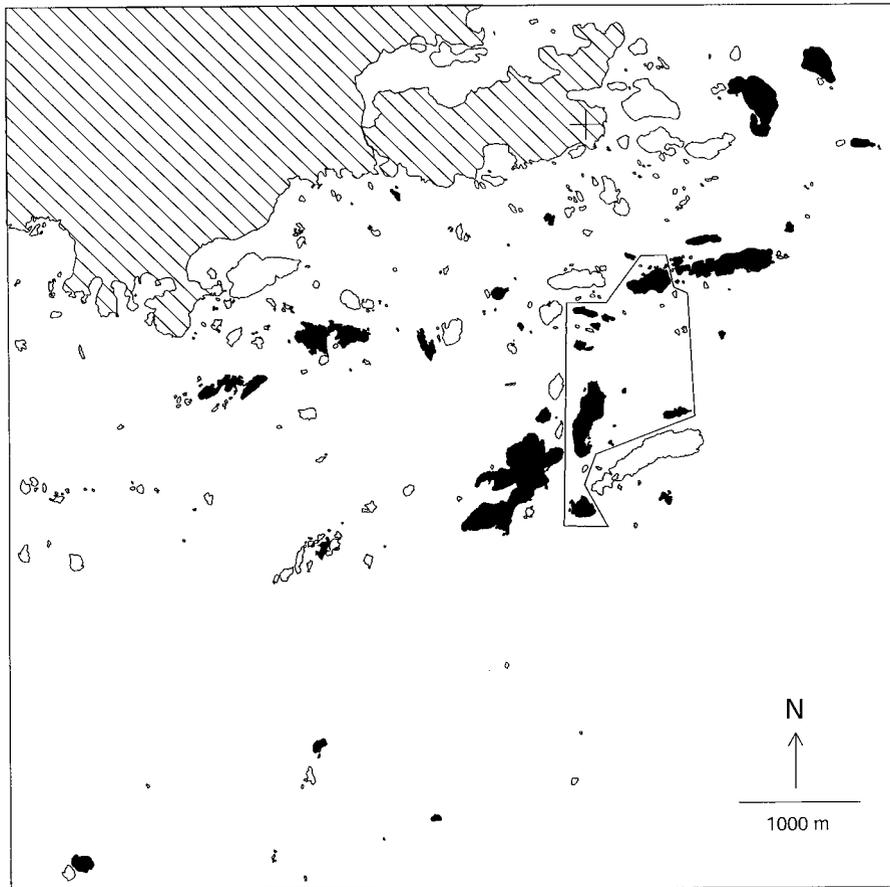


FIG. 1. Map of the study area on the Baltic coast of southern Finland. The mainland and the Tvärminne peninsula are filled with hatched lines. Islands from which we collected samples are shown in black. The polygon surrounds islands of the core area. The cross indicates the Zoological Station Tvärminne at 59°50' N and 23°15' E. To our knowledge, there is no *Daphnia magna* population in the hatched region, but there are populations on islands not included in the study.

by a number of different endoparasites (e.g., bacteria, microsporidia, protozoa) and epibionts (e.g., fungi, algae, peritrich ciliates) (Green 1957, 1974, Bengtsson and Ebert 1998), most of which are *Daphnia*-specific or even species-specific. The epibionts of *Daphnia* are not ectoparasites in the usual sense, as they use the host only as a substrate to hold on and to be carried around. However, intensities of epibionts are often very high, and they can cause a considerable reduction in host fecundity and survival (Green 1974, Kankaala and Eloranta 1987, Allen et al. 1993, Chiavelli et al. 1993, Threlkeld and Willey 1993, Threlkeld et al. 1993, Weissman et al. 1993, Stirnadel and Ebert 1997). Although, epibiont life style suggests that they could attach to any aquatic organism, their populations seem closely connected to the presence of the *Daphnia* host (Green 1957, 1974, Stirnadel and Ebert 1997). That other hosts are less suitable seems also be supported by the epibionts' life history, which seems to have evolved to match the *Daphnia* life history patterns (Green 1974, Chiavelli et al. 1993, Threlkeld and Willey 1993, Threlkeld et al. 1993).

In this study we use the term parasites to include endoparasites and epibionts, but highlight the differences between these two groups by analyzing richness patterns not only for all parasites, but also for epibionts and endoparasites separately. For our analysis we use data from a 16-yr study on the metapopulation dynamics of *Daphnia*, plus data on various geographical, physical, chemical, and biological properties from 137 populations of *D. magna* living in rock pools.

MATERIALS AND METHODS

Study area

We studied a metapopulation on the coast of the Baltic Sea in Southern Finland, at Tvärminne on the Hanko Peninsular (59°50' N, 23°15' E; Fig. 1). Roughly 40% of the rock pools in this area are inhabited with at least one *Daphnia* species (Pajunen 1986). Rock pools belonging to our study area fall into two categories (Fig. 1): rock pools in the core area, which includes 13 islands; and rock pools in the outer area, which includes data from 19 further islands. The rock pools in the core

area have been studied since 1982 (Pajunen 1986); the pools of the outer area were studied only in 1998. In the core area, we studied all rock pools; in the outer area, we usually included only two rock pools per island (on large islands (longest axis > 800 m) up to eight pools). With increasing distance from the core area, we adopted a less dense sampling strategy. The greatest distance between two pools in the outer area is 8940 m. For the study of the parasites of *D. magna*, we have data from 137 rock pools; however, we have temporal data (years 1982 to 1998) on *Daphnia* presence and absence only for 86 rock pools from the core area. We included all pools from the core area that were found to be inhabited by *D. magna* during our sampling trips in the summer of 1998. Thirty-four percent of all pools also had either *D. longispina* or *D. pulex*. None of the pools harbored all three *Daphnia* species.

Data collection

For each rock pool we recorded the geographic location, either with the use of a differential global positioning system, or with hand-drawn maps (scale 1:1250). We recorded the distance to the sea and the distance to the next tree. Rock pools are located in the rocky parts between the sea and the trees on an island. The width of this treeless area is an indication of the impact of the sea on the land and it varies from 3 m in wind- and wave-protected parts of the coast to ~80 m in exposed parts of the coast. As an estimate of the average impact of the sea on the rock pools (e.g., spray of seawater), we calculated the relative distance to the sea, which is the rock pool's distance to the sea divided by the total distance from the sea to the nearest tree. This assumes that the progression of trees is limited by the impact of the sea. As some islands do not have any trees, we calculated this measure only for 116 of the 137 rock pools. We measured the longest axis of each pool, the widest dimension perpendicular to this and the maximal water depth. These data were used to calculate the volume of the rock pool assuming it has the shape of an inverted pyramid (length \times width \times depth/3). We measured the water conductivity (an estimate for salinity) using a portable electronic measuring device. Many rock pools have a brownish water color, because the water is stained by humic acids from terrestrial plants. To quantify this effect, we judged water color on a nine-step scale ranging from clear water (sea water as control) to very dark (about the color of strong tea; compare Bengtsson and Ebert [1998] for a similar method) by holding a glass beaker (5.8-cm diameter) filled with pool water against a light background. As this is a subjective measure, we judged our ability to quantify water brownness by letting two investigators independently rate water samples from 26 rock pools. The correlation of these water color estimates was $r = 0.90$ ($P < 0.0001$).

To investigate *Daphnia* for the presence of parasites, we collected a sample of all *Daphnia* species from each

rock pool that harbored *D. magna*, cooled it on ice, and brought it to the laboratory where it was kept at 12°C and inspected within 3 d. A large sample (>150 adult hosts) was first screened for endoparasites with strong visual effects, for example the bacteria *Spirobacillus cienkowskii*, which makes the hosts bright red, and the bacterium causing the white bacterial disease, which makes the hosts bright white. Both usually occur in low prevalence. Then we investigated 10 adult female hosts from each sample (10 from each *Daphnia* species) for endoparasites and epibionts (compare Stirnadel and Ebert [1997] and Bengtsson and Ebert [1998]). Briefly, each host was first investigated for external epibionts (25 \times and 50 \times magnification) and then dissected and investigated with phase-contrast microscopy (100–400 \times magnification). Only presence or absence of any particular parasite taxon was recorded. We used the papers by Green (1957, 1974), and by Larsson and coworkers (Larsson 1981, 1988, Larsson et al. 1996a, b, 1997, 1998) for identification of parasites. As some parasites could not be identified to the species level, we classified them according to pathology and morphological traits to the nearest taxon possible. We believe that our groups usually include single species, except for the filamentous bacteria, which are likely to include several taxa. Screening a large sample for conspicuous infections and dissecting 10 females per sample, we might have missed some parasite species. However, these species would be without conspicuous pathology, with low prevalence, and only present in few rock pools. Therefore, it seems unlikely that their absence from the data set would influence our results.

Screening for parasites was done between 14 June and 30 July 1998. We use the word "prevalence" to describe the proportion of adult females infected within a sample. Host specificity was judged from those pools in which *D. pulex* or *D. longispina* occurred as well. For the purpose of this study, a parasite was classified as specific when it occurred only on *D. magna*, despite the presence of other *Daphnia* species in the same pool. We report here only on parasite species that include *D. magna* in their host range. In total, 1840 female *Daphnia* were dissected for this study.

In the core area, one of us (V. I. Pajunen) collected data since 1982 on the presence and absence of *Daphnia* species in 508 rock pools (see Pajunen [1986] for details of methods). Briefly, all pools were visited and searched for *Daphnia* twice during the summer season (usually early June and August). If *Daphnia* were present, samples were taken to the laboratory to identify species (*D. pulex* and *D. longispina* are difficult to distinguish in the field). Using these data we calculated host population age (= duration [in years] of continuous inhabitation) for all rock pools with *D. magna* present in 1998. We calculated the *D. magna* population age as well as the time (in years) since a given rock pool was continuously colonized with any *Daphnia*

TABLE 2. Descriptive summary of variables used in this study.

Variable	Mean	Range	N
Dependent variables			
Total parasite richness	2.030	0–7	137
Endoparasite richness	0.664	0–4	137
Epibiont richness	1.004	0–6	137
Epidemiological variables			
Pool volume of water (m ³)	1.52	0.006–27.9	137
Number of <i>Daphnia</i> species	1.34	1 or 2	137
Network size (local pool density)			
Pools with <i>D. magna</i> within 10-m radius	1.54	0–6	97
<i>D. magna</i> pools on the same island	16.76	0–33	86
Temporal component			
Years since <i>Daphnia</i> colonization	8.84	0–16	86
Years since <i>D. magna</i> colonization	7.4	0–16	86
Patch quality			
Conductivity (mS)	1.27	0.018–12.4	137
Water color (on a step ordinal scale)	1.38	0.5–3	137
Relative distance to sea	0.32	0.048–1.0	116
Geographic location			
Location of pool	137
Island on which pool is located	137

Notes: All variables, except “Number of *Daphnia* species” and “Island” are continuous. Sample size is 137 when data from all pools were available and 86 when only data from core area pools were available. Relative distance to sea could only be assessed for islands with trees. The measure of “number of pools within 10-m radius” assumed knowledge of all pools within the area. This was only available for 97 pools.

species. A *Daphnia* species was considered to be absent from a pool if it was not seen for at least 1 yr (two checks).

Using geographic coordinates, we calculated two measures of rock pool network size: We counted the number of *D. magna*-inhabited rock pools per island, and we counted the number of *D. magna*-inhabited rock pools within a radius of 10 m around each rock pool. Volume of pools, conductivity, water color, and number of pools per island were log₁₀-transformed prior to statistical analysis. Table 2 gives a summary of the variables used in this study.

Statistical analysis

Total parasite richness, as well as endoparasite and epibionts richness data, showed a Poisson distribution. Therefore, we tested their dependence on the explanatory variables listed in Table 2 by using Poisson regression (Proc GENMOD, dist = poisson, link = log, type 3 [SAS Institute 1993]). The regression parameters for endoparasite and epibionts were compared with a *t* test. For eight common parasite taxa, we also ran the analysis for each taxon separately using logistic regression (presence/absence data, Proc LOGISTIC [SAS Institute 1990]). “Island” and “Number of *Daphnia* species” per pool were treated as class variables.

We used two approaches to test for correlation between richness measures and the explanatory variables. First we tested for associations between the parasites and each of the explanatory variables separately (Poisson and logistic regressions). Second, we used a multiple regression model, which included all variables (except geographic location). The multiple Poisson and

logistic regressions were done with a stepwise selection procedure (exclusion criterion $P > 0.05$). The multiple regression analysis was only possible for the subset of pools for which we had all variables (see Table 2). As white bacterial disease (= WBD) was rare in the core area, we did not perform the multiple regression for it. The multiple regression permits the identification of those variables that explain most of the variance in the dependent variable. In the tables we indicate significance of tests with and without correcting for multiple tests (Sokal and Rohlf 1981). For each multiple logistic regression we calculated an approximate r^2 (also called “pseudo r square”) estimate following the method by Nagelkerke (1991). For the multiple Poisson regression we calculated pseudo r square estimates from the deviance of the intercept-only model (D_i) and the deviance of the fitted model (D_m) (Kleinbaum et al. 1988) as $r^2 = (D_i - D_m)/D_i$.

Associations among parasite species.—To test whether the occurrence of certain parasite species is positively or negatively associated with the occurrence of other species, we performed Fisher exact tests for all possible combinations of parasite pairs (2×2 tables). We included all parasites that occurred in >10% of the pools in this analysis. If we found that these tests indicated an association between two species, we repeated the multiple regression analysis but included “competitor” variables. This variable gives the number of potential competing species (those with $P < 0.1$ in the Fisher exact tests) (0 for no competitors, 1 for one competitor species, 2 for two, and 3 for three competitors). We report those multiple logistic regressions

TABLE 3. Endoparasite and epibiont taxa recorded for *Daphnia magna* in 137 rock pools.

Symbiont	Taxonomic group	Infected tissue	Mode of transmission†	Percentage infected pools	Prevalence in infected pools (%)	Other <i>Daphnia</i> hosts
Endoparasites						
<i>Pasteuria ramosa</i>	bacteria	body cavity	horizontal	0.7	<10	?
<i>Spirobacillus cienkowski</i>	bacteria	haemolymph	? (horizontal)	3.6	<2	<i>D. pulex</i> , <i>D. longispina</i>
White bacterial disease	bacteria	fat cells	horizontal	5.1	14.2	none
Bacterium 2	bacteria	haemolymph	?	0.7	<2	?
Bacterium 3	bacteria	haemolymph	?	0.7	<2	?
<i>Octosporea bayeri</i>	microsporidia	ovaries, fat cells	vertical and horizontal	44.9	44.4	none
<i>Ordozpora colligata</i>	microsporidia	gut epithelium	horizontal	2.1	100	none
<i>Larssonia</i> sp.	microsporidia	muscle tissue	? (intermediate host?)	8.0	21.8	<i>D. pulex</i> , <i>D. longispina</i>
Epibionts						
Filamentous bacterium‡	bacteria	carapace, antennae	horizontal	5.8	55	<i>D. pulex</i> , <i>D. longispina</i>
<i>Vorticella octava</i>	ciliata	carapace, antennae	horizontal	38.3	88.4	<i>D. pulex</i> , <i>D. longispina</i>
<i>Epistylis helenae</i>	ciliata	carapace, antennae	horizontal	24.0	80.9	<i>D. pulex</i> , <i>D. longispina</i>
<i>Rhabdostylis</i> sp.	ciliata	carapace, antennae	horizontal	6.7	86.6	<i>D. pulex</i> , <i>D. longispina</i>
<i>Amoebidium parasiticum</i>	fungus	antennae (carapace)	horizontal	26.2	60.2	<i>D. pulex</i> , <i>D. longispina</i>
<i>Chlorangiella</i> sp.	algae	carapace, antennae	horizontal	18.9	66.5	<i>D. pulex</i> , <i>D. longispina</i>
<i>Colacium vesiculosum</i>	algae	carapace, antennae	horizontal	13.1	93.8	<i>D. pulex</i> , <i>D. longispina</i>
<i>Protoderma</i> sp.	algae	carapace	horizontal	3.6	40	?

Notes: Entries are sorted according to taxonomic group. A question mark (?) indicates that we did not have enough information on this aspect.

† Horizontal indicates transmission through waterborne transmission stages; vertical indicates transmission through the eggs from mother to offspring. A question mark (?) indicates unknown mode of transmission. Parentheses indicate cases where vertical transmission was experimentally excluded (offspring were healthy), but horizontal transmission was not achieved.

‡ This group is likely to include several species.

in which this competitor variable entered as a significant factor in the stepwise selection procedure.

Spatial autocorrelation.—For all common parasite taxa we tested for spatial autocorrelation using the software R-Package (Legendre and Vaudor 1991). Moran's autocorrelation coefficient *I* was calculated for various distance classes. *I* ranges from -1 to 1 , with zero indicating no autocorrelation, negative values indicating negative autocorrelation, and positive values indicating positive autocorrelations. A positive autocorrelation indicates that pools are more similar to each other (a parasite occurs in both or a parasite occurs in neither) than expected by random. Initially we used distance with a stepwise increasing class width (0–10, 10–20, 20–30, . . . 90–100, 100–200, 200–300, . . . 900–1000, 1000–2000, 2000–3000, . . . 8000–9000 m). However, since we found effects only on a very local scale (<100 m), we present only data for distances ≤ 100 m, with a class width of 10 m. Using the distance classes and Moran's *I*, we show for each species a correlogram, i.e., the change in *I* across distance classes (for discussion, see Sokal and Oden [1978], Upton and Fingleton [1985], and Legendre and Fortin [1989]).

RESULTS

Sixteen parasite taxa were identified, including eight endoparasites (five bacteria and three microsporidia) and eight epibionts (one bacterium, three ciliates, one fungus, and three algae) (Table 3). Generally epibionts were more common than endoparasites, with five out of eight epibionts being present in >10% of the pools, while only one of eight endoparasites was common. However, the endoparasitic microsporidium *Octosporea bayeri* was the most abundant parasite in the entire area (see Plate 1, middle), occurring in nearly 45% of the pools. This is the only parasite known to be both horizontally (through water-borne spores) and vertically (through resting and parthenogenetic eggs) transmitted (*D. Vizoso* and *D. Ebert*, unpublished data).

Host specificity appears low for the epibionts, which generally infect all three *Daphnia* species recorded from the rock pools (Table 3). The endoparasites range from being specific to *D. magna* (e.g., *Ordozpora colligata*, *Octosporea bayeri*) to being unspecific (e.g., *Larssonia* spp.).

Before analyzing the effects of the variables listed

TABLE 4. Matrix of correlations among for independent variables in a study of a *Daphnia* parasite metacommunity.

Independent variable	Independent variable							
	2	3	4	5	6	7	8	9
1) Pool volume	0.29**	-0.07	0.02	0.28**	0.37***	0.05	-0.13	0.13
2) Number of <i>Daphnia</i> species		0.19	0.19	0.10	0.19	-0.19	0.13	0.42***
3) No. pools within 10-m radius			0.38***	0.014	0.02	0.07	0.05	-0.08
4) No. pools per island				0.05	0.13	0.13	0.14	0.09
5) Age of <i>D. magna</i> population					0.88***	-0.04	0.28**	0.19
6) Age of <i>Daphnia</i> population						-0.11	0.31**	0.27*
7) Water conductivity							-0.37***	-0.19
8) Water color								0.36**
9) Relative distance to sea								

Notes: After adjustment for multiple tests, only the correlations shown in boldface type are significant. Numbers in italic indicate correlations among variables of the same category (e.g., variables 7, 8, and 9 all indicate the influence of the marine environment).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

in Table 2 on the parasite community, we tested to what degree these variables are independent from each other. Table 4 lists the Spearman correlation matrix for all variables that can be measured on a quantitative scale. Of the six correlations computed within the four ecological groupings listed in Table 2 (epidemiological variables, network size, temporal components, and patch quality, five were significant (entries along the diagonal in Table 4), while only six (two after correcting for multiple tests) out of 30 correlations among variables belonging to different groups were significant. These correlations have to be taken into account

in the interpretation of the multiple regression analysis. However, in general the correlations appear to us not strong enough (the correlation between the two age measures is the only exception) to justify excluding one of the variables or combining them into compound variables (e.g., using principal components analysis).

Associations with single explanatory variables

Epidemiological factors.—Pool volume was positively correlated with the number of all parasites and endoparasite richness (Table 5). The number of all parasites and the number of epibionts was correlated pos-

TABLE 5. Tests for associations (Poisson regression) between *Daphnia*-parasite richness measures and single explanatory variables.

Explanatory variable	Type of data	Association statistic	Richness (number of)			<i>t</i> test
			All parasites	Endoparasites	Epibionts	
Epidemiological variables						
Pool volume	continuous	slope	+0.291	+0.606	+0.107	2.94**
		Wald χ^2	12.81***	19.01***	1.13	
No. <i>Daphnia</i> species/pool	class	
		Wald χ^2	4.83*	1.09	3.78*	
Network size						
No. pools within 10-m radius	continuous	slope	+0.047	+0.005	+0.066	0.57
		Wald χ^2	0.921	0.002	1.26	
No. pools per island	continuous	slope	+0.361	+0.60	+0.263	0.90
		Wald χ^2	5.00*	3.94*	1.90	
Population age						
Colonization by <i>D. magna</i>	continuous	slope	+0.013	+0.054	+0.032	0.82
		Wald χ^2	9.98**	5.94*	4.73*	
Colonization by any <i>Daphnia</i>	continuous	slope	+0.061	+0.071	+0.055	0.58
		Wald χ^2	25.41***	11.08***	14.79***	
Patch quality						
Conductivity	continuous	slope	-0.204	-0.163	-0.212	0.22
		Wald χ^2	4.00*	0.84	2.89	
Water color	continuous	slope	+0.983	+0.052	+1.38	1.22
		Wald χ^2	3.70	0.003	4.88*	
Relative distance	continuous	slope	+0.619	+1.180	+0.294	1.67
		Wald χ^2	5.40*	7.54**	0.76	

Notes: Two entries are given in each cell of the richness columns where parameter estimates are possible. The first number is a regression slope; the second is a Wald χ^2 value. The last column shows *t* tests for the comparison of the regression parameters of the endoparasite and the epibionts. After adjustment for multiple tests, only the correlations shown in boldface type are significant.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

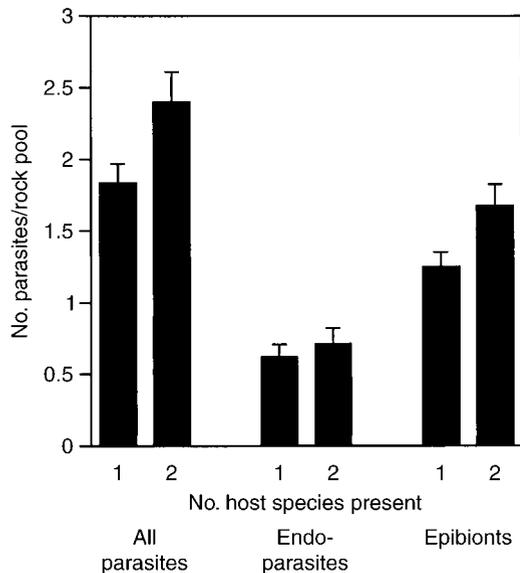


FIG. 2. Number of species of parasites, endoparasites, and epibionts (mean \pm 1 SE) found on *Daphnia magna* in relation to the number of host (*Daphnia*) species per rock pool. The difference in the number of parasites per rock pool for pools with one or two host species for all parasites and epibionts is significant (Table 5).

itively (but weakly) with the number of *Daphnia* species per rock pool (Fig. 2). However, while the first difference between endoparasites and epibionts was significant, the latter was not (Table 5).

The presence of all three common endoparasites was correlated positively with pool volume (Table 6, Fig. 3), while presence of none of the common epibionts was correlated with pool volume. In contrast, three epibionts were significantly associated with the number of *Daphnia* species in the pools, while for the three common endoparasites no such trend was apparent. Interestingly the association between *Vorticella octava* and the number of *Daphnia* species was negative, while it was positive for *Epistylis helenae* and *Chlorangiella* sp. All three epibionts infect all *Daphnia* species in the study area.

Network size.—The variables describing network density and size generally showed poor associations with richness and presence/absence measures. There was a weak positive association between the number of inhabited rock pools per island and both the total and endoparasite richness (Table 5). None of the three richness measures was correlated with the number of pools within a 10-m radius.

E. helenae and *Amoebidium parasiticum* were the only parasites whose presence was correlated with the local density of inhabited rock pools (Table 6). Interestingly, however, this association was positive for *E. helenae* and negative for *A. parasiticum*. There was also a weak positive association between *Octosporea*

bayeri and the number of inhabited pools per island (Table 6).

Temporal variables.—The number of all parasites, endoparasites, and epibionts was correlated positively with both measures of host population age (Table 5, Fig. 4), indicating that older host populations harbor more parasite species. There appears a difference in the shape of the relationship. While the number of endoparasites increases with time since colonization linearly, the number of epibionts is low in young *Daphnia* populations, but reaches an asymptote after only 3 yr, suggesting that the epibiont community is rapidly saturated. Accordingly, the population age effect for epibionts disappeared when we excluded young populations (<3 yr old) from the analysis ($P > 0.3$).

Given the strong associations between host population age and richness, it is surprising to see that hardly any of the parasite species alone revealed an association with host population age (Table 6). The strongest association is between the presence of *Octosporea bayeri* and the age of host population, disregarding which *Daphnia* species arrived in the rock pool first (Table 5). As the two age measures were highly correlated with each other (Table 3), it is not surprising that presence/absence of *Octosporea bayeri* is significantly correlated with both variables, although it was never found to infect *D. longispina* or *D. pulex*.

Patch quality.—There was a weak indication that rock pools with a stronger marine influence (higher conductivity, lighter water color, and shorter distance to the sea) have fewer parasite species (Table 5). Total parasite richness was negatively correlated with conductivity and positively correlated with the relative distance to the sea. Water color was correlated positively with the number of epibionts and the relative distance to the sea with the number of endoparasites.

Table 6 reveals a number of correlations between epibiont species and variables related to the impact of the sea on the rock pools, but there was no single significant correlation between an endoparasite species and these variables. Thus, it appears that epibionts are more strongly influenced by the external environment than endoparasites, although not with a consistent pattern. *Vorticella octava* appears to be found more often in light colored water in pools close to the sea, while the opposite seems the case for *Colacium vesiculosum* and *Epistylis helenae*.

Multiple regression analysis

The multiple Poisson regression with stepwise selection revealed a strongly simplified pattern of associations between the number of parasites and the independent variables. For all three richness measures, the age of the host population entered the regression first and remained significant (Table 7). Total richness was correlated further with the number of other *Daphnia* species in the pools, the endoparasite richness was further explained by pool volume, while epibiont rich-

TABLE 6. Tests for associations between parasite presence/absence data and single explanatory variables in a study of parasites in a *Daphnia* metapopulation.

Explanatory variable	Type of data	Endoparasites			Epibionts				
		<i>Octosporea bayeri</i>	<i>Larssonia</i>	White bacterial disease	<i>Vorticella octava</i>	<i>Epistylis helenae</i>	<i>Amoebidium parasiticum</i>	<i>Chlorangiella</i>	<i>Colacium</i>
Epidemiological variables									
Pool volume	continuous	0.513 6.71**	0.234 9.91**	0.347 4.10*	1.660 3.64	0.66 2.17	0.816 0.55	0.588 3.09	0.823 0.30
No. <i>Daphnia</i> species/pool	class	+0.181 0.74	+0.048 0.02	+0.19 0.24	-0.65 9.24**	+0.77 13.04***	-0.088 0.18	+0.76 11.21***	+0.307 1.37
Network size									
No. pools within 10-m radius	continuous	0.962 0.07	0.724 2.17	...	0.971 0.04	0.539 11.37***	2.081 8.09**	0.865 0.70	0.985 0.01
No. pools per island	continuous	0.33 5.34*	0.621 0.27	...	1.55 0.916	0.200 6.147*	2.034 1.80	0.447 1.89	3.088 3.13
Population age									
Colonization by <i>D. magna</i>	continuous	0.89 8.93**	0.914 1.66	...	1.003 0.01	0.940 2.50	0.953 1.21	0.960 0.97	0.941 1.27
Colonization by any <i>Daphnia</i>	continuous	0.878 12.64***	0.857 2.74	...	1.035 1.03	0.927 3.87*	0.917 3.59	0.895 6.07*	0.920 2.18
Patch quality									
Conductivity	continuous	1.230 0.51	1.227 0.14	0.764 0.18	0.613 2.505	2.540 5.49*	1.888 3.19	2.101 3.44	2.049 2.21
Water color	continuous	1.700 0.13	1.908 0.06	0.898 0.01	192.95 8.30**	0.027 3.88*	0.13 5.60*	0.247 0.56	<0.001 10.50**
Relative distance	continuous	0.237 2.76	0.118 3.26	0.128 1.83	16.58 6.22*	0.278 1.94	0.201 3.13	0.186 3.32	0.063 6.75**

Notes: We used logistic regressions, except for the class variable “No. *Daphnia* species/pool,” which was tested with a generalized linear model with a binomial error distribution and a logit link function. The first entries in each data cell for endoparasites and epibionts are odds ratios, except for number of *Daphnia* species/pool, where regression slopes are given. Odds ratios < 1 indicate positive associations; ratios > 1 indicate negative associations. In the second line of each cell Wald χ^2 values are given. After adjustment for multiple tests, only the correlations shown in boldface type are significant. Ellipses indicate that no estimate was possible due to the rareness of parasites in the core area.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ness was further explained by conductivity (Table 7). When excluding young populations from the analysis (<3 yr), population age no longer entered the regression for epibiont richness, supporting the impression

from Fig. 4 that epibiont richness reaches an asymptote after a few years. In this case epibiont richness was only explained by the number of *Daphnia* species ($\chi^2 = 5.75, P = 0.016$).

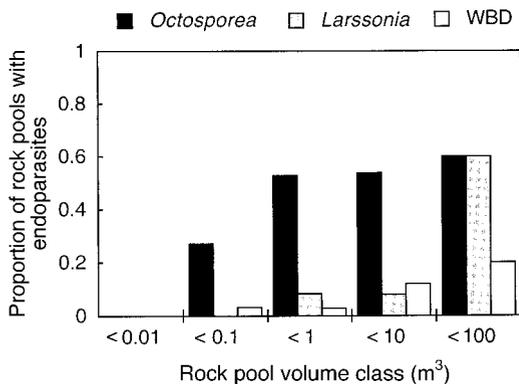


FIG. 3. Relationship between rock pool volume (in size classes) and the proportion of *D. magna* populations infected with *Octosporea bayeri*, *Larssonia*, or WBD. We sampled $N = 137$ rock pools. The increase in the proportion of parasitized populations is significant for all three parasites (Table 5).

The multiple regression of the seven parasites common in the core area showed strong variation among species (Table 7). The regression for *Octosporea bayeri* included host population age as the only factor, while the *Larssonia* regression included pool volume and the number of inhabited rock pools within a radius of 10 m. The regressions for two epibionts included the number of inhabited pools within a 10-m radius but with opposite sign. The regression for three epibionts included a measure of water quality. All three epibionts prefer pools that are lighter or less saline. *V. octava* showed a negative association with the number of *Daphnia* species in the pool. This is surprising, as *V. octava* is an unspecific parasite for which we expected a positive association with the number of host species (Table 1).

Association among parasite species

We tested pairs of common parasites (found in >10% of pools) for independence of associations. All seven

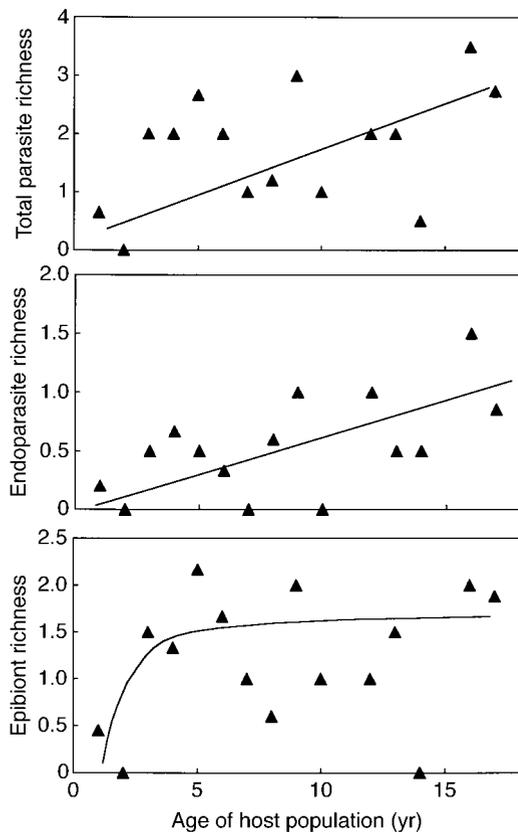


FIG. 4. The number species of parasites (top), endoparasites (middle), and epibionts (bottom) found in the *Daphnia magna* rock pools in 1998 plotted against the time that a pool has been continuously inhabited by *Daphnia*. The mean number of parasite species is given for each age class of the x -axis. Note that the oldest age class includes populations that were founded in 1982 or earlier. Curves were fitted by hand. For statistics, see Tables 5 and 7.

significant associations were due to a lack of populations in which two parasites co-occurred (Table 8). All of the strong negative associations ($P < 0.01$) were among epibiont species, which share the same resource, the host body surface. To test for the effect of competition, we reran the multiple regression for each species, but with an additional variable, called "competitor," included. This variable was zero when none of those species that showed a negative association ($P < 0.1$) with the tested species were present in the population (compare Table 8A). It increased by one with each competitor species present. For two of seven species, the results of the multiple regression changed when the competitor variable was added: The *V. octava* presence/absence pattern is better explained by the distribution of three other epibionts (*E. helena*, *Chlorangiella*, *Colacium vesiculosum*), with which it occurred less often together than by chance, than by the number of *Daphnia* species (compare Tables 7 and 8). However, the fit of the regression model only marginally improved (increasing from $r^2 = 0.14$ to $r^2 = 0.18$).

As the competitor variable was not significant for *E. helena*, it seems that the lack of co-occurrence of *V. octava* and *E. helena* (five co-occurrences in of 137 pools; expected 12.6) is due to competitive exclusion of *V. octava* by *E. helena* and not the other way around.

A much stronger improvement of the model fit was found for *Colacium vesiculosum*. In addition to water color, the competitor variable was significant and increased the fit from $r^2 = 0.19$ to $r^2 = 0.47$ (Table 8).

Spatial effects

The spatial autocorrelation analysis did not reveal any striking pattern. Significant positive autocorrelations were found only in the distance classes ≥ 10 m for *V. octava* and *E. helena* (Fig. 5, Moran's $I = 0.3-0.4$, $P < 0.05$).

To further test for geographic variation, we tested whether islands differ in the average parasite richness per pool. None of the three richness measures varied significantly among islands (total richness: Wald $\chi^2 = 35.13$, $P > 0.1$; endoparasites: $\chi^2 = 35.13$, $P > 0.1$; epibionts: $\chi^2 = 35.13$, $P > 0.1$). This did not change when we first corrected for those variables that were significant in the multiple regression (Table 7) and then tested for the island effect ($P > 0.4$ in all cases). Additional analysis using Mantel tests (*not shown*) to search for associations among parasite community measures and geographic distance between pools did not reveal any spatial effects. Overall, taking these results and the results from the analysis of network size and density into account (Tables 5, 6), it seems that spatial patterns do not strongly shape the parasite community of the *D. magna* metapopulation in Tvärminne.

DISCUSSION

Total parasite richness and the colonization time hypothesis

Of all variables considered, population age explained by far the most variance in total parasite richness. The dominance of this effect is not surprising given that the rock pool *Daphnia* populations form a highly dynamic metapopulation with on average 20% extinction per year (Pajunen 1986; V. I. Pajunen, *unpublished manuscript*). These dynamics are a consequence of the inherent instability of the rock pool environment, caused by frequent drying up, the arrival of rainwater, or the sudden invasion of brackish water from the sea. Thus, most *Daphnia* populations are short lived and from the parasite's point of view, highly unpredictable resources.

The relationship between parasite richness and host population age is likely to be caused by the time delay parasites experience in reaching newly founded host populations (Guégan and Kennedy 1993). A common problem when testing the colonization time hypothesis are confounding variables, e.g., extreme habitats may

TABLE 7. Results of multiple regressions for environmental parameters of a *Daphnia* parasite community.

Dependent variable	Independent variable	Sign of relationship	Estimate	r^2	χ^2
All parasites	time since <i>Daphnia</i> colonization (yr)	+	0.054	0.55	19.40**
	no. <i>Daphnia</i> species	+	0.388		5.92*
Endoparasites	time since <i>Daphnia</i> colonization (yr)	+	0.059	0.56	6.024*
	pool volume	+	0.392		3.57*
Epibionts	time since <i>Daphnia</i> colonization (yr)	+	0.052	0.42	12.82**
	conductivity	-	0.381		4.30*
<i>Octosporea bayeri</i>	time since <i>Daphnia</i> colonization (yr)	+	0.879	0.20	11.04**
	pool volume	+	0.097	0.40	8.28**
<i>Larssonia</i> sp.	pools within 10-m radius	+	0.384		7.05**
	no. <i>Daphnia</i> species	-	4.20	0.14	7.45**
<i>Vorticella octava</i>	pools within 10-m radius	+	0.469	0.38	9.98**
	no. of <i>Daphnia</i> species	+	0.173		7.88**
<i>Epistylis helenae</i>	water color	+	0.001	0.24	5.84*
	pools within 10-m radius	-	2.098		4.82*
Chlorangiella	no. <i>Daphnia</i> species	+	0.114	0.33	9.32**
	conductivity	-	4.54		3.94*
<i>Colacium vesiculosum</i>	water color	+	<0.001	0.19	6.56**

Notes: Data included numbers of parasites, endoparasites, and epibionts (all three, Poisson regression) and presence/absence for each of the common endoparasites and epibionts. Regressions were run with stepwise selection. Only those independent variables with significant ($P < 0.05$) effects in the final model are listed. The basic model included the following variables: number of *Daphnia* species, pool volume, water color, conductivity, number of inhabited pools per island, number of pools within 10-m radius, time since colonization by *D. magna*, time since colonization by any *Daphnia* species, and relative distance to the sea. A plus sign (+) indicates a positive relationship between the independent and the dependent variables, a minus sign (-) indicates a negative relationship. The estimates give the regression parameter for the three richness measures (Poisson regressions), while for the individual parasites the odds ratios are given. The r^2 column lists pseudo r^2 values, which are approximations of the total amount of variance explained by the model.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

be colonized last or novel host populations are often isolated in space (Kennedy and Bush 1994). Our analysis does not suffer from this problem and therefore gives clear support for the colonization-time hypothesis. We believe that the colonization-time effect in our study area is best explained by "isolation by encounter

probability." Evolutionary processes (e.g., host range expansion) might contribute as well, but seem to us less likely to explain this effect.

The colonization-time hypothesis plays a role mainly in populations with limited dispersal. If dispersal is high among populations, host population age is likely

TABLE 8. Impact of competitor presence/absence on parasites and epibionts of *Daphnia*, for species occurring in >10% of the rock pools.

A) Tests of independence of occurrence					
Parasite	<i>Vorticella octava</i>	<i>Epistylis helenae</i>	<i>Amoebidium parasiticum</i>	<i>Chlorangiella</i>	<i>Colacium vesiculosum</i>
<i>Octosporea bayeri</i>	0.85	0.03	0.69	0.13	1.0
<i>V. octava</i>		0.001	0.68	0.04	0.005
<i>E. helenae</i>			0.48	0.005	0.23
<i>A. parasiticum</i>				0.32	0.04
<i>Chlorangiella</i>					0.02

B) Regression results with competitor variable included					
Dependent variable	Independent variable	Sign of relationship	Odds ratio	r^2	χ^2
<i>V. octava</i>	Competitors	-	3.20	0.18	8.35**
<i>Colacium vesiculosum</i>	Water color	+	<0.001	0.47	7.26**
	Competitors	-	35.29		5.29*

Notes: (A) Tests of independence for each pair of the common endoparasites and epibionts. P values of Fisher's exact tests are given. All cases with $P < 0.1$ had a deficiency of *Daphnia magna* populations with double infections. (B) Results of logistic regression with the competitor variable included. For *Vorticella octava*, the competitor variables included *E. helenae*, *Chlorangiella*, and *Colacium vesiculosum*. For *Colacium vesiculosum*, the competitor variables included *V. octava*, *Chlorangiella*, and *A. parasiticum*. For further details on the logistic regression see *Methods: Statistical analysis* and Table 6.

* $P < 0.05$; ** $P < 0.01$.

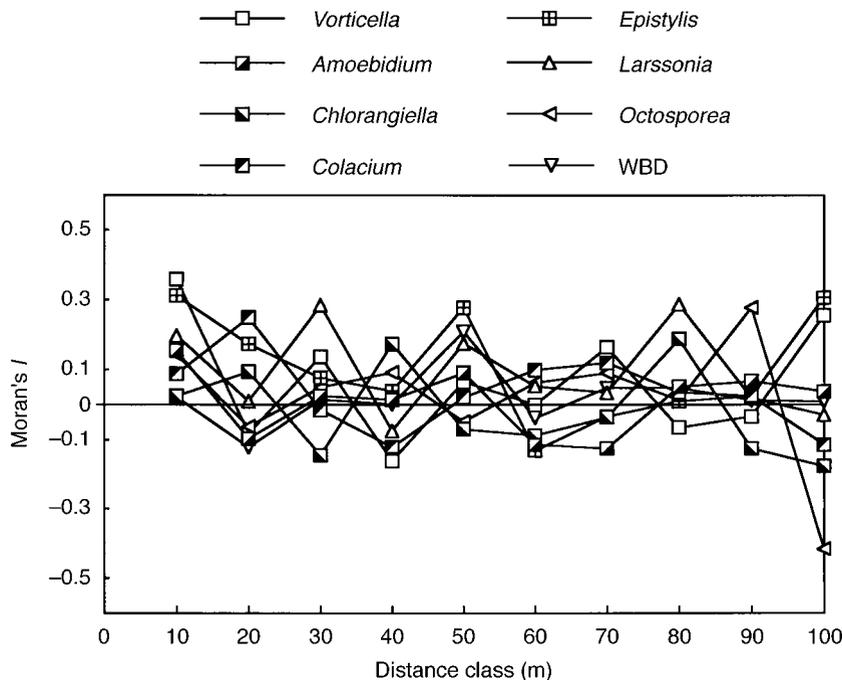


FIG. 5. Correlogram for the spatial autocorrelation of the common parasites of *D. magna* in rock pools. Moran's autocorrelation coefficient I is shown in relation to 10 distance classes.

to have an effect on richness only in new patches, for older populations may have already reached saturation. Endoparasite richness does not seem to saturate in 16 yr, while the epibionts saturate within ~ 3 yr (Fig. 4). It is, however, important to point out that in our study the oldest group of host populations includes populations that are *at least* 16 yr old, but many may be older. As the mean number of endoparasites for this oldest class (1982 and older) is not above the regression line across the entire range of ages, not much more of an increase would be expected if the data set were extended further back in time.

For all cases where population age played a significant role, the age of the *Daphnia* population (any *Daphnia* species) explained more variance than the age of the *D. magna* population. The date of population founding by any *Daphnia* species is always equal to or earlier than the date for foundations by *D. magna*. There are two likely reasons for this. First, for generalist parasites it may not be important which *Daphnia* species is present. This explanation is likely to play a role for the correlations with total parasite richness and epibiont richness, but it fails to explain the good correlations between *Daphnia* population age and endoparasites. A second reason, which would explain this finding, is that the presence of any host species may be a better indicator of host population persistence than the presence of *D. magna* alone. Population age estimates based on recordings of one host species are noisier than estimates based on recordings from three species, and less noisy data give more reliable age esti-

mates. This might explain why the correlation between the presence/absence pattern of the host-specific endoparasite *Octosporea bayeri* is much stronger with *Daphnia* population age than with *D. magna* population age (Table 6).

Differences between endoparasites and epibionts

Host population age.—An important difference between endoparasite and epibiont richness in our data set is the shape of the curve relating richness to the time since the pools were colonized by the host. While there was no further increase in the number of epibionts after ~ 3 yr, the number of endoparasites continued to increase over the entire period of the study (Fig. 4). We believe that this difference is mainly caused by differences in rates and modes of dispersal, resulting in epibionts having greater colonization success than endoparasites. First, epibionts have very high transmission rates, not only among individual hosts of the same species, but also across species barriers. Every time a *Daphnia* molts, the epibionts detach from the carapace, remain for some time in a motile or floating stage, and then attach to the same or another host individual (Green 1974, Chiavelli et al. 1993, Threlkeld et al. 1993, Threlkeld and Willey 1993). Thus, every few days epibionts are transmitted to other hosts. The high epibiont prevalences found within populations (Table 2) is consistent with this. Second, although *Daphnia* are the preferred hosts for most of the epibionts in our study, other host species are occasionally encountered and may be used as dispersal vehicles

among rock pools. In particular, aquatic insects (>60 species of beetles and dipterans [Lindberg 1944, Ranta 1982]), which breed in the rock pools and disperse as adults to other rock pools, are potential epibiont vectors. For example, epibionts have been observed to attach occasionally to the body surface of the larvae of the very common corixids *Arctocorisa carinata* and *Callicorixa producta* (V. I. Pajunen, unpublished data). Further, there is a very abundant amphipod species (*Gammarus duebeni*), individuals of which actively migrate between rock pools along the wet surface of the rocks (V. I. Pajunen, unpublished data). Thus, while, the relatively unspecific epibionts could use numerous host species as dispersal vehicles, the more specific endoparasites in our study area may be more restricted in this respect. Third, experimental work has shown that endoparasites of *Daphnia* need high doses for successful transmissions (Ebert et al. 1998, 2000). A few spores carried from one pool to the next by a dispersing insect are unlikely to reach the necessary minimal infective doses (often several 100 or 1000 spores/mL). In contrast, one epibiont could successfully colonize a new host. This difference might be related to the fact that *Daphnia* epibionts are not subject to the immune response of the host.

An exceptional endoparasite with an apparently higher dispersal rate is *Octosporea bayeri*, which is transmitted both horizontally and vertically and may thus co-disperse with its host. This additional mode of dispersal may be the reason why *Octosporea bayeri* is the most common parasite in the study area (Table 2). Vertical transmission through resting eggs may also increase the chance to survive temporary absence of hosts, e.g., during droughts or in winter.

In summary, we suggest that the rapid saturation of epibionts after pool colonization is a consequence of their higher dispersal rates and the fact that the poorly dispersing, exclusively horizontally transmitted, endoparasites take longer to reach saturation. The need for a high dispersal rate follows from the inherent instability of the rock pool environment, which may allow only parasites with high dispersal capacities to persist. Other *Daphnia* parasites commonly found in permanent ponds and lakes (Green 1974, Stirnadel and Ebert 1997) may not be able to persist in *Daphnia* rock pool populations.

Pool volume.—A significant difference in the patterns explaining endoparasite and epibiont richness is found in the pool volume effect. Larger pools, which harbor larger *Daphnia* populations, have more endoparasites (Fig. 3) but not more epibionts (Tables 5, 6). This effect was found for each endoparasite species (Table 6) and was even apparent when host population age was statistically controlled for (Table 7). A possible explanation for this might be within-pool transmission rates. The higher the transmission rate the lower is the parasite-specific population threshold size that determines whether a parasite can persist ($R_0 > 1$) (Anderson

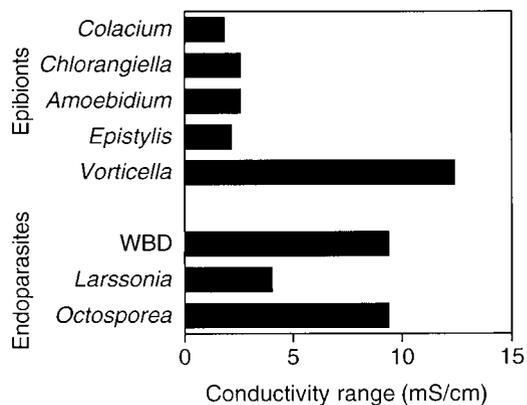


FIG. 6. Maximum water conductivity in which the eight common parasites were recorded. The *D. magna* rock pool with the highest conductivity had 12.4 mS/cm. Note that the lowest conductivities were for all parasite species <0.05 mS/cm.

and May 1991, Dobson and Pacala 1992, Simberloff and Moore 1996). The larger the host population size, the more parasite species may pass their specific threshold host-population size and thus persist (Dobson and Pacala 1992). This might be the case for the endoparasite species (Fig. 3). In contrast to endoparasites, epibionts have extremely high within-pool transmission rates. If the specific threshold host-population sizes for the epibionts are below the size in our smallest rock pools, no correlation between epibiont richness and pool volume is expected.

Patch quality.—None of the endoparasites showed a correlation with water quality variables that describe the influence of the brackish seawater on the rock pools. In contrast, several significant correlations between epibionts and water quality measures were found (Table 6, Fig. 6), and conductivity was significant in the multiple regression explaining epibiont richness (Table 7). This contrast between endoparasites and epibionts is likely to be a consequence of the epibionts being much more dependent on the external environment than are the endoparasites. It is also consistent with earlier reports of decreasing species richness in rock pools with higher salinity (Järnefelt 1940, Lindberg 1944, Ghilarov 1967, Ranta 1982). However, the epibionts differ in their associations with patch quality measures.

Number of host species per pool.—For total epibiont richness and for two of the five common epibionts, significant positive associations were found with the number of recorded *Daphnia* species (Tables 5, 6). It may be that low host specificity may promote epibiont persistence in *Daphnia* rock pools. Several factors may contribute to this. With more host species living in a rock pool, the effective host population size increases and therefore more parasites may be able to persist. However, we speculate that host population size seems not to be important for the rock pool epibionts. It may be more important that being able to utilize different

hosts reduces the dependency on each single host species. For example, the likelihood of extinction of a particular epibiont during a temporary extinction of one host species is strongly reduced. Also, competition with other parasites with a different but overlapping host range is reduced (parasites may have different reservoir hosts). We cannot distinguish which hypothesis is more likely. The more host-specific endoparasites showed no clear association with the number of *Daphnia* species present (Tables 5, 6).

Species-wise presence/absence patterns

Interspecific competition.—If the factors listed in Table 1 are of general importance for parasites, one would expect to find support for them also on a species-wise analysis. This is not the case in our study. The results from the species-wise analysis differ strongly from the results of the three richness parameters, and single species in turn differ strongly in their presence/absence pattern from each other. For example, the age of the host population, which explained parasite richness better than any other variable, is not significant for six of seven parasite species (Tables 6, 7). Several factors may explain this discrepancy, among them certainly the lower statistical power associated with tests of single species as compared to the entire data set. We have, however, evidence for the presence of one biological factor causing such discrepancies, namely interspecific competition, which was suggested to be strong among parasites with ecologically similar niches (e.g., Kuris and Lafferty 1994, Lafferty et al. 1994, Poulin 1998). Interspecific competition can lead to exclusion of species and thus influence species presence/absence patterns in rock pool populations (see Pajunen and Pajunen [1993] for an example of competitive exclusion among rock pool corixid species).

It appears as if interspecific competition occurs among epibionts that colonize the body surface of their hosts and by this contribute to explaining their presence/absence patterns. The three epibiont species (*V. octava*, *E. helena*, and *Colacium vesiculosum*) that had showed strong negative associations (Table 8A) colonize mainly the head region and the dorsal parts of the host carapace. *V. octava* is much less often found together with *E. helena* and *Colacium vesiculosum* than would be expected by chance (Table 8A). This result agrees with earlier findings for epibionts sampled from the rock pools in study region (Green 1957). Further, as was the case in our data set, Green (1957) found that *E. helena* and *Colacium vesiculosum* occur independently of each other. He suggested that this might be due to the partially different space requirements of these epibionts on the hosts body surface. *Colacium vesiculosum* has a short stalk, while *V. octava* and *E. helena* have long stalks (see Plate 1, right) and may form a canopy over *Colacium vesiculosum*. Moreover, *E. helena* has a noncontractile stalk, while *V. octava* has a contractile stalk. When the stalk contracts, it

forms a spiral that takes up much more space than the diameter of the stalk. Contraction of the stalk may cause a mechanical disturbance to both species and thus lead to stronger competition (Green 1957). Thus, *V. octava* may suffer from strong interspecific competition because it interferes mechanically with both *E. helena* and *Colacium vesiculosum*, while the two latter species do not compete as strongly with each other because they are somewhat separated in space. Earlier, Green (1955) had experimentally shown that peritrichs (species not given) compete with *Colacium vesiculosum* and that light is an important factor in determining the outcome of competition between algal epibionts (favored under strong light) and peritrich ciliates (favored under poor light conditions).

Interspecific competition is, however, not the only reason for non-independent distribution of parasites across host populations. Niche differences seem to play a role as well. These epibionts showed contrasting associations with the variables that indicate the impact of the marine environment on the rock pools. *V. octava* was found mainly in pools relatively near the sea with light water color, while the opposite was the case for *Colacium vesiculosum* and *E. helena* (Table 6). Further, *E. helena* was more often found in pools with more than one *Daphnia* species, whereas *V. octava* was mainly found in pools with *D. magna* only (Tables 6, 7). However, the realized niche of *V. octava* seems to be influenced by the presence of *E. helena* and *Colacium vesiculosum*. In all rock pools with more than one *Daphnia* species and *V. octava* as the only epibiont, *V. octava* is found on all hosts. This seems to contrast with the negative association between this species and the number of host species in a pool (Tables 6, 7), but may be explained with the finding that rock pools with two *Daphnia* species often harbor the presumably competitively stronger *E. helena* or *Colacium vesiculosum*. Further, the tendency of *V. octava* to occur more often in rock pools with a stronger marine influence might also be a consequence of competitive replacement in less brackish pools. The potential niche of *V. octava* seems to be independent of water conductivity, as it was found in pools with conductivities from 0.043 to 12.4 mS/cm, while all other epibionts were found only in pools with <3 mS/cm (Fig. 6). A similar observation was made by Green (1957). It seems likely that the shift of the realized niche of *V. octava* towards light-colored pools close to the sea may be the result of competitive exclusion from dark-colored, low-conductivity rock pools far from the sea, which often harbor *E. helena* and *Colacium vesiculosum*. The multiple logistic regression including the competitor variable revealed that this variable explains most of the variance of the *V. octava* presence/absence pattern (Table 8). This indirect evidence for interspecific competition among epibionts suggests that an experiment done by manipulating rock pool populations would be worthwhile.

Interspecific competition has been widely discussed as an important factor in shaping parasite communities (see Poulin [1998] for a recent review), and it seems a reasonable explanation for some of the patterns described here as well. Thus, we have to be careful in interpreting the associations of richness with the explanatory variables listed in Table 1. Lack of support might not indicate that the hypothesis is wrong, but rather that other factors explain more variance.

Spatial patterns.—If species occur in a stochastic balance between local extinction and colonization, patch isolation and network size become translated into patterns of patch occupancy (Hanski 1999). In our case, however, the spatial arrangement of the rock pools appeared not to explain much of the variation in parasite richness or presence/absence patterns of individual parasite species. Total parasite richness and endoparasite richness showed positive associations with the network size (number of pools per island), but the correlations were weak and were not found in the multiple regression approach (Table 7). Further, the three richness measures did not differ among islands (no significant island effects), indicating once more that geographic differentiation is of little importance for the *Daphnia* rock pool parasites in our study area. Only *E. helena* and *Larsson* (the latter only after correcting for the volume effect, Table 7) confirmed our hypothesis that a high density of pools will increase the likelihood that these parasites will be found (Tables 6, 7). Another parasite, *A. parasiticum*, had a negative association with local pool density (Tables 5, 6). We have no explanation for this finding.

The spatial autocorrelation addressed the question of how similar two rock pools are with respect to the presence or absence of a parasite. (Presence or absence in a pair of pools indicates a high similarity; presence in only one pool indicates low similarity). Although all eight common parasites showed positive autocorrelation indices for distances ≤ 10 m, the estimates were generally low (maximum $I = +0.36$) and mostly not significant (except for *V. octava* and *E. helena*, Fig. 5). In an earlier rock pool study, the presence of *Larsson* was shown to be positively autocorrelated over short distances (Bengtsson and Ebert 1998). In our study *Larsson* had the third highest autocorrelation index in the first distance class (Fig. 5). As the other analyses (Tables 5, 6, and 7) showed that presence/absence patterns depend strongly on many variables, it might be that a pattern of spatial autocorrelation is masked by these factors.

The search for general patterns

By using data collected across many taxa, we were able to give correlational support for some of the general hypotheses stated in Table 1 and to draw a statistical picture of a "typical *Daphnia* rock pool parasite". While we need this form of generalization to understand the diversity of biological interactions, we have

to interpret this statistical picture with caution, because it might not necessarily reflect the biology of individual species, or might be confounded by other factors, e.g., that interspecific competition increases with species richness. It has also to be kept in mind that different parasite species contribute unequally to the overall variance in richness. Rare and very common parasite species influence variance in richness variables less strongly than parasites with intermediate commonness.

We believe that our analysis of total parasite richness might not properly reflect the biology of *Daphnia* parasites in rock pools. The pictures drawn for endoparasites and epibionts appear to capture more of the biology of these two groups. The more host-specific endoparasites appear to represent typical microparasites (Anderson and May 1978, 1979) which depend on their host dynamics. In the rock pools they seem to represent a metapopulation characterized by limited dispersal among pools and by the population size of their hosts. In contrast, the mostly host-unspecific epibionts depend more strongly on the external environment (water quality) and appear strongly influenced by interspecific competition. Their dispersal rates are much higher than those of the endoparasites, and their metapopulation dynamics may be driven more by patch quality and interspecific competition than by dispersal limitation.

The high dispersal rates of *Daphnia* combined with the inherent instability of the rock pool environment produce a highly dynamic picture of a metapopulation (Hanski and Ranta 1983, Pajunen 1986). Although our analysis revealed several factors that modify parasite presence/absence patterns in the rock pool *Daphnia* populations, the variable that explained by far the most variance in parasite richness is directly coupled to the dynamics of the *Daphnia* metapopulation, namely the age of the host populations. Parasites with high colonization rates are clearly favored under such conditions.

ACKNOWLEDGMENTS

We thank the staff of the Tvärminne Zoological Station for their technical assistance. Myriam Riek, Christoph Haag, and Irmeli Pajunen helped in collecting data. Heide Stirnadel and Tom Smith helped us with the statistics. Tom Little, Steve Stearns, Wolfgang Weisser, Roger Nisbet, and Janne Bengtsson improved earlier versions of the manuscript. D. Ebert and J. Hottinger were supported by the Swiss Academy for Natural Sciences (SANW) and by grant No. 31-53595.98 from the Swiss Nationalfond.

LITERATURE CITED

- Allen, Y. C., B. T. De Stasio, and C. W. Ramcharan. 1993. Individual and population level consequences of an algal epibiont on *Daphnia*. *Limnology and Oceanography* **38**: 592–601.
- Anderson, R. M., and R. M. May. 1978. Regulation and stability of host–parasite population interactions I. regulatory processes. *Journal of Animal Ecology* **47**:219–247.
- Anderson, R. M., and R. M. May. 1979. Population biology of infectious diseases: Part I. *Nature (London)* **280**:361–367.

- Anderson, R. M., and R. M. May. 1991. Infectious diseases of humans. Oxford University Press, Oxford, UK.
- Arneberg, P., A. Skorping, B. Grenfell, and A. F. Read. 1998. Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London Series B: Biological Sciences* **265**:1283–1289.
- Bengtsson, J. 1993. Interspecific competition and determinants of extinction in experimental populations of three rockpool *Daphnia* species. *Oikos* **67**:451–464.
- Bengtsson, J., and D. Ebert. 1998. Distribution and impacts of microparasites on *Daphnia* in a rockpool metapopulation. *Oecologia (Berlin)* **115**:213–221.
- Bengtsson, J., and G. Milbrink. 1995. Predicting extinctions: interspecific competition, predation and population variability in experimental *Daphnia* populations. *Oecologia (Berlin)* **101**:397–406.
- Chiavelli, D. A., E. L. Mills, and S. T. Threlkeld. 1993. Host preference, seasonality, and community interactions of zooplankton epibionts. *Limnology and Oceanography* **38**:574–583.
- Dobson, A. P., and S. W. Pacala. 1992. The parasites of *Anolis* lizards of the northern Lesser Antilles: II. the structure of the parasite community. *Oecologia (Berlin)* **91**:118–125.
- Doig, V. A. 1964. General parasitology. Oliver and Boyd, Edinburgh, UK.
- Ebert, D., C. D. Zschokke-Rohringer, and H. J. Carius. 1998. Within and between population variation for resistance of *Daphnia magna* to the bacterial endoparasite *Pasteuria ramosa*. *Proceedings of the Royal Society, London, Series B* **265**:2127–2134.
- Ebert, D., C. D. Zschokke-Rohringer, and H. J. Carius. 2000. Dose effects and density dependent regulation of two microparasites of *Daphnia magna*. *Oecologia (Berlin)* **122**:200–209.
- Ghilarov, A. M. 1967. The zooplankton of arctic rockpools. *Oikos* **18**:82–95.
- Green, J. 1955. Studies on a population of *Daphnia magna*. *Journal of Animal Ecology* **24**:84–97.
- Green, J. 1957. Parasites and epibionts of Cladocera in rock pools of Tvärminne archipelago. *Archivum Societatis Zoologicae Botanicae Fennicae "Vanamo"* **12**:5–12.
- Green, J. 1974. Parasites and epibionts of Cladocera. *Transactions of the Zoological Society of London* **32**:417–515.
- Gregory, R. D. 1990. Parasites and host geographic range as illustrated by water fowl. *Functional Ecology* **4**:645–654.
- Guégan, J.-F., and C. R. Kennedy. 1993. Maximum and local helminth parasite community richness in British freshwater fish: a test of the colonization time hypothesis. *Parasitology* **106**:91–100.
- Guégan, J.-F., and C. R. Kennedy. 1996. Parasites richness/sampling effort/host range: the fancy three piece jigsaw puzzle. *Parasitology Today* **12**:367–369.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Hanski, I., and E. Ranta. 1983. Coexistence in a patchy environment: three species of *Daphnia* in rock pools. *Journal of Animal Ecology* **52**:263–279.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, London, UK.
- Järnefelt, H. 1940. Beobachtungen über die Hydrologie einiger Scharentümpel. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **9**:79–101.
- Kankaala, P., and P. Eloranta. 1987. Epizootic ciliates (*Vorticella* sp.) compete for food with their host *Daphnia longispina* in a small polyhumic lake. *Oecologia (Berlin)* **73**:203–206.
- Kennedy, C. R., and A. O. Bush. 1994. The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* **109**:187–196.
- Kleinbaum, D. G., L. L. Kupper, and K. E. Muller. 1988. *Applied regression analysis and other multivariate methods*. Duxbury, Belmont, California, USA.
- Korpelainen, H. 1986. Competition between clones: an experimental study in a natural population of *Daphnia magna*. *Hereditas* **105**:29–36.
- Kuris, A. M., A. R. Blaustein, and J. J. Alió. 1980. Hosts as islands. *American Naturalist* **116**:570–586.
- Kuris, A. M., and K. D. Lafferty. 1994. Community structure: larval trematodes in snail hosts. *Annual Review in Ecology and Systematics* **25**:189–217.
- Lafferty, K. D., D. T. Sammond, and A. M. Kuris. 1994. Analysis of larval trematode communities. *Ecology* **75**:2275–2285.
- Lagerspetz, K. 1955. Physiological studies on the brackish water tolerance of some species of *Daphnia*. *Archivum Societatis Zoologicae Botanicae Fennicae "Vanamo"* **9**:supplement:138–143.
- Larsson, J. I. R. 1981. A new microsporidium *Berwaldia singularis* gen. et sp. nov. from *Daphnia pulex* and a survey of microsporidia described from Cladocera. *Parasitology* **83**:325–342.
- Larsson, J. I. R. 1988. Identification of Microsporidia genera (Protozoa, Microspora)—a guide with comments on the taxonomy. *Archiv für Protistenkunde* **136**:1–37.
- Larsson, J. I. R., D. Ebert, K. L. Mangin, and J. Vavra. 1998. Ultrastructural study and description of *Flabelliforma magnivora* n. sp. (Microspora, Dubosqiidae), a microsporidian parasite of *Daphnia magna* (Crustacea, Cladocera, Daphniidae). *Acta Protozoologica* **37**:41–52.
- Larsson, J. I. R., D. Ebert, and J. Vavra. 1996a. Ultrastructural study of *Glugea cladocera* Pfeiffer, 1895, and transfer to the genus *Agglomerata* (Microspora, Dubosqiidae). *European Journal of Protistology* **32**:412–422.
- Larsson, J. I. R., D. Ebert, and J. Vavra. 1997. Ultrastructural study of *Ordospora colligata* Gen. et Sp. Nov. (Microspora, Ordosporidae Fam. Nov.), a new microsporidian parasite of *Daphnia magna* (Crustacea, Cladocera). *European Journal of Protozoology* **33**:432–443.
- Larsson, J. I. R., D. Ebert, J. Vavra, and V. N. Voronin. 1996b. Redescription of *Pleistophora intestinalis* Chatton, 1907, a microsporidian parasite of *Daphnia magna* and *Daphnia pulex*, with establishment of the genus *Glugoides* (Microspora, Glugeidae). *European Journal of Protistology* **32**:251–261.
- Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* **80**:107–138.
- Legendre, P., and A. Vaudor. 1991. *The R Package: multi-dimensional analysis, spatial analysis*. Université de Montréal, Montréal, Canada.
- Levander, K. M. 1900. Zur Kenntnis des Lebens in den stehenden Kleingewässern auf den Skäreninseln. *Acta Societatis pro Fauna et Flora Fennica* **18**:1–107.
- Lindberg, H. 1944. Ökologisch-geographische Untersuchungen zur Insektenfauna der Felsentümpel an den Küsten Finnlands. *Acta Zoologica Fennica* **41**:1–180.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* **78**:691–692.
- Pajunen, V. I. 1986. Distributional patterns of *Daphnia* species in a rock-pool environment. *Annales Zoologici Fennici* **23**:131–140.
- Pajunen, V. I., and I. Pajunen. 1993. Competitive interactions limiting the number of species in rock pools experiments

- with *Sigara nigrolineata*. *Oecologia* (Heidelberg) **95**:220–225.
- Poulin, R. 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* **65**:283–302.
- Poulin, R. 1998. *Evolutionary ecology of parasites*. Chapman & Hall, London, UK.
- Price, P. W. 1980. *Evolutionary biology of parasitism*. Princeton University Press, Princeton, New Jersey, USA.
- Price, P. W., and K. M. Clancy. 1983. Patterns in numbers of helminth parasite species in freshwater fishes. *Journal of Parasitology* **69**:449–454.
- Ranta, E. 1979. Niche of *Daphnia* species in rock pools. *Archiv für Hydrobiologie* **87**:205–223.
- Ranta, E. 1982. Animal communities in rock pools. *Annales Zoologici Fennici* **19**:337–347.
- SAS Institute. 1990. SAS/STAT, Version 6.06. SAS Institute, Cary, North Carolina, USA.
- SAS Institute. 1993. SAS technical report P-243. SAS/STAT software: the GENMOD procedure, release 6.09. SAS Institute, Cary, North Carolina, USA.
- Simberloff, D., and J. Moore. 1996. Community ecology of parasites and free-living animals. Pages 174–197 in D. H. Clayton and J. Moore, editors. *Host-parasite evolution: General principles and avian models*. Oxford University Press, Oxford, UK.
- Sokal, R. R., and N. L. Oden. 1978. Spatial autocorrelation in biology I. methodology. *Biological Journal of the Linnean Society* **10**:199–228.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. Freeman, New York, New York, USA.
- Stirnadel, H. A., and D. Ebert. 1997. Prevalence, host specificity and impact on host fecundity of microparasites and epibionts in three sympatric *Daphnia* species. *Journal of Animal Ecology* **66**:212–222.
- Threlkeld, S. T., D. A. Chiavelli, and R. L. Willey. 1993. The organisation of zooplankton epibiont communities. *Trends in Ecology and Evolution* **8**:317–321.
- Threlkeld, S. T., and R. L. Willey. 1993. Colonization, interaction, and organization of cladoceran epibiont communities. *Limnology and Oceanography* **38**:584–591.
- Upton, G. J. G., and B. Fingleton. 1985. *Spatial data analysis by example. Volume 1. Point pattern and quantitative data*. John Wiley and Sons, Chichester, UK.
- Weider, L. J., and P. D. N. Hebert. 1987. Ecological and physiological differentiation among low-arctic clones of *Daphnia pulex*. *Ecology* **68**:188–198.
- Weissman, P., D. J. Lonsdale, and J. Yen. 1993. The effect of peritrich ciliates on the production of *Acartia hudsonica* in Long Island sound. *Limnology and Oceanography* **38**:613–622.
- Wilson, C. C., and P. D. N. Hebert. 1992. The maintenance of taxon diversity in an asexual assemblage: an experimental analysis. *Ecology* **73**:1462–1472.
- Wilson, C. C., and P. D. N. Hebert. 1993. Impact of copepod predation on distribution patterns of *Daphnia pulex* clones. *Limnology and Oceanography* **38**:1304–1310.