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Species composition of freshwater snail communities in lakes of southern and western Finland

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The niche relations of 20 snail species and the species composition of snail communities in the shallow littoral zone of 72 Finnish lakes was studied. The analysis showed that only a few species can be regarded as specialists for the niche dimensions measured (lake area, calcium content of lake water, content of humus substances), but most of them showed no preference for lake size, and showed a wide tolerance with respect to water quality.

The species were arranged according to the size of the communities they occupy; as species which were found in communities of all sizes (type *a*), or as species of species-rich lakes (type *b*). The type *b* species, 10 in all, occupy the most productive lakes, whereas the type *a* species tolerate the oligotrophic lakes, too. Thus the community size is due not so much to the biological coherence of different species, as to the euryoecious-stenoecious properties of the species.

An analysis of habitat niche overlap revealed three groups of species, which differed with respect to the lowest tolerated calcium content. Within the groups most species showed differences with respect to crude autecological features. The result supports the conclusion that the species composition of gastropod communities deviates from random subsets of species from the species pool, this being primarily affected by abiotic components of the habitat.

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1. Introduction

Species equilibrium theory (MacArthur & Wilson 1967) has proved to be a useful theoretical framework on which to account for patterns of species diversity on islands and habitats distributed as islands. The theory has recently also been applied to freshwater snail communities, with lakes being regarded as island analogues (Lassen 1975, Aho 1978a, b, c, d).

In Finland, the applicability of the theory was tested in a marginal area of gastropod distribution, where the composition of lake water sets physiological limits on the occurrence of the species (Aho 1978a, b). In the most oligotrophic lakes the species richness was best predicted by the hydrochemical composition of lake water, the most important components being total hardness, alkalinity and humus substances. On the other hand, in the lakes where the calcium content exceeded about 7 mg/l the number of species was largely predicted by the spatial variables (lake area, degree of isolation) of the equilibrium theory.

In Finnish lakes the hydrochemical and spatial variables jointly accounted for 73—89 % of the variation in the snail species richness of unpolluted lakes (Aho 1978b). This means that the number of snail species of the lake communities in Finland is primarily determined by the properties of the physical environment.

2. Study area

Niche relations and species distribution were studied in two areas in southern and western Finland which were further divided into four subareas. The characterization of the lakes of the different subareas is given in Table 1 and in Aho (1978b).

Table 1. Characterization of the different subareas.

		Number of species per lake	Specific conductivity ($\varkappa_{20}$)	Total hardness (°dH)	Colour of water (mg Pt/l)	Lake area (km^2)
Subarea I	mean ± *SD*	1.1±0.4	75.2±14.1	1.44±0.26	166±23	14.180±11.291
	min	0	37	0.68	50	0.30
	max	5	233	4.20	320	147.300
Subarea II	mean ± *SD*	1.9±0.4	37.4± 2.2	0.65±0.05	98± 7	3.190± 1.104
	min	0	20	0.3	70	0.229
	max	5	50	1.0	160	14.820
Subarea III	mean ± *SD*	4.5±0.8	45.5± 3.0	0.94±0.07	68± 7	0.092± 0.040
	min	0	26	0.47	30	0.0003
	max	12	71	1.39	180	0.790
Subarea IV	mean ± *SD*	10.5±0.6	70.9± 5.4	1.53±0.11	45± 5	38.639± 7.545
	min	6	34	0.67	11	8.420
	max	15	111	2.30	83	119.150

The lakes of the first two subareas belong partly to the same watercourses. Subarea I is situated in South Bothnia and includes 14 lakes in which the total number of gastropod species was 5 *(Lymnaea stagnalis, L. peregra, L. palustris, Bathyomphalus contortus, Gyraulus albus)*, mean 1.1 species per lake (range 0 to 5). In these lakes 77 % of the variation in the number of gastropod species was accounted for by lake area and isolation (Aho 1978c).

The lakes ($n = 14$) of subarea II are situated in the Suomenselkä region, one of the most important watershed districts in Finland. The total number of gastropod species was 7 *(Lymnaea stagnalis, L. peregra, L. truncatula, Bathyomphalus contortus, Gyraulus acronicus, Bithynia tentaculata, Valvata piscinalis)*, mean 1.9 species per lake (range 0 to 5). In this area 65 % of the variation in the species richness was predictable according to the alkalinity, humus content and altitude (Aho 1978b).

Subareas III and IV belong to the Finnish lake district, and partly to the same watercourse. Area III consists of 22 small lakes in the Tampere district. They compose a distinct series from eutrophic water bodies to polyhumous dys-oligotrophic woodland lakes. The total number of gastropod species was 18 (shown in Table 2, excluding *Planorbarius corneus* and *Bythinella steini*). The number of species per lake ranged from 0 to 12, the mean being 4.5. In the lakes of subarea III 73 % of the variation in the species richness was explained by total hardness and lake area (Aho 1978b).

The fourth subarea includes 22 large lakes (mean area 38.6 km^2) of the southern drainage basin of the river Kokemäenjoki. The number of gastropod species is 20 (Table 2), 10.5 species per lake (range 6 to 15). This subarea is divided into two different parts, one of them quite heavily loaded by waste waters and the other in a more or less natural condition. The total hardness explains 72 % of the number of species in unpolluted lakes, whereas in the large lakes overloaded with waste waters the negative correlation between species richness and total hardness indicates the adverse effect of pollution on the occurrence of gastropod fauna (percentage of explanation 51 %) (Aho 1978b).

3. Material

The material used in this study was collected by Aho (1978b), and by Mutka (1966; subarea II). The collection consisted of 18,200 specimens, of which 9.9 % originated from 75 sample plots of subarea I, 4.4 % from 64 sample plots of subarea II, 22.8 % from 89 sample plots of subarea III and 64.9 % from 135 sample plots of subarea IV. The collection technique has been described in detail by Aho (1966, 1978a, b, c) and Mutka (1966).

The total number of freshwater gastropod species in Finland is 31. In this article we deal with the distribution of the 20 species living in the lakes of the study area (Table 2). The abundances of the species are disregarded and only the presence or absence of the species in the lakes studied are taken into account.

The analysis is restricted to the material collected from macrophyte associations and stony bottoms. The freshwater snails can be ranked as a series showing progressively greater degrees of adaptation to aquatic life (Hunter 1953, 1957). At one end of the spectrum there are such marsh-dwelling species as *Lymnaea truncatula* and at the other end *Valvata piscinalis*, which lives mainly on soft bottom sediments, and thus at greater depths than the other gastropod species studied. The sampling technique used here did not catch these two species with the same efficiency as the other species and therefore their occurrence is underestimated. *Planorbarius corneus* is a new immigrant to the study area, and, therefore, its position in the communities is not yet stable. Thus, these three species are discussed with a certain degree of caution.

4. Niche relations and species distribution

4.1. Niches of gastropod species along three selected axes

The niche of a species can be indicated by studying the actual distribution of the species over a gradient of environments (Levins 1968). The basic method used here is as follows. The presence of each gastropod species in the lakes was determined and a frequency distribution was constructed for each species on all environmental gradients studied. The position of the niche is indicated by the median of the frequency distribution and the niche width is defined as within the limits of the lower and upper quartiles. By defining the central parameters of the niche in this way we avoided the conflict between the distributional patterns of field data (in most cases non-gaussian) and the conventionally used estimates of niche parameters (mean and standard deviation as position and width of the niche, respectively).

Since a description of the complete ecological niche for a species would include an infinite set of biological characteristics and physical parameters, the concept is most useful in terms of differences between species with regard to a few practically significant features (Levins 1968). Three niche dimensions were selected for a detailed analysis: lake area, total hardness and colour of water. The coefficient of partial correlation between lake area and total hardness was 0.28 ($df = 70$; non-significant), after any effect of water colour was eliminated. The corresponding coefficient between lake area and colour of water was —0.33 ($P < 0.05$), and between total hardness and colour of water 0.06 (non-significant).

Lake area. Lake area is a spatial variable which has a positive correlation with species richness (Lassen 1975, Aho 1978a). This parameter implies the number of habitat types in the lake ecosystem. However, as the distribution of some species may be limited to either small, intermediate or large lakes, it is relevant to study the distribution of a species over lakes of different sizes. The values of lake area varied from 0.3 ha to 119 km^2. Most of the gastropod species (15/20) demonstrated a wide occurrence over this habitat dimension (Fig. 1a). The narrow range of *Valvata piscinalis* is due to the sampling technique; it also lives in the large lakes, but at a greater depth (1—5 m) than in small lakes, and is therefore absent from the shallow littoral samples of the largest lakes. *Planorbarius corneus* and *Bythinella steini* were the species with the narrowest ranges. Thus, their distribution may be limited to large lakes, but the result is also due to the small number of lakes (n = 1—2) occupied by them (Table 2). The other species recorded as specialists with respect to this dimension are *Gyraulus riparius* (n = 17), *Lymnaea auricularia* (n = 21) and *Bithynia tentaculata* (n = 11). All these

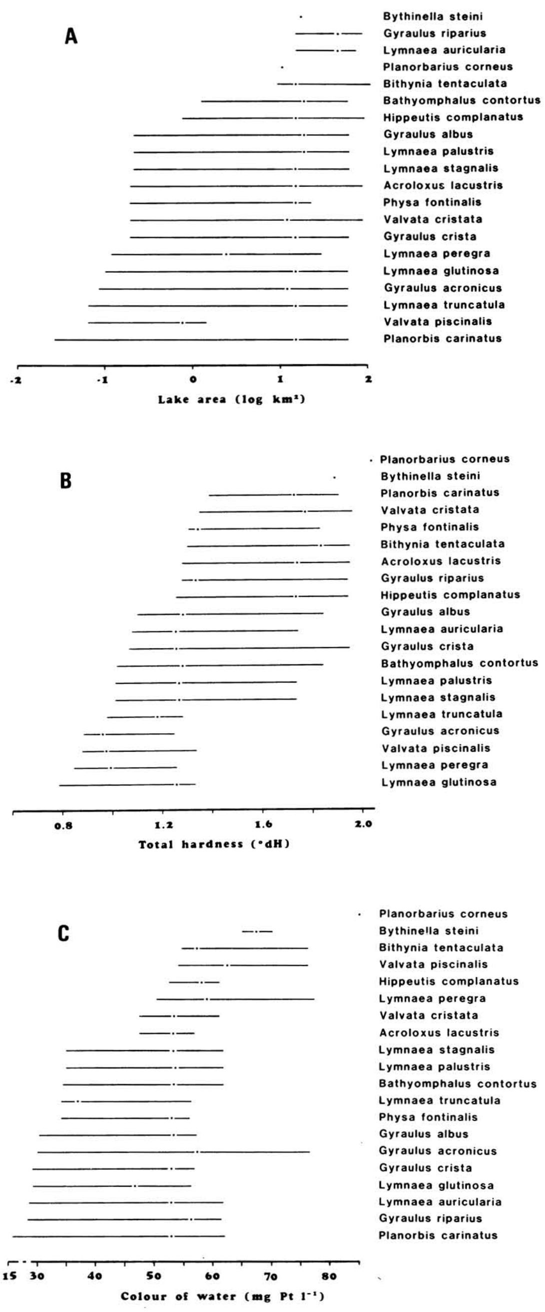

Fig. 1. Distribution of the gastropod species along three selected dimensions: A = lake area in km^2 ($\log_{10}$ transformation), B = total hardness (°dH units; 1 °dH = 7.1 mg Ca/l), C = colour of water (mg Pt/l). Position of the niche is given by the median of the observed frequency distribution, and the width is given by the limits of lower and upper quartiles (see text). Note that with regard to the colour of water the critical limit for distribution of gastropod species is at the high values of mg Pt/l.

species have concentrated into large lakes.

Total hardness. The calcium content of lake water is regarded as one of the most important environmental factors limiting the occurrence of gastropod species, especially at the margins of distribution (e.g. Boycott 1936, Hubendick 1947, Hunter 1964). In Finnish lakes the total hardness (indicating the calcium content; 1 °dH = 7.1 mg Ca/l) is a chemical variable with which the species richness has a highly significant positive correlation (Aho 1966). The values of total hardness clustered in the range 0.3—4.2 °dH. In lakes with a total hardness of less than 1.0 °dH, calcium is a limiting factor for the gastropod fauna (Aho 1966). Most of the species (14/20) had intermediate or wide niches along this axis. When *Planorbarius corneus* and *Bythinella steini* (because they occupy only 1—2 lakes which have high total hardness) and *Valvata piscinalis* are excluded from the analysis, *Lymnaea peregra* (n = 54), *L. truncatula* (n = 8), *L. glutinosa* (n = 21) and *Gyraulus acronicus* (n = 30) form the group of species mainly found in lakes with low values of total hardness (Fig. 1b).

Colour of water. The values of water colour indicate primarily the content of humus substances, but they also correlate strongly with the pH of the lake water (r = —0.95, $P < 0.001$; in Aho 1966). There is a negative correlation between colour of water and species richness (Aho 1978d). Most frequently the gastropod species have their niches positioned around 50—55 mg Pt/l (Fig. 1c). *Gyraulus acronicus* (n = 30) is a generalist with respect to this dimension, which indicates a high tolerance to those properties of lake water caused by humus substances. *Hippeutis complanatus* (n = 9), *Valvata cristata* (n = 13) and *Acroloxus lacustris* (n = 17) occur in a narrow range of intermediate values of water colour, but this perhaps has no ecological relevance. In this connection, *Planorbarius corneus* and *Bythinella steini* are again excluded from consideration.

In general, the differences between species seemed to be quite insignificant. When the two species with limited occurrence are excluded from consideration, there are only 1—4 species on each niche dimension which have a somewhat specialized occurrence. This observation supports the opinion that freshwater snails are an ecologically homogeneous group of organisms, which react in parallel but with different sensitivity to the different properties of their environment (Hubendick 1947). Therefore, all or nearly all species are potentially able to live together in the same littoral communities.

4.2. Community size

In the present study, community size is defined as the number of species which occur together with species i. Community size analysis reveals the distributional patterns of different species. Certain species may occur only in the most species-poor lakes; at the other extreme, certain species occur only in species-rich communities. The analysis somewhat resembles the incidence analysis proposed by Diamond (1975). We counted the number of species in the communities where species i occurred and arranged them by frequency. The community size preference patterns for each species are given in Fig. 2, and the mean number of species present in the communities where species i was living can be seen in Table 2.

The snail fauna of the study area can be grouped into the species which occur in communities from low to high number of species (type *a* distribution) and into the species which occur only in communities with a high number of species (type *b* distribution). The criterion for the classification is the coefficient of variation for the mean of community size; when it is greater than 30 %, the species belongs to type *a*, otherwise to type *b*. In this particular case 10 species have type *a* distribution and 10 type *b* distribution (Table 2, Fig. 2). The species which occupied 30 or more lakes belong to type *a* (Table 2). However, four species

Table 2. Mean number of specimens per lake (N), number of lakes occupied by different gastropod species (n), and the mean number of species (s) and the coefficient of variation (CV) when the species i is present in the community. Classification of species into the distribution types *a* and *b* are indicated (see section 4.2).

	N	n	s	CV	Distr. type
Lymnaea stagnalis (L.)	31	38	9.2	38.3	*a*
L. peregra (Müller)	68	54	7.0	64.6	*a*
L. auricularia (L.)	30	21	11.2	23.2	*b*
L. palustris (Müller)	71	37	9.1	43.2	*a*
L. truncatula (Müller)	10	8	9.8	36.7	*a*
L. glutinosa (Müller)	83	21	9.6	44.9	*a*
Physa fontinalis (L.)	97	13	12.5	15.2	*b*
Planorbarius corneus (L.)	29	1	12.0	—	*b*
Planorbis carinatus (Müller)	78	4	13.8	15.0	*b*
Bathyomphalus contortus (L.)	94	35	9.2	42.5	*a*
Gyraulus albus (Müller)	21	32	9.9	33.3	*a*
G. acronicus (Férussac)	47	30	6.8	56.4	*a*
G. crista (L.)	9	19	10.4	32.6	*a*
G. riparius (Westerl.)	30	17	12.1	16.5	*b*
Hippeutis complanatus (L.)	2	9	11.6	19.4	*b*
Acroloxus lacustris (L.)	11	17	11.5	24.2	*b*
Bithynia tentaculata (L.)	49	11	12.3	26.6	*b*
Bythinella steini (Martens)	56	2	15.5	4.6	*b*
Valvata cristata (Müller)	66	13	12.5	19.7	*b*
V. piscinalis (Müller)	3	8	9.0	53.4	*a*

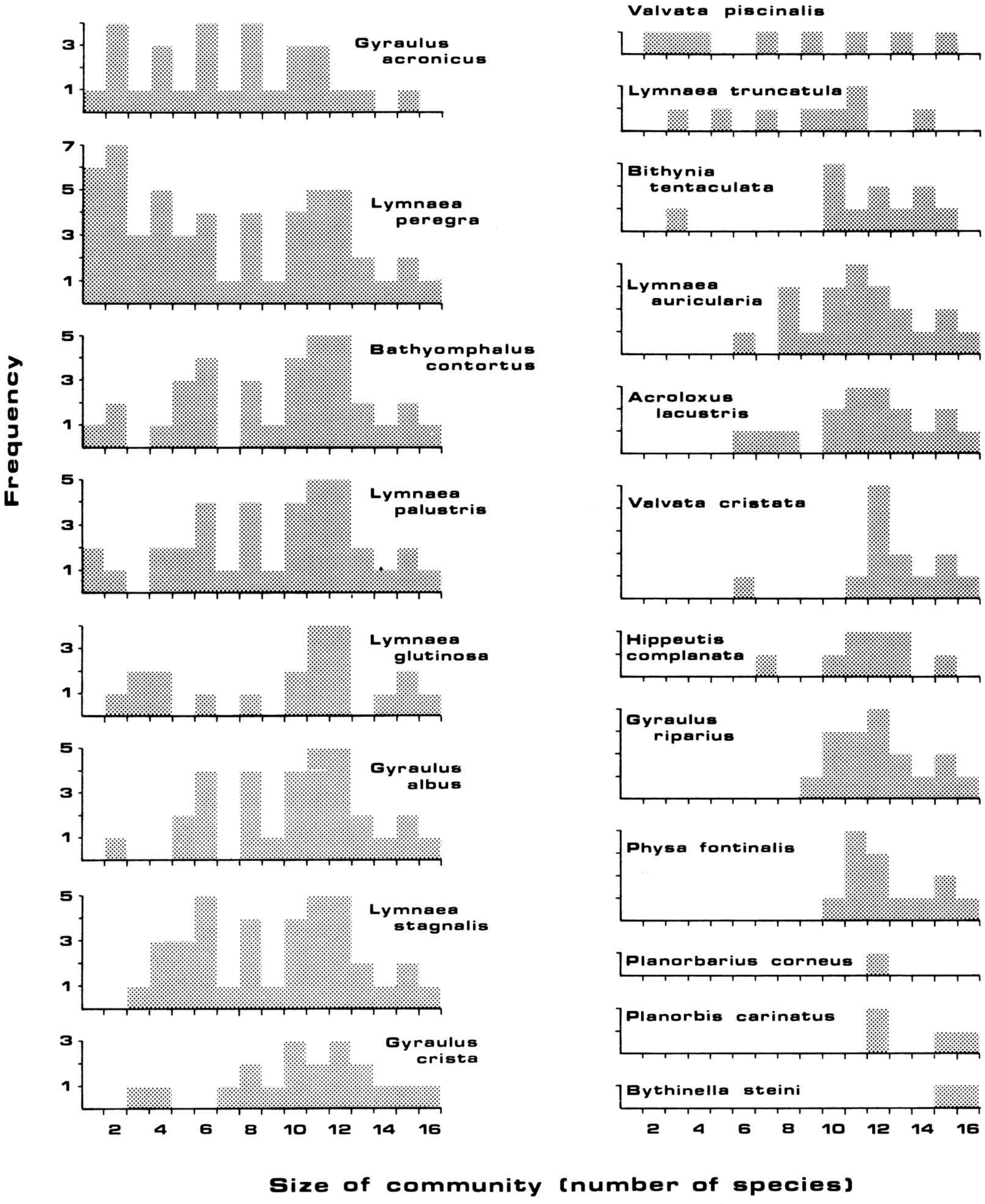

Fig. 2. Frequency distributions of community size preferences for each species.

(*Lymnaea truncatula, L. glutinosa, Gyraulus crista* and *Valvata piscinalis)* with sparse distribution (8—21 lakes) also belong to the type *a* species.

The foremost factor dividing the species into these two distributional types seems to be water quality. The type *a* species (especially *Lymnaea peregra, L. truncatula, L. glutinosa, Gyraulus acronicus* and *Valvata piscinalis*) tolerate water with low electrolyte concentrations (cf. Fig. 1b). The type *b* species, on the other hand, live in the most electrolyte-rich lakes. An additional explanation for this type of distribution pattern might be that the type

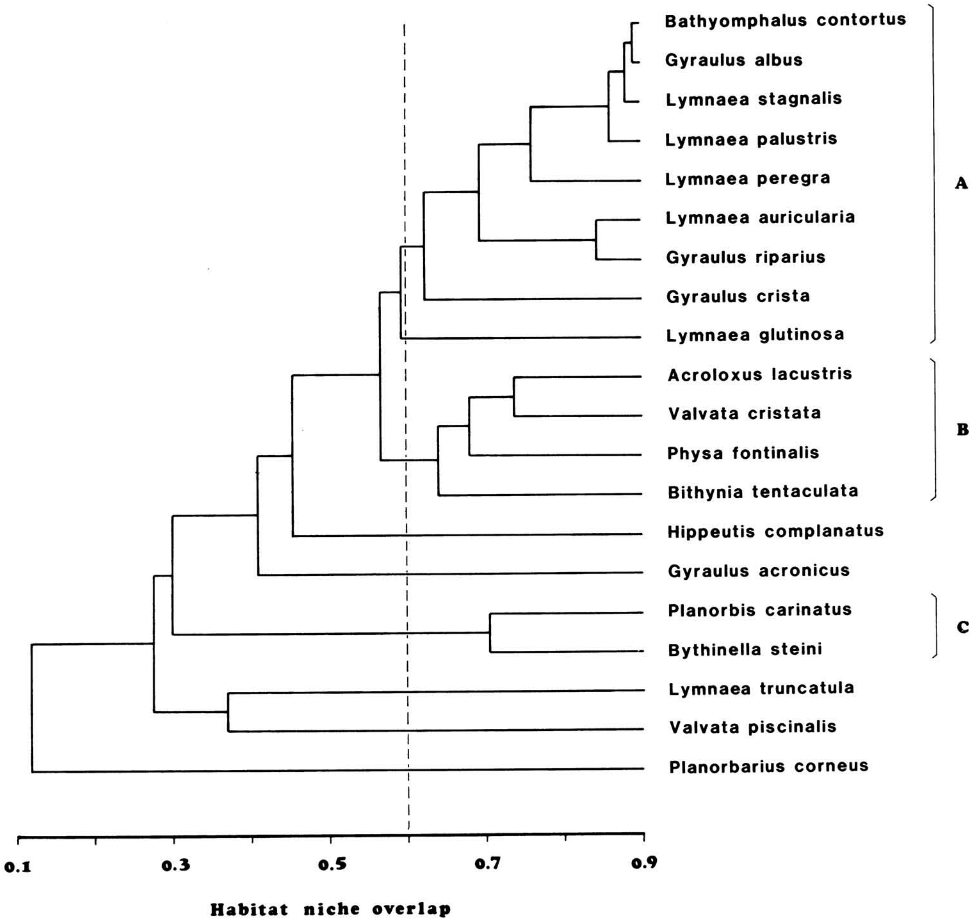

Fig. 3. Dendrogram summarizing the distributional similarities between the snail species studied. A, B and C indicate the species clusters (see text).

b species allocate more on effective habitat utilization and the type *a* species allocate on migration and/or on support of high population densities, which minimize the probability of local extinction. Among the 10 most abundant species in the whole material there are 7 type *a* species and 3 type *b* species. However, verification of this hypothesis is not possible on the basis of the present data.

4.3. Habitat niche overlap

To simultaneously analyse all the environmental gradients mentioned above we performed an analysis of the similarity of the habitat niches. This analysis takes into account the distributional patterns of the species and also explicit and implicit niche dimensions (Cody 1974). In the calculations we used the following measure of similarity:

$$a_{ij} = n_{ij}/(n_i \times n_j)^{1/2} ,$$

where a_{ij} is the distributional similarity between the species i and j (range from 0 to 1), n_{ij} is the number of lakes where both species occur, n_i is the number of lakes occupied by species i, and n_j is the same for species j. The suitability of this kind of index is briefly discussed by Clifford & Stephenson (1975). On the basis of the habitat niche overlap matrix we drew a similarity dendrogram (group average method; Sneath & Sokal 1973).

The analysis revealed three clusters of species (habitat overlap $\geq$ 60 %), with 9, 4 and 2 species, respectively (Fig. 3). Five species *(Lymnaea*

Table 3. Some properties of the gastropod species belonging to the clusters revealed by the analysis of habitat niche overlap. Maximum size from Hubendick (1949), habitat preference from Aho (unpubl.)

		Maximum size in mm	Habitat preference	Lowest total hardness (°dH)	Highest humus content (mg Pt/l)	Preference
Cluster A	*Bathyomphalus contortus*	6	—	0.63	240	
	Gyraulus albus	6	—	0.67	140	
	Lymnaea stagnalis	60	macrophyte	0.63	90	
	Lymnaea palustris	25	macrophyte	0.58	280	
	Lymnaea peregra	20	—	0.55	160	low °dH values
	Lymnaea auricularia	20	—	0.67	85	large lakes
	Gyraulus riparius	3	stony bottom	0.89	85	
	Gyraulus crista	3	—	0.55	80	
	Lymnaea glutinosa	15	macrophyte	0.55	90	
Cluster B	*Acroloxus lacustris*	7	stony bottom	0.94	80	intermediate water colour
	Valvata cristata	3	—	1.01	85	
	Physa fontinalis	10	macrophyte	1.15	80	only macrophyte associations,
	Bithynia tentaculata	12	—	1.01	85	large lakes
Cluster C	*Planorbis carinatus*	15	—	1.39	75	
	Bythinella steini	3	stony bottom	1.73	75	large lakes, high °dH values

truncatula, Planorbarius corneus, Gyraulus acronicus, Hippeutis complanatus and *Valvata piscinalis)* remained outside these clusters. The sampling technique used did not catch *L. trunculata* and *V. piscinalis* with the same efficiency as the other species. The position of *P. corneus* has not yet become stabilized in the lake communities of the study area. *H. complanatus* generally has a quite sparse and somewhat irregular pattern of distribution. *G. acronicus* is better adapted to low electrolyte and high humus concentrations than the other species (see section 4.1), and it occurs mainly in species-poor communities (Fig. 2).

Cluster A. Bathyomphalus contortus, Gyraulus albus, Lymnaea stagnalis, L. palustris, L. auricularia, L. peregra, L. glutinosa, G. riparius and *G. crista* belong to this group of species (Fig. 3). The habitat overlap within this cluster is very coherent, especially between *B. contortus, G. albus, L. stagnalis* and *L. palustris.* Of the two small species, *G. riparius* has the type *b* distribution, and has a preference for stony bottoms, thus differing from *G. crista* (type *a* species), which has no substrate preference (Table 3). Within the species which prefer macrophyte habitats *(L. stagnalis, L. palustris* and *L. glutinosa)* there are pronounced size differences. *L. auricularia* (type *b* species; found mainly in large lakes), *L. peregra* (type *a* species; concentrated in lakes with low values of total hardness), *B. contortus* and *G. albus* appear to have no habitat preference. *B. contortus* and *G. albus,* which have the highest habitat overlap (0.895), are also most similar with regard to the autecological features given in Table 3. A common denominator of the species of cluster A is that they tolerate very low values of total hardness (range of minimum values from 0.55 to 0.89 °dH) compared with other groups of species (Table 3). *B. contortus, G. albus, L. palustris* and *L. peregra* also tolerate extremely high humus contents of lake water.

Cluster B. These four different-sized species *(Acroloxus lacustris, Valvata cristata, Physa fontinalis, Bithynia tentaculata)* form a taxonomically and morphologically heterogeneous group. All are type *b* species by distribution. *P. fontinalis* lives exclusively on macrophytes, whereas *A. lacustris* prefers stony bottoms, and the other two have no substrate preferences. *B. tentaculata* prefers large lakes. The species of this cluster have a uniform tolerance to humus substances, highest tolerated value being 80—85 mg Pt/l (Table 3). The lowest tolerated value of total hardness (range 0.94 to 1.15 °dH) is also a unifying factor in this group of species, being about 60 % higher than in cluster A (Table 3).

Cluster C. The species of this group *(Planorbis carinatus* and *Bythinella steini)* differ notably in size. *B. steini* is restricted to stony bottoms. Not a single specimen of *B. steini* was found either on soft bottoms or on macrophytes. Both species are found in lakes with total hardness equal to or greater than 1.39 °dH. In addition, their distribution is limited to very restricted areas of the large lakes of subarea IV.

The cluster structure described above cannot, however, be due only to the total hardness. When the habitat overlap analysis was performed without the lakes where the total hardness was below the critical limit of 1 °dH (Aho 1966), the cluster structure remained nearly unchanged.

5. Discussion

In Finnish lakes the main part of the variation in snail species richness is accounted for by the physical environment (Aho 1978d). This analysis indicates that the primary factor classifying the species into the clusters and the distribution types of community size also seems to be physical environment. This fits well with a previous snail study done in some of these lakes at species level (Aho 1966). The limnic snail species are relatively slightly specialized for various substrates and environments (Hubendick 1947) and, furthermore, they show much adaptive flexibility in respiration, growth cycles, reproduction and other aspects of their physiology (Hunter 1953, 1957, 1961a, b, 1964, Aho 1978c). As the supply of calcium is the most essential environmental factor for the limnic gastropod fauna in lakes of Northern Europe (Hubendick 1947), it is not surprising that the species clusters presented in this paper are primarily formed on the basis of the physical environment.

Despite the general ecological homogeneity of the limnic gastropod fauna, the species differ from each other in many respects, even within the species clusters. It has often been argued that biological interactions between species, viz. competition, play a pronounced role in the distribution of animal species (e.g., Diamond 1975; for gastropod species Boycott 1936, Fenchel 1975a,b, Lassen 1975). In the material of this study, a taxonomically and morphologically related pair of species (sibling species), *Gyraulus albus* and *G. acronicus,* differ by habitat occupation to such an extent that they do not fall in the same cluster. In contrast, two species, *Bathyomphalus contortus* and *Gyraulus albus,* with the highest distributional similarity are also fairly similar with regard to morphological and autoecological features. Likewise, a closely related pair of species, *Lymnea peregra* and *L. auricularia,* have a high degree of similarity in their distribution. Hence, with the present material one can find support both for and against competition as a factor affecting the species composition of gastropod communities in Finnish lakes. However, near the limits of the distributional range of most of the gastropod species some other mechanisms may serve as more likely explanatory factors for their distribution (such as association to certain macrophytes, Pip 1978).

Almost all species of the species pool of southern and western Finland are able to live in most of the water bodies where gastropods are found. The presence or absence of species in a certain community depend not only on the water quality but also on the colonization and extinction rates of the species (Lassen 1975, 1978, Aho 1978c). Whether competition has any effect on species composition of the communities should be studied more closely, preferably with controlled experiments. The results by Aho (1978c) suggest that extinction of gastropod populations in lakes of certain properties might be a common phenomenon. Together with the patchy distribution of small lakes this emphasizes the role of migration in maintaining species populations in the species pool of certain areas.

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