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Freshwater snail populations and the equilibrium theory of island biogeography. II. Relative importance of chemical and spatial variables

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The aim of this study was to analyse how far the local distribution of the freshwater gastropods in southern and western Finland is determined by water quality and how far by the spatial variables (area, degree of isolation) of the MacArthur-Wilson equilibrium model. The analysis was performed in four different lake groups comprising 70 lakes. The statistical tool was stepwise multiple regression analysis.

In the most oligotrophic lakes, where total hardness was < 1.0 °dH (1 °dH $=$ 7.1 mg Ca l^{-1}), the best predictors for the local occurrence of the gastropod fauna were the chemical variables of lake water. By contrast, in the group of lakes where total hardness exceeded this critical limit, the explained variation in the number of species was nearly all accounted for by the spatial variables of the equilibrium theory. The equilibrium model does not hold for the large, non-isolated lakes of the Finnish lake district. Thus, no single formula will explain the occurrence of gastropods in southern and western Finland, but each "archipelago" of lakes behaves ecologically and biogeographically as a functional entity.

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1. Introduction

Previous studies have shown that the numbers of gastropod species in some Finnish lake communities can be explained both by the theory of limiting factors (AHO 1966), and by the equilibrium theory of island biogeography (AHO 1978a). In Finland, which lies at the northern margin of the range of the freshwater snail fauna, both the properties of lake water and the spatial parameters (lake area, distances from other lakes) forming the basis of the equilibrium model (MACARTHUR & WILSON 1963, 1967) regulate the distribution and diversity of species in lakes that are more or less isolated.

The theory of dynamic equilibrium was evolved for bird populations of the Pacific islands, where climatic conditions are uniform. Lakes, considered as habitat islands, are "climatically" very heterogeneous, even in a limited area. Thus, when the equilibrium model is applied to lake communities, water quality constitutes an additional dimension, especially in the Finnish lakes, which tend to be oligotrophic (JÄRNEFELT 1963, LAAKSONEN 1972). Presumably in the poorest lakes the occurrence of gastropod species is limited predominantly by chemical variables, whereas in the more eutrophic lake ecosystems spatial parameters have a stronger impact. As these two independent studies (AHO 1966, 1978a) were made in areas that partly overlapped, a further attempt was made to analyse the relative importance of chemical and spatial variables for the gastropod fauna in a greater variety of lakes.

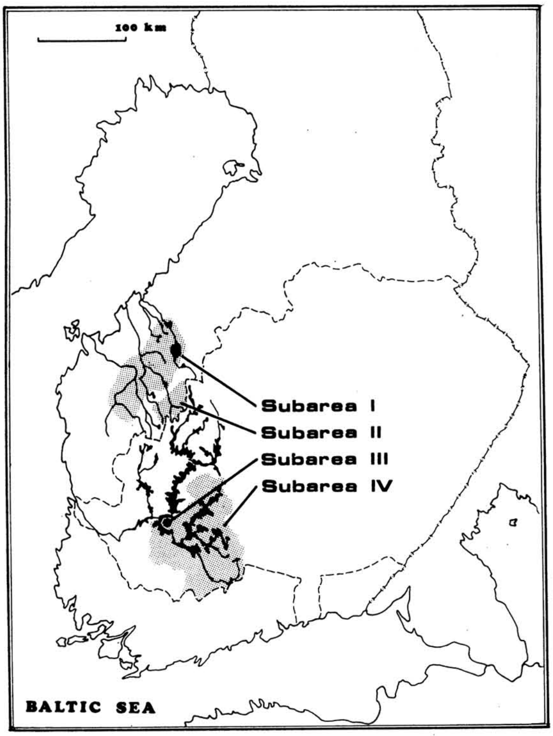

Fig. 1. Map showing the positions of the lakes studied. Dashed lines = boundaries of the Finnish lake district.

2. Study area

The species diversity and the factors influencing it were studied in four different lake groups consisting in all of 70 lakes in southern and western Finland (Fig. 1). The lake groups studied were selected by two criteria. Firstly, these subareas were to represent marginal areas of gastropod distribution in Finland. A subarea was regarded as a marginal area if it included at least one lake without any gastropod populations. Secondly, the marginal areas were to differ from each other in regard to some important limiting factor. For this criterion the best factor was considered to be the calcium content, expressed as total hardness. The critical limit of total hardness in the study area is 1.0 °dH (Aho 1966). Therefore, the waters of the lakes in at least one subarea should, if possible, all be softer than 1.0 °dH, in another subarea should fall on both sides of this critical limit, and in a third subarea should all be significantly above 1.0 °dH.

Three of the subareas chosen for this study can be regarded as marginal areas (subareas I—III), because each includes lakes without a single gastropod species. One subarea (IV) forms a contrast to the marginal areas; this consists of large lakes, such as are typical of the Finnish lake district.

A. Subarea I. Lakes in South Bothnia

The lakes of the first two subareas belong partly to the same watercourses. The criterion separating subareas I and II was the highest shoreline of the Littorina Sea, the precursor of the recent Baltic, which was formed about 7300 years ago (Eronen 1974, Donner 1977).

Nowadays this shoreline lies about 90 m above sea level in South Bothnia (Mölder & Salmi 1954). The lakes of subarea I are situated below this ancient shoreline, and those of subarea II above it.

Subarea I includes 14 lakes belonging to four drainage basins (for details, see Aho 1978b). The electrolytic conductivity, total hardness, and humus content of the water tend to be higher than in the other marginal areas. Furthermore, the study area is characterized by long distances separating the lakes from the presumed source

Table 1. Characterization of the different subareas.

		Number of species per lake	Electrolytic conductivity ($\varkappa_{20}$)	Total hardness (°dH)	Colour of water (mg Pt l^{-1})	Lake area (km^2)	Proximity to source areas of species (km)	Altitude (m)	Lake percentage (%)
Subarea I South Bothnia	$\bar{x}$	1.1±0.4	75.2±14.1	1.44±0.26	166±23	14.180±11.291	25.3±4.7	65.4±3.7	4.6±1.3
	min	0	37	0.68	50	0.030	0	40.0	0.2
	max	5	233	4.20	320	147.300	50.0	84.0	12.2
Subarea II (Suomenselkä)	$\bar{x}$	1.9±0.4	37.4± 2.2	0.65±0.05	98± 7	3.190± 1.104	15.8±2.7	125.2±6.5	6.3±0.7
	min	0	20	0.3	70	0.229	2.7	93.3	3.2
	max	5	50	1.0	160	14.820	36.7	170.1	11.5
Subarea III (Tampere)	$\bar{x}$	4.5±0.8	45.5± 3.0	0.94±0.07	68± 7	0.092± 0.040	3.4±0.4	103.0±3.7	3.2±1.0
	min	0	26	0.47	30	0.003	0.5	77.2	0.4
	max	12	71	1.39	180	0.790	6.1	136.2	3.8
Subarea IV (large non-isolated lakes)	$\bar{x}$	10.5±0.6	70.9± 5.4	1.53±0.11	45± 5	38.639± 7.545	0	81.2±0.6	14.1±1.0
	min	6	34	0.67	11	8.420	0	77.2	6.3
	max	15	111	2.30	83	119.150	0	83.8	23.7

Table 2. Data about the collections.

Subarea	Sampling period	Number of sample plots	Number of specimens	Mean number of specimens per sample plot
Subarea I	25 July — 31 July 1977 3 » — 29 » 1961	75	1437	21
Subarea II	3 » — 29 » 1961	64	807	13
Subarea III	12 June — 31 Aug. 1960	89	4138	47
Subarea IV	10 July — 20 Aug. 1965 11 » — 16 » 1966 31 » — 1 » 1977	135	11798	87

areas of species, and by a wide range of lake areas (Table 1). The helophyte associations are vast and well developed, resembling in this respect the littoral vegetation of the large lakes of the Finnish lake district (subarea IV).

B. Subarea II. Lakes in the district of the Suomenselkä watershed

The subarea includes 14 lakes in the drainage basin of the river Lapuanjoki: Ristijärvi, Mutkanjärvi, Ponnejärvi and Iso Liesjärvi in the commune of Töysä, and Kaitavesi, Sapsalampi, Alavudenjärvi, Edesjärvi, Rantatöysänjärvi, Vetämäjärvi, Iso Vehkajärvi, Iso Allasjärvi, Kuotesjärvi and Kuorasjärvi in the commune of Alavus. Biogeographically the lakes are situated in the Suomenselkä region, one of the most important watersheds in Finland.

The study area is the least productive of the subareas, with electrotic conductivity $\leqq$ 50 μS and total hardness $\leqq$ 1.0 °dH (Table 1). The lakes are shallow, with depths ranging mostly from 1 to 5 m, Sapsalampi being the only one with a depth exceeding 10 m (Mutka 1966). The few aquatic plant species form, as a rule, sparse helophyte associations.

C. Subarea III. Lakes in the Tampere district

This subarea consists of 20 small lakes belonging to the drainage basin of the river Kokemäenjoki (see Aho 1966). These lakes, which are richer in electrolytes than those in subarea II, but poorer than those in subarea I, are distinctly the smallest in this study. Also, they are situated closer to the dispersal centre than the lakes in the other marginal areas (Table 1).

D. Subarea IV. Large lakes of the drainage basin of the river Kokemäenjoki

The fourth subarea includes the large (> 8.4 km^2) lakes of the drainage basin of the Kokemäenjoki (for details, see Ryhänen 1962, Aho 1966, 1978c). Collections were made at 22 stations, 11 of which were heavily loaded with waste waters, and 11 in more or less natural condition. The electrolytic conductivity and the total hardness were at the same level as in subarea I, but the humus content was lower than in the other areas studied. Here lakes form a higher percentage of the total area than elsewhere, and the average area of a lake is also highest (Table 1).

3. Material and methods

A. Gastropods

The material was collected by the author, except in subarea II and from Kuortaneenjärvi in subarea I, which were originally sampled for another purpose (Mutka 1966). Details of collections are presented in Table 2.

The collection technique has been described by Aho (1966, 1978a, 1978c) and Mutka (1966). In general, the two collectors worked in the same manner. The only slight difference was in the sieving technique. Mutka (1966) used a sieve with a 1.0-mm mesh, whereas my sieve had a 0.8-mm mesh. This difference can hardly have had a significant effect on the number of species (S) used as the dependent variable in this study.

B. Independent variables

The chief purpose of this study was to ascertain how far the variation in the number of species was explained by chemical variables (water quality) and how far by spatial variables (lake area and distance from other lakes). Therefore, the number of parameters characterizing water quality was restricted. In the light of results of a previous paper (Aho 1966), two variables were chosen for the preliminary analysis: electrolytic conductivity, which had the highest positive correlation with the number of species (r = 0.904***, df = 27), and colour of water (mg Pt l^{-1}) indicating the humus content, which, in contrast, had the highest negative correlation (r = —0.592**, df = 20). As calcium is regarded as a very important factor regulating the distribution of gastropods (e.g. Boycott 1936, Hubendick 1947, Hunter 1964), and as there was also a high positive correlation between number of species and total hardness (r = 0.872***, df = 27; cf. Aho

1966), the correlations were calculated after combining all the gastropod data, the aim being to identify the chemical factor with the strongest favourable influence on gastropods. This factor was used for the multiple regression analysis. One of the two variables with positive correlations had to be eliminated from the multiple regression analysis for a high intercorrelation ($r = 0.975$***, df = 68). In the light of the examination, electrolytic conductivity was eliminated, because its influence on the number of gastropod species was less significant ($r = 0.264$**) than that of total hardness ($r = 0.382$***). Thus, the parameters describing water quality in this study are total hardness (WQ_1) and colour of water (WQ_2). In addition, the values of alkalinity (WQ_3; mval l^{-1}) were used in the lakes of the Suomenselkä district (see p. 160).

The spatial parameters used were the lake area (A) and the degree of isolation. The latter can be estimated in many ways (e.g. POWER 1972). In this study two parameters were used: The first was the shortest possible distance between the lake and the presumed centre of dispersal (I_1) and the second the total area of the lakes in relation to the total area of the drainage basin, called the lake percentage (I_2). The centre of dispersal was assumed to be either the greatest lake in the subarea (Lappajärvi in subarea I) or the nearest large lake of the main watercourses of the Finnish lake district (Toisvesi and Ähtärinjärvi in subarea II, and Pyhäjärvi in subarea III). Toisvesi was chosen as the dispersal centre of Jalasjärvi and Hirvijärvi, because these lakes were nearer to Toisvesi than to Lappajärvi. The lakes of subarea IV are regarded as the dispersal centre itself. The definition of a dispersal centre is based on two criteria: (1) The number of species must be greater than in the other lakes of the subarea, and (2) all gastropod species living in the habitat islands must also be found in the dispersal centre.

The altitude of the lakes is a third type of independent variable. Primarily, the altitude indicates the age of the lake, but in some cases it is also inversely proportional to the productivity (see Table 4).

The values for the hydrochemical variables have mainly been taken from other papers (Hämeen vesiensuojeluyhdistys 1964, 1965, 1966, 1968, AHO 1966, MUTKA 1966, Maataloushallitus 1967, 1968a, 1968b, 1969, 1970, Kokemäenjoen vesistön vesiensuojeluyhdistys 1969, 1970, and the files of the Water Authority of Finland). In addition, I analysed the water quality of the lakes studied in 1977, adopting the technique used by the Water Authority of Finland. Samples were taken at depths of 0.5—1.0 m.

The areas of the lakes, the parameters describing the degree of isolation and the values for altitude have been taken from the papers of ODENWALL (1934), SIRÉN (1955), KAJOSAARI (1964) and AHO (1966), or determined from topographic maps (scale 1 : 20 000 or 1 : 100 000).

C. Statistical procedures

Two statistical processes were used, correlation matrices and stepwise multiple regression analysis. A useful technique for assessing relationships between biological and physical variables is stepwise multiple regression. This analytical tool has been widely employed for analysing the numbers of species in the different groups of organisms on both oceanic archipelagos and continental habitat islands (e.g. HAMILTON *et al.* 1964, JOHNSON *et al.* 1968, VUILLEUMIER 1970, 1973, BROWN 1971, POWER 1972, JOHNSON & RAVEN 1972, SEPKOSKI & REX 1974, SIMPSON 1974, JÄRVINEN 1977). The technique is most useful for considering the properties of single archipelagos (MACARTHUR & WILSON 1967).

The components with the greatest weight in predicting variation in the numbers of freshwater gastropod species were identified by stepwise multiple regression analysis, with the number of species (S) as the dependent variable. The stepwise procedure admits independent variables into the regression model according to the amount of variation they explain in the dependent variable. Further interpretation was performed with the equations in which all partial regression coefficients (t values) as well as the whole regression model (F value) were statistically significant.

This type of analysis is subject to a number of statistical limitations (POOLE 1974). The data from each separate subarea fulfilled the requirements for multiple regression analysis, but the data as a whole did not, because the dependent variable was not normally distributed. Therefore regression models have been calculated for the four subareas separately, but not for all the lakes together. The regression equation also assumes that the independent variables are independent of each other. However, some independent variables showed quite high, although often entirely spurious, intercorrelations (Table 3). In practice, this requirement is not rigid, and does not seriously affect the predictive value of the regression equation (POOLE 1974). Because the ecological data are not ideally suited to multiple regression, I regard the stepwise regression analysis only as a heuristic aid to understanding the biogeographic system of the four lake groups studied (cf. also SEPKOSKI & REX 1974).

Stepwise multiple regressions were performed with the HYLPS system for the UNIVAC 1108 computer of the Ministry of Education via the Computing Centre of the University of Joensuu.

4. Results

A. Correlations among variables

For the material as a whole the number of snail species is positively correlated with total hardness, lake area and lake percentage at the highest level of probability, and at the same level negatively correlated with humus content and with distance from the hypothetical dispersal centre (Table 3). The correlation with altitude, however, is not so strong. So, for the material as a whole, the number of species shows statistically significant correlations with all independent variables.

When the polluted large lakes are excluded, the positive correlation with lake percentage is still above the probability limit of 0.1 %,

Table 3. Intercorrelations (r) of the variables in the different subareas.

Subarea I (South Bothnia)	1	2	3	4	5	6
1 Total hardness (WQ_1)	–					
2 Colour of water (WQ_2)	−0.079	–				
3 Lake area (A)	−0.193	−0.467	–			
4 Distance from dispersal center (I_1)	0.410	0.684**	−0.486	–		
5 Lake percentage (I_2)	−0.319	−0.573*	0.543*	−0.699**	–	
6 Altitude (E)	−0.444	−0.042	0.080	−0.253	0.146	–
Number of species	−0.369	−0.500	0.816***	−0.484	0.712**	0.131

Subarea II (Suomenselkä)	1	2	3	4	5	6	7
1 Total hardness	–						
2 Colour of water	−0.158	–					
3 Lake area	−0.206	0.160	–				
4 Distance from dispersal center	−0.195	0.387	0.729**	–			
5 Lake percentage	−0.204	−0.216	0.599*	0.338	–		
6 Altitude	0.043	−0.523	−0.427	−0.686**	0.183	–	
7 Alkalinity (WQ_3)	0.738**	0.035	−0.325	−0.498	−0.370	0.108	–
Number of species	0.421	−0.125	−0.016	−0.217	−0.346	−0.292	0.602*

Subarea III (Tampere)	1	2	3	4	5	6	7
1 Total hardness	–						
2 Colour of water	−0.518*	–					
3 Lake area	0.077	−0.356	–				
4 Distance from dispersal center	−0.737***	0.063	0.059	–			
5 Lake percentage	−0.191	0.334	0.351	−0.236	–		
6 Altitude	−0.744***	0.566**	0.040	0.482*	0.379	–	
7 Alkalinity	0.920***	−0.488*	−0.037	−0.746***	−0.862***	−0.178	–
Number of species	0.740***	−0.640**	0.482*	−0.605**	0.208	−0.584**	0.680***

Subarea IV (Large lakes)	1	2	3	4	5	6	Number of species in polluted lakes
1 Total hardness	–	−0.200	−0.106	0.000	−0.021	0.705*	−0.716*
2 Colour of water	−0.220	–	−0.408	0.000	−0.513	−0.237	0.220
3 Lake area	−0.259	−0.537	–	0.000	−0.264	0.080	0.407
4 Distance from dispersal center	0.000	0.000	0.000	–	0.000	0.000	0.000
5 Lake percentage	0.350	−0.758**	0.395	0.000		−0.345	−0.402
6 Altitude	−0.431	0.805**	−0.258	0.000	−0.380	–	−0.499
Number of species in unpolluted lakes	0.848***	−0.453	−0.037	0.000	0.416	−0.528	

Totals (Subareas I–IV)	1	2	3	4	5	6	Number of species (n = 70)
1 Total hardness	–	−0.036	0.275*	0.061	0.132	−0.583***	0.389***
2 Colour of water	0.086	–	−0.326**	0.763***	−0.455***	−0.167	−0.586***
3 Lake area	−0.012	−0.341**	–	−0.325**	0.524***	−0.296*	0.538***
4 Distance from dispersal center	0.303*	0.758***	−0.278*	–	−0.417***	−0.352**	−0.590***
5 Lake percentage	−0.083	−0.433***	0.663***	−0.319*	–	−0.169	0.506***
6 Altitude	−0.556***	−0.225	−0.265*	−0.320*	−0.093	–	−0.298*
Number of species (unpolluted, n = 59)	0.113	−0.633***	0.382**	−0.557***	0.471***	−0.196	

whereas the correlation with lake area decreases and that with total hardness disappears entirely. On the other hand, the number of species is still negatively correlated with humus content and distance. Thus, in general, humus content (WQ_2), the variables describing isolation (I_1 and I_2), and also lake area (A) seem to be the most important factors regulating the distribution of the gastropod fauna in southern and western Finland.

But the separate subareas differ greatly from each other and from the lakes as a whole (Table 3). In the Suomenselkä watershed district (subarea II) the number of gastropod species was not significantly correlated with any of the basic independent variables (variables 1—6 in Table 3). In South Bothnia (subarea I) the number of species was dependent on lake area and lake percentage. In the Tampere district (subarea III), on the other hand, the number of species bore a statistically significant correlation with nearly all independent variables. The correlation was highest with total hardness, then with humus content, distance from the dispersal centre and altitude, and thirdly with lake area. It was in this subarea that the correlations between the independent variables were closest, especially those between distance and total hardness, altitude and total hardness, and altitude and humus content.

In the large non-isolated lakes of the Finnish lake district (subarea IV) the number of species was significantly correlated only with total hardness. In the unpolluted lakes the correlation was positive, but in the polluted lakes negative. If these large lakes are treated as a unit, the only factor significantly correlated with the number of species was altitude ($r = -0.564$**, df $= 20$), the number of species increasing downstream.

In the Suomenselkä watershed district, because there was no significant relation between the number of species and the chemical and spatial variables already tested, alkalinity was added to the analysis on the ground that only alkalinity had been found to have a statistically significant correlation with the number of species (MUTKA 1966). A clear correlation with alkalinity was observed in the Tampere subarea, too (Table 3, see also AHO 1966).

Thus, the results obtained by means of intercorrelations are quite inconsistent. The correlations are very different in different subareas, and the figures given in Table 3 do not exhibit any logical trends.

B. Multiple regressions

Stepwise multiple regression analyses were carried out with the number of species (S) as the dependent variable and all the other components as independent variables. In the results to follow, the amount of variation in the dependent variable explained by the simultaneous effect of independent variables in the regression equations is given in parentheses for each case. Statistical significance of partial regression coefficients is indicated by asterisks:

$* = 0.01 < p < 0.05$, $** = 0.001 < p < 0.01$, $*** = p < 0.001$.

In South Bothnia (subarea I) the regression model for the gastropod species was

$$S = 0.202 + 0.024A^{**} + 0.128I_3^{*} \quad (76.8\ \%).$$

Lake area (A) accounted for 66.5 % of the variation in S, and lake percentage (I_2) for the remaining 10.3 %.

In the Suomenselkä watershed district (subarea II) the basic independent variables did not provide a statistically significant regression model at all. Therefore, in this case only the values for alkalinity were added to the independent variables. The simplest regression model was

$$S = -2.000 + 15.000 WQ_3^{*} \quad (36.2\ \%).$$

The next two variables to enter the equation after alkalinity (WQ_3) were altitude (E; explaining 12.9 %) and humus content (WQ_2; explaining 15.7 %), although the associated partial regression coefficient for humus content was not quite statistically significant ($0.05 < p < 0.10$), but the percentage of explained variation in S increased by a total of 28.6 percentage units:

$$S = 5.927 + 17.043 WQ_3^{**} - 0.044E^{*} - 0.031 WQ_2 \quad (64.8\ \%).$$

When the calculations were performed for all the data of MUTKA (1966), which includes Kuortaneenjärvi ($n = 15$), the partial regression coefficient of WQ_2 was also significant:

$$S = 5.244 + 17.602 WQ_3^{**} - 0.039E^{*} - 0.032 WQ_2^{*} \quad (63.5\ \%).$$

In this study Kuortaneenjärvi falls into subarea I. According to the model, alkalinity is of great importance in extremely poor lakes where the species have to live in abiotic environmental conditions approaching their lower limits of tolerance.

For the data of the lakes in the Tampere district (subarea III) the best regression model was

$$S = -3.765 + 8.143 WQ_1^{***} + 9.450A^{**} \quad (72.9\ \%).$$

The most important factor was total hardness (WQ_1), which explained 54.7 % of the variation in S, the remaining 18.2 % being due to lake area (A).

The large lakes of the Finnish lake district (subarea IV) were treated as three subgroups, (a) unpolluted lakes, (b) polluted lakes, and (c) all large lakes together:

(a) $S = 0.989 + 8.028 WQ_1$*** (71.8 %),

(b) $S = 36.992 - 12.907 WQ_1$* (51.3 %),

(c) $S = 40.278 - 0.364E$* (31.8 %).

In unpolluted lakes total hardness will function as a very strong favourable factor. But in the lakes overloaded with waste waters the negative correlation between number of species and total hardness indicates the adverse effect of pollution on the distribution of the gastropod species in general. When the large lakes are examined as a group the best predictor is altitude, the number of species increasing downstream along the lake channels.

The percentage of variation in S explained by the simultaneous effects of all 6 independent variables (7 in subarea II) was:

Subarea I	84.5 %
Subarea II	72.8 "
Subarea III	88.3 "
Subarea IV (unpolluted)	89.4 "
Subarea IV (polluted)	83.3 "
Subarea IV (total)	41.7 "

As shown by the results presented above, the most important predictor of species diversity differs from one subarea to another, being lake area in South Bothnia, alkalinity in the Suomenselkä watershed district, and total hardness in the small lakes of the Tampere district. In the large, non-isolated lakes of the Finnish lake district, furthermore, the most important factor is altitude, or if they are considered as two groups, the first predictor in the unpolluted lakes is total hardness, and in the polluted lakes the waste water itself (here the evidence is indirect). Thus multiple regression analyses gave the same inconsistencies as the correlation matrices.

5. Discussion

The assemblage of species found in any particular locality is determined by physical environment, migrations and colonizations, interspecific competition and extinctions (HORN & MACARTHUR 1972, LEVIN 1974, SLATKIN 1974). A satisfactory community theory must integrate all these processes, but interspecific competition is not discussed in this paper, which is concerned — directly or indirectly — with the other determinants mentioned. The main problem in this paper was to estimate the relative importance of chemical and spatial factors in determining the local distribution of the gastropod fauna in southern and western Finland.

The subareas differ from each other in regard to several factors, one of the most important being total hardness (see p. 156, and Table 1). In the Suomenselkä watershed district the total hardness ranged from 0.3 to 1.0 °dH, with a mean of 0.65±0.05 °dH. This means that in all the lakes of this subarea the main limiting factor is calcium (Fig. 2). In these conditions the occurrence of gastropods was also dependent on alkalinity and humus content together with altitude. As regards the relative contributions of chemical and spatial variables to the explained variation of S, spatial variables accounted for only 5 %, and water chemistry

Table 4. Relative contributions of different groups of independent variables to the multiple correlation coefficient (R^2). Chemical variables = $WQ_1 + WQ_2 + WQ_3$; spatial variables = $A + I_1 + I_2$; altitude = E.

Subarea	Chemical variables		Spatial variables		Altitude		
	Contribution to R^2	%	Contribution to R^2	%	Contribution to R^2	%	Total R^2
Subarea I	0.0528	6.3	0.7913	93.7	0.0007	0.1	0.8448
Subarea II	0.5634	77.4	0.0357	4.9	0.1286	17.7	0.7277
Subarea III	0.6338	71.7	0.2410	27.3	0.0086	1.0	0.8834
Subarea IV	0.0344	8.3	0.0639	15.3	0.3184	76.4	0.4167

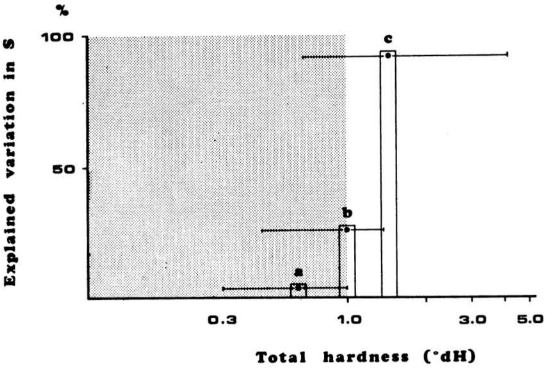

Fig. 2. The relative importance of the spatial variables on the occurrence of the gastropod fauna in different marginal areas of the study, a = subarea II, b = subarea III, c = subarea I. The means and ranges of total hardness are indicated at the top of each column. Shaded area = the range of total hardness where calcium is the limiting factor.

for as much as 77 %. Another factor playing an importance role in these lakes was altitude (Table 4). Thus, in the unproductive lakes of Suomenselkä the local distribution of gastropods depends on the water chemistry and altitude and not on the spatial variables of the equilibrium model of island biogeography (see also Fig. 2).

In the Tampere district the total hardness ranged from 0.47 to 1.39 °dH, the mean value, 0.94±0.07 °dH, being very near the critical limit (Aho 1966). In this case, total hardness is the most important factor, but one of the variables of the equilibrium theory, lake area, is a close second. In these lakes, which are intermediate in total hardness between the subareas of South Bothnia and Suomenselkä, water quality accounts for 72 % and spatial variables for 27 % of the explained variation (Table 4 and Fig. 2).

In the third marginal area, South Bothnia, the lakes had quite high values of total hardness, ranging from 0.68 to 4.20 °dH, the mean being 1.44±0.26 °dH. Nearly all lakes had a calcium content above the critical limit. It is in this group of lakes, where calcium does not act as a limiting factor, that the number of species is most clearly dependent on lake area and degree of isolation, the variables of the equilibrium theory. Spatial variables explained 94 % and water chemistry only 6 % of the explained variation in *S*. Thus, here the situation is just the opposite of that in the unproductive lakes of the Suomenselkä watershed district (Table 4).

This analysis indicated that both chemical and spatial factors regulate the numbers of species in the lakes of southern and western Finland. In the most oligotrophic lakes it is water quality that sets the physiological limits for the occurrence of gastropods, whereas in the most eutrophic lakes the numbers of species present is determined by spatial parameters.

6. Conclusions

1) As regards the distribution of gastropod species in the Finnish lakes, the theory of dynamic equilibrium and the theory of limiting factors are both applicable.

2) In the most oligotrophic lakes, with a total hardness of < 1.0 °dH, the local gastropod fauna was best predicted by the composition of the lake water. In these lakes 77 % of the explained variation in the number of species was due to water quality and only 5 % to spatial factors. Altitude accounted for 18 % of the explained variation in *S*.

3) In lakes where the total hardness exceeded the critical limit mentioned in (2), the number of species was largely predicted by the spatial variables of the equilibrium theory. In these lakes the spatial variables accounted for 94 % of the explained variation in the number of snail species and the water quality for only 6 %.

4) The equilibrium theory does not hold good in the large lakes of the Finnish lake district, which are probably insufficiently isolated from each other. The low value of the species-area exponent *z* measured previously for the same lakes (Aho 1978a) pointed in the same direction.

5) Alkalinity was more important as a stabilizing agent in the extremely oligotrophic lakes, where the freshwater gastropods live near the extreme limit of their range.

6) No single rule will explain the occurrence of gastropods in southern and western Finland. Each lake "archipelago" behaves ecologically and biogeographically as a functional entity. Each lake group therefore also has its own particular combination of factors regulating the local distribution of the freshwater gastropod species.

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