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Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland

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The applicability of the equilibrium theory of island biogeography to freshwater snail populations was tested in an area on the margin of gastropod distribution in the Finnish lake district. The study concerned 20 small lakes and ponds (mean area about 0.1 km^2) treated as "habitat islands", and a system of 21 large lakes (mean area about 40 km^2) regarded as a "mainland analogy".

The species-area relations agreed with those found in other studies of habitat islands. The slope of the log-log line was a little steeper for the small lakes (z = 0.163) than for the lakes as a whole (z = 0.149). In the large lakes the area effect was almost non-existent (z = 0.061). Water quality was also taken into consideration in the analysis.

The existence of a dynamic equilibrium was tested with the variance-to-mean ratios of the numbers of species. These ratios gave strong support to the MacArthur-Wilson equilibrium theory. They also showed that the rates of extinction and immigration are modified by a further variable, water quality. Thus, in the small lakes the presence of gastropod species is determined simultaneously by water composition and spatial variables (area, distances).

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1. Introduction

The number of species on oceanic islands is thought to represent a dynamic equilibrium between contemporary rates of immigration and extinction (MACARTHUR & WILSON 1963, 1967; see also PRESTON 1962a, 1962b). Analogously, some mainland habitats can be regarded as islands (e.g. CULVER 1970, VUILLEUMIER 1970, BROWN 1971, FORMAN *et al.* 1976). The equilibrium theory of island biogeography has also been applied to freshwater communities (e.g. BARBOUR & BROWN 1974, SEPKOSKI & REX 1974, LASSEN 1975, PATRIC 1975, KEDDY 1976), but, as MAGNUSON (1976) points out, few investigators have so far taken lakes as models of islands.

A previous paper (AHO 1966) showed that the distribution of freshwater mollusc species is correlated significantly with lake water composition in conditions of low electrolyte and high humus concentrations, which characterize Finnish lakes in general. That paper concerned the mollusc fauna of one large lake and 22 small lakes and ponds which harboured widely differing numbers of molluscan species, from 0 to 33.

The study indicated that the occurrence of gastropod species could also be explained by the equilibrium theory of island biogeography. In the large lake there were 19 gastropod and 10 sphaerid species. In the small lakes and ponds, by contrast, the number of gastropod species varied from 0 to 14, and the number of sphaerids from 0 to 10. The area effect could still be seen in the mean numbers of gastropod species when the results were standardized for total hardness, a parameter which is correlated with the calcium concentration of lake water (AHO 1966:310—311).

Elsewhere, too, the molluscan fauna is richer in species in large lakes than in smaller bodies of water with equal calcium concentrations (BOYCOTT 1936, ARCHER 1939, MACAN 1950, TUCKER 1958). The same is true of other water organisms, for example, fishes and fish parasites in the small isolated lakes of Karelia (PETRUSHEVSKIJ & BYKHOVSKAYA 1935, BYKHOVSKAYA 1936).

Recently, the distribution of Danish freshwater snails has been studied in the light of the MacArthur-Wilson theory of island biogeography (LASSEN 1975). These data indicated that the snail fauna represents a dynamic equilibrium sustained by immigration and extinction within the main area of gastropod distribution where biotic interrelations are probably the chief factors governing the diversity of the local fauna.

The lakes of the present study, in contrast, are situated in a marginal area of gastropod distribution where the composition of the lake water constitutes the ultimate physiological limit for the occurrence of a species. Some of the lakes contain no gastropods. The aim of this study is to test whether in such circumstances the equilibrium model proposed by MACARTHUR & WILSON (1963) will account for the variation in the number of species in lakes differing in area, degree of isolation and water quality.

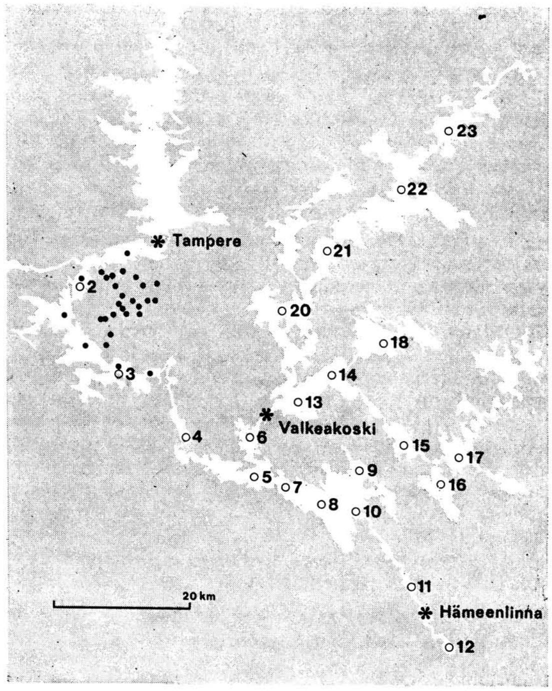

Fig. 1. The southern drainage basin of the river Kokemäenjoki. Filled circles = lakes, mainly small ones, studied in 1960–1963 (AHO 1966); open circles = large lakes, studied in 1965–1967 (AHO 1978). The cities of Tampere, Valkeakoski and Hämeenlinna are indicated in the figure.

2. Study area

The study is based on two collections described in other papers: A) material collected in 1960—1963 (AHO 1966), and B) material collected in 1965—1966 (AHO 1978). The two collections were made in the southern drainage basin of the river Kokemäenjoki. Collection A covers the small lakes (n = 22) with areas ranging from 0.003 to 0.790 km², mean 0.092 km². Collection B covers the large lakes (n = 21) with areas ranging from 8.4 to 119.2 km², mean 38.6 km². One lake, Pyhäjärvi (area 111.5 km²), was included in both collections (Fig. 1, stations 2 and 3).

General descriptions of both groups of lakes are to be found elsewhere (AHO 1966, 1978).

3. Collection technique and material

The sampling technique in the two collections was identical, except that for collection B the number of samples taken at each station was fixed. The whole set of samples for a station comprised three samples from helophyte associations (each from an area of 4 m²), and three samples from stony bottoms (sampling time 0.5 h in each case) (for details see AHO 1966, 1978).

Collection A from the Tampere district was gathered with slightly greater intensity than the material from the large lakes (collection B). The former study area is distinctly smaller than the latter. Nevertheless, the former collection (based on 187 samples) comprised about 21 000 gastropod specimens, while the latter collection (based on 125 samples) comprised 11 600 specimens. The difference in intensity of collection can be deduced from the numbers of gastropods collected from Pyhäjärvi, stations 2 and 3 (Table 1), because both collections included material from these stations. The number of gastropod species found in collection B was 17 % smaller than the maximum number of species at station 2, and 18 % smaller at station 3. Collection B did not

Table 1. Effect of differences in collection intensity on the number of species at stations 2 and 3 in Pyhäjärvi. S = total number of gastropod species, % = percentage of gastropod species found in relation to total number of species, n = number of sample units.

	Collection A 1960–1963			Collection B 1965–1967			Totals	
	S	%	n	S	%	n	S	n
Station 2	18	100	14	15	83	8	18	22
Station 3	17	100	9	14	82	6	17	15

include a single species which had not already been found during collection A (Table 1).

When testing whether the equilibrium theory of island biogeography would explain the distribution and diversity of the snail fauna in the Finnish lake district, I assumed that Pyhäjärvi, with its large area and great number of gastropod species, functions as a source for colonization of the smaller lakes and ponds. Thus the smaller water bodies were considered as habitat islands.

The small lakes are connected with Pyhäjärvi by narrow brooks, which does not mean that these freshwater habitats are ecologically less insular (cf. HUBENDICK 1962). Only two of them (Vähälammi and Isolammi, see Fig. 2 in AHO 1966) are connected with Pyhäjärvi by a short, wide stream. The littoral communities of these two small lakes form a continuum with the littoral community of Pyhäjärvi. In addition, the surfaces of these three lakes are at exactly the same level. Thus, for these two small lakes isolation is incomplete and, not surprisingly, they have the greatest number of gastropod species of all the small lakes studied (Vähälammi 12 and Isolammi 14 species). Because of insufficient isolation Vähälammi and Isolammi were excluded from the testing of the hypothesis.

4. Results and discussion

A. Species—area relations

The problem is first considered with regard to the static aspects of the equilibrium biota by examining empirical relations between the island area (A) and the number of species present (S). The relation between species and area can be described by the equation $S = CA^z$, or in the converted form $\log S = \log C + z \log A$ (ARRHENIUS 1921, MACARTHUR & WILSON 1967, DONY 1977). C is a proportionality constant and varies with the dimensions in which A is measured and with the taxonomic group studied. z is a dimensionless parameter describing the slope of the line relating $\log S$ and $\log A$. The actual equation for the small lakes is

$$S = 6.237\ A^{0.163},$$

for the large lakes

$$S = 8.318\ A^{0.061},$$

and for all lakes

$$S = 6.026\ A^{0.149}.$$

In oceanic islands the empirical z values cluster in the range 0.20—0.35. In the habitat islands a similar relation exists between S and A, except that z is smaller, usually falling between 0.12 and 0.17 (MACARTHUR & WILSON 1967). In the Danish lakes studied by LASSEN (1975) the slope of the species-area curve for gastropods was 0.09 in eutrophic waters, and as high as 0.25 in oligotrophic waters. BARBOUR & BROWN (1974), studying the species-area relations of fishes, found that z was 0.15 for a sample of 70 of the whole world's lakes and 0.16 for the North American lakes. The same values were found in this paper for the small lakes and for all lakes (z = 0.15—0.16). In the large lakes z was smaller ($z = 0.06$), which indicates that they have higher immigration rates (cf. GILPIN & DIAMOND 1976).

However, the mathematical relation between S and A is complicated (MAY 1975), and the equation is most reliable when S is greater than 20 (DIAMOND & MAY 1976). In addition, the species-area curve does not take into consideration the chemical heterogeneity of the lakes studied. For these two reasons the species-area relation was also analysed in another way.

As a first step, the large lakes (stations 2—23 in Fig. 1) were divided into two subgroups according to surface area, and the mean numbers of species in the subgroups were compared. In the larger lakes ($\bar{x} = 64.1 \pm 9.9$ km², n = 11) the mean number of gastropod species was

Table 2. Some parameters of water quality in large lakes and small lakes of the southern drainage basin of the river Kokemäenjoki. Min = minimum value, $\bar{x}$ = mean value, max = maximum value, n = number of lakes, t = t value between means. Measurements were made at 1 m depth during the summer stagnation period (for details see AHO 1966, 1978).

	Large lakes				Small lakes				
	Min	$\bar{x}$	Max	n	Min	$\bar{x}$	Max	n	t
Electrolytic conductivity ($\varkappa_{20}$)	33	69.4	180	21	26	45.3	71	22	3.96***
Total hardness (°dH)	0.67	1.53	2.30	21	0.47	0.94	1.39	22	4.65***
pH	5.7	6.99	7.8	21	4.7	6.29	7.0	16	4.64***
Colour of water (mg Pt l^{-1})	5	45	100	21	30	68	180	22	2.66*
$KMnO_4$ consumption (mg l^{-1})	11	49.3	193	21	30	51.3	113	22	0.26

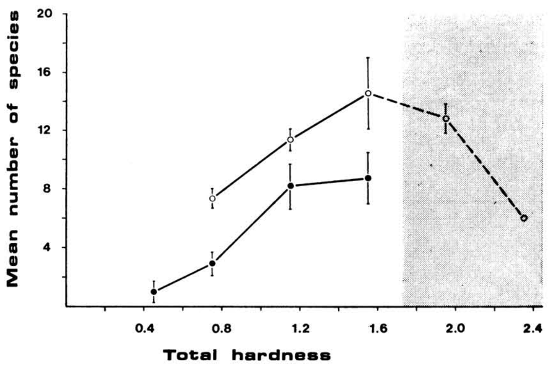

Fig. 2. The relation of the mean number of gastropod species to the lake area in different total hardness classes. Open circles = large lakes; filled circles = small lakes; shaded area above 1.7 °dH = polluted lakes.

10.7±0.9, and in the smaller ones ($\bar{x}$ = 20.1±4.4 km², n = 10) 10.6±0.7. Thus, there was no difference between the two subgroups, as was also suggested by the low z value (0.06) of these lakes.

The second step was to compare the numbers of species in the large and small lakes. The mean number of gastropod species in the large lakes was 10.7±0.6 (n = 21), and in the small lakes 4.5±0.8 species (n = 20). The difference in the mean numbers of gastropods between these two lake groups was statistically significant (t = 4.929***, df = 39). The difference might have been even greater if the two collections had been made with the same relative intensity.

The interpretation of the result mentioned above is complicated, however, because the lake groups in question differ in water quality (see Table 2). The small lakes have softer and more acid water containing larger amounts of humus, and their electrolyte content is at a lower level. In the lakes studied the number of gastropod species is positively correlated with such properties as water hardness, electrolytic conductivity, pH and alkalinity, and negatively correlated with the colour of the water and with $KMnO_4$ consumption (Aho 1966). Is the mean number of species determined primarily

Table 3. Occurrence of freshwater gastropods in lakes differing in total hardness (°dH). Values are numbers of small lakes (a), and of large lakes (b). The decline in species diversity with total hardness of 2.2–2.5 °dH is the result of heavy pollution caused by the wood-processing industry.

	Classes of total hardness (°dH)								
	≧0.5	0.6–0.9		1.0–1.3		1.4–1.7		1.8–2.1	2.2–2.5
	a	a	b	a	b	a	b	b	b
Lymnaea stagnalis	—	2	3	7	6	3	2	9	1
L. peregra	1	6	2	8	6	3	2	9	1
L. auricularia	—	—	3	1	6	2	2	7	—
L. palustris	—	3	3	6	6	2	2	9	1
L. truncatula	—	—	—	4	1	1	—	1	—
L. glutinosa	1	3	1	4	5	1	2	3	—
Physa fontinalis	—	—	—	4	2	1	1	5	—
Planorbarius corneus	—	—	—	—	—	—	—	1	—
Planorbis carinatus	—	—	—	—	1	1	1	1	—
Bathyomphalus contortus	—	—	3	5	6	2	2	9	1
Gyraulus albus	—	—	3	6	6	3	2	9	1
G. acronicus	1	2	3	3	6	1	1	5	1
G. crista	1	2	1	4	3	—	1	8	—
G. riparius	—	—	—	2	6	1	2	7	—
Hippeutis complanatus	—	1	—	2	—	—	2	5	—
Acroloxus lacustris	—	1	—	4	1	1	2	8	—
Bithynia tentaculata	—	—	—	1	2	—	1	7	—
Bythinella steini	—	—	—	—	—	—	1	1	—
Valvata cristata	—	—	—	3	1	2	1	6	—
V. piscinalis	—	1	1	2	3	2	2	5	—
Average number of species	1.0	2.9	7.3	8.1	11.3	8.7	14.5	12.8	—
Total number of species	4	9	10	17	17	15	18	20	6
Number of lakes	4	7	3	8	6	3	2	9	1

Table 4. Average number of gastropod species in lakes of different areas but the same total hardness. $\bar{x}$ = mean number of species, S = total number of species, A = mean size of lakes studied (km^2), n = number of lakes. (According to the material of AHO 1966)

	Total hardness (°dH)															
	0.4—0.7				0.8—1.1				1.2—1.5				1.6—1.9			
	$\bar{x}$	S	A	n	$\bar{x}$	S	A	n	$\bar{x}$	S	A	n	$\bar{x}$	S	A	n
Small lakes in the Tampere study area																
— the smaller ones	0.8	3	0.028	4	2.7	5	0.029	3	5.7	15	0.016	3	—	—	—	—
— the larger ones	2.0	5	0.092	4	7.0	13	0.308	3	10.7	17	0.117	3	—	—	—	—
Pyhäjärvi (dispersal centre)	—	—	—	—	—	—	—	—	14.3	16	55	3	16.7	18	55	3

Table 5. Some aspects of water quality in different groups of small lakes.

	Small lakes of different sizes					Small lakes of different degrees of isolation				
	Smaller		Larger			Lakes farther from Pyhäjärvi		Lakes nearer to Pyhäjärvi		
	$\bar{x}$	n	$\bar{x}$	n	t	$\bar{x}$	n	$\bar{x}$	n	t
Electrolytic conductivity ($\varkappa_{20}$)	43.0	10	45.7	10	0.412	35.0	10	53.7	10	3.906**
Total hardness (°dH)	0.90	10	0.90	10	0.027	0.69	10	1.10	10	3.599**
Alkalinity (mval l^{-1})	0.16	10	0.15	10	0.215	0.09	10	0.22	10	4.012***
pH	5.9	6	6.5	8	2.173	6.3	8	6.3	6	0.047
Water colour (mg Pt l^{-1})	84	10	56	10	1.936	72	10	68	10	0.279
$KMnO_4$ consumption (mg l^{-1})	57.3	10	46.1	10	1.410	51.8	10	51.6	10	0.022

by lake area or water quality, or by the simultaneous effect of both variables?

To settle this question the lakes were classified in relation to total hardness (1 °dH = 0.178 mmol l^{-1} $CaCO_3$), the abiotic factor of greatest significance (Table 2). The mean numbers of species were consistently lower for the small lakes (Table 3, Fig. 2). Up to 1.7 °dH the number of species increased with hardness, but at higher values it declined (shaded area in Fig. 2); the hardness above 1.7 °dH is due to pollution from the towns of Hämeenlinna and Valkeakoski. The mean number of gastropod species was found to have a similar relation to water hardness in the large and small lakes. Thus, the difference in the mean numbers of species between the mainland analogies and island analogies is probably explained by lake area.

As a third step the area effect was studied within the group of small lakes, which were divided into two equal subgroups according to lake area (Table 4). In the aspects of water quality studied the two subgroups did not show statistically significant differences (Table 5). Nevertheless, there was a significant difference in number of species (t = 2.140*, df = 18; see also Fig. 3). Thus, the influence of area upon species diversity was also seen within the group of habitat islands.

The above tests of the hypothesis were done by comparing the mean numbers of species in different lake groups. But when the curves for mean number (Fig. 2) are compared with those for total number of species in each class of total hardness (Fig. 4), it emerges that there are no differences between the large lakes and the small lakes. Thus, the gastropod species are equally able to live in large and small lakes, and the differences in their distribution cannot be accounted for by an adaptive or autecological explanation.

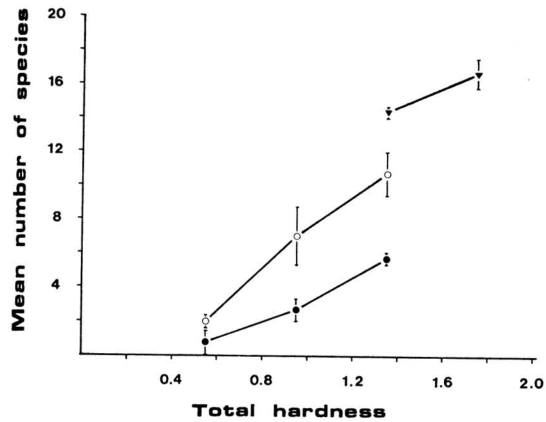

Fig. 3. The effect of area on the number of gastropod species among the small lakes in different total hardness classes. Filled circles = the smaller island analogies; open circles = the larger island analogies; filled triangles = the mainland analogy (Pyhäjärvi).

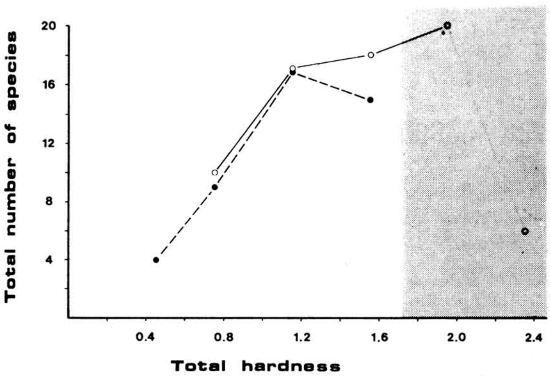

Fig. 4. The total number of gastropod species in the large lakes (open circles) and the small lakes (filled circles) in different total hardness classes.

B. Species equilibrium in the small lakes

Preston (1962a, 1962b) and MacArthur & Wilson (1963) have independently pointed out that the number of species on an island depends on a dynamic balance between immigration and extinction, so that in some biotas, at least, the species diversity can be regarded as an equilibrium. However, Preston failed to take account of the precise distance effect (MacArthur & Wilson 1963). The distance effect, combined with the area effect, is one of the central concepts of the equilibrium model. The greater the distance from the source that supplies the species for colonization, the lower the immigration rate, and consequently the smaller the number of species present when equilibrium ($\hat{S}$) is reached.

The distance effect was first studied in the same way as the area effect in the previous section. The small lakes were divided into two equal subgroups according to their distance from Pyhäjärvi. These subgroups differed in the number of species present ($t = 4.105$***, df = 18), but they also differed in electrolytic conductivity, total hardness and alkalinity (Table 5). Thus, the differences in water quality hampered the statistical establishing of the distance effect. Further studies by partial correlation analysis showed that when the interaction between the abiotic factors mentioned above was eliminated, the statistically significant negative correlation between the number of species and the degree of isolation of a lake disappeared. Therefore, the study area under consideration was not suitable for direct statistical analysis of the distance effect, because water quality deteriorated with increasing distance from the centre of dispersal of the gastropod species. Lassen (1975) was likewise unable to demonstrate a distance effect among the snail populations of the Danish lakes. However, these negative results do not rule out the existence of a distance effect.

A second procedure for testing whether the snail populations were in dynamic equilibrium was based on the variance-to-mean ratio of numbers of species (MacArthur & Wilson 1963, 1967, Lassen 1975). The equilibrium model predicts a low variance, so an observed variance that is significantly smaller than the mean supports the equilibrium explanation. According to MacArthur & Wilson (1963, 1967), if the extinction and immigration curves have slopes about equal in absolute value, then the variance-to-mean ratio should equal 0.5.

For the test the 20 small lakes were divided into four equal groups of 5, according to lake area and distance from Pyhäjärvi (large-near, large-far, small-near, small-far). The shortest possible distance from a habitat island to Pyhäjärvi was used. The mean distance for the near lakes (n = 10) was 2.3 km, and for the far lakes (n = 10) 5.1 km. The mean number of species ($\bar{x}$), its variance (s^2) and the variance-to-mean ratio ($s^2/\bar{x}$) were calculated for each lake group:

Lake group	$\bar{x}$	s^2	$s^2/\bar{x}$	n
large, near	8.6	11.8	1.37	5
large, far	3.6	13.3	3.69	5
small, near	3.4	9.8	2.88	5
small, far	2.4	1.3	0.54	5

The means for the different lake groups formed a logical sequence, the large-near lakes having the greatest and the small-far lakes the smallest number of species, the other two lake groups falling in between. However, the variance-to-mean ratio was over 1 in three of the groups and under 1 only in one. The result suggests that, although dynamic equilibrium is possible, the spatial parameters (area and distance) are not the only factors regulating the occurrence of the gastropod species.

Therefore, the distances were measured in another way, along the outlets of the small lakes. In this analysis the mean distance for the near lakes was 4.2 km and for the far lakes 7.9 km. Then the calculations were performed as before:

Lake group	$\bar{x}$	s^2	$s^2/\bar{x}$	n
near, large	9.8	5.2	0.53	5
near, small	4.2	6.2	1.48	5
far, large	2.4	1.3	0.54	5
far, small	1.6	1.3	0.81	5

In this case, too, the sequence of the means was logical, and the differences between mean values were more distinct. In three lake groups the variance-to-mean ratio strongly supports the MacArthur-Wilson model. But the group of near-small lakes includes on extremely poor lake with no gastropod species at all. If this lake is excluded, the variance-to-mean ratio for the remaining four lakes is as low as 0.17 ($\bar{x}$ = 5.3, n = 4).

Of the 20 lakes, 16 were in the same lake groups in both analyses. Only 4 lakes were placed in different groups, two among the larger and two among the smaller habitat islands. The latter grouping of the small lakes also takes account of altitude, and so the water quality in each lake group is more homogeneous. Thus, the latter analysis takes into consideration not only lake area and degree of isolation but also, to some extent, water quality.

Comparison of the water quality in the lake groups formed above supports the equilibrium explanation:

Lake group	$\bar{x}$	Total hardness (°dH)	Electrolytic conductivity ($\varkappa_{18}$)	Colour of water (mg Pt l^{-1})
near, large	9.8	1.16	60	47
near, small	4.2	1.05	52	88
far, large	2.4	0.63	35	64
far, small	1.6	0.75	38	80

The comparison indicates that the lakes with the smallest number of gastropod species are not the most oligotrophic lakes, which strengthens the impression that water quality is not the sole factor accounting for the diversity of snail species in the lakes of the Tampere district.

This result implies that in the small lakes studied dynamic equilibrium prevails, the MacArthur-Wilson model representing one of the mechanisms regulating the local occurrence of the gastropod fauna.

C. Effect of water quality on the equilibrium model

The equilibrium model assumes the extinction rate to be a function of island size, and the immigration rate to be a function of isolation. But island size, too, may have a slight effect on the immigration rate, because a larger island forms a larger target for immigrants to hit (MacArthur 1972). When the immigration rate is sufficiently high, the degree of isolation may also influence the extinction rate via the rescue effect (Brown & Kodric-Brown 1977). Thus, at the equilibrium point ($\hat{S}$) the number of species on an island is determined by two opposing forces, immigration and extinction, which are affected by many different factors.

If water quality affects the equilibrium, it must change the rates of immigration and/or extinction, i.e. the slopes of the extinction and immigration curves in the model, which, in turn, will shift $\hat{S}$ on the abscissa. The immediate effect of water quality will be to alter the slope of the extinction curve, for if the water of a lake is unsuitable for the immigrating species, the propagules will be unable to colonize the lake successfully. There are noticeable differences in water quality between the large and the small lakes, but also among the small lakes (Tables 2 and 5). Owing to the more severe abiotic conditions prevailing in the small lakes, the extinction curves become steeper as we

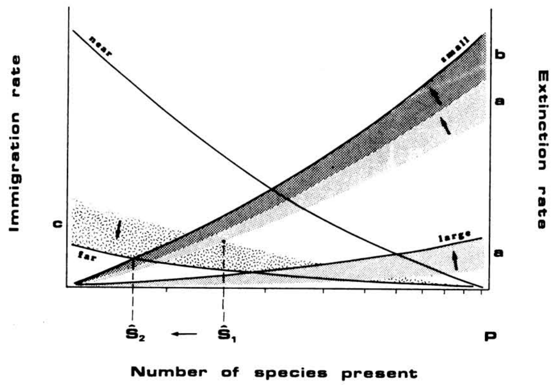

Fig. 5. Supposed effect of water quality on immigration and extinction rates. a = adverse effect of low concentrations of electrolytes; b = adverse effect of high concentrations of humus substances; c = indirect adverse effect of poor water quality on the immigration rate. A hypothetical example: $\hat{S}_1$ = number of species at equilibrium without the adverse effect of water quality, $\hat{S}_2$ = actual number of species at equilibrium, P = size of the species pool.

approach the limits of gastropod distribution. A model of the situation is given in Fig. 5.

Between the near and far lakes there is a statistically significant difference in water quality (Table 5). The most isolated lakes are significantly more oligotrophic than those close to the dispersal centre. The two curves describing the extinction rates in Fig. 5 (for small and for large habitat islands) include equal numbers of the poor far lakes, and therefore the modifying effect of water quality makes the extinction curves steeper in both large and small habitat islands. Furthermore, the humus content is greater in the small habitat islands than in the large ones (Table 5), which makes the extinction curve for the smallest water bodies even steeper (Fig. 5).

But the modifying effect of water quality may also alter the immigration rate. Freshwater snails are efficiently dispersed by passive means (e.g. BOYCOTT 1936, HUBENDICK 1950). LASSEN (1975) estimated the immigration and extinction rates in two ponds in Denmark. The turnover rates were 0.8 and 1.7 species per year. Aquatic birds are generally regarded as the chief agents in aerial dispersal (HUBENDICK 1947, REES 1965). As the productivity of the lakes is strongly correlated with water quality, the population densities of aquatic bird species are greatest in the small lakes close to Pyhäjärvi. In addition, the birds nesting in Pyhäjärvi probably visit the near small lakes more frequently than the far ones. Thus, because the numbers of resident and visiting birds are lower in the far habitat islands, the immigration curve for these lakes is depressed (Fig. 5).

5. Conclusions

1) The equilibrium theory of island biogeography can be applied to the small lakes of the Finnish lake district, even though they are situated close to the limit of distribution of the gastropod fauna.

2) Water quality modifies the MacArthur-Wilson equilibrium model, oligotrophy increasing the probability of extinction in both larger and smaller habitat islands, and indirectly decreasing the probability of immigration into the most distant lakes, which at the same time have the poorest water quality. The relative importance of the chemical and spatial variables is not analysed in this paper.

3) The equilibrium model did not apply to the large lakes of the main watercourses in the Finnish lake district.

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