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Freshwater snail populations and the equilibrium theory of island biogeography. III. An explanation for the small number of species in South Bothnia, western Finland

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The small numbers of gastropod species in the inland lakes of South Bothnia is enigmatic. The whole snail fauna consists of only 5 species, the mean number in 14 lakes studied being 1.1 species. Northernmost Lapland is the only other part of Finland where the snail fauna is as poor as in South Bothnia. The lakes, which became separated from the ancient Baltic Sea about 3700—6800 years ago, have been regarded as analogous with land-bridge islands. The present paucity of snail species is attributed to postglacial changes. The consequences of land uplift are clearly seen in South Bothnia, where the land rises at a rate of 0.8—0.9 m per 100 years. Correspondingly, the shoreline of the Baltic Sea has receded from the lakes by about 1 km per 100 years.

Evidently the number of species was greater in ancient times than today, and has gradually decreased to the present level primarily as a consequence of the increasing isolation of the lakes. The immigration rates and the species pool have been reduced. As the lake water has changed towards oligotrophy and dystrophy, the extinction curves have steepened. In addition to the palaeo-ecological processes, a further factor that has probably influenced the numbers of species is the adaptation of the snail populations to the changing conditions, which should be incorporated into the equilibrium model of island biogeography.

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1. Introduction

One of the most interesting observations in my previous study (AHO 1978b) was the very small number of gastropod species in the lakes of South Bothnia, western Finland. Although conditions were favourable, the total number of snail species was only 5, and the mean number per lake was as low as 1.1. In the Finnish lake district, in contrast, the corresponding values were 20 and 10.7 in the larger water bodies, and 18 and 5.3 in the smaller lakes and ponds (AHO 1966, 1978a, 1978b, 1978c).

In this paper, an attempt is made to find out why there was such a noticeable difference in the gastropod fauna between these two districts, which are situated at almost the same latitude and are quite close geographically. The attempt is based on the theory of island biogeography (MACARTHUR & WILSON 1963, 1967), which appears to account for the distribution of snails in Finnish lakes (AHO 1978b). The present paucity of snail species in South Bothnia has been ascribed to the postglacial changes in the area. In this sense, the lakes are analogous to oceanic (e.g. MACARTHUR 1972, MACARTHUR *et al.* 1972, DIAMOND 1973, TERBORGH 1974, DIAMOND & MAY 1976) and continental (BROWN 1971, SIMPSON 1974) land-bridge islands.

2. Study area

South Bothnia is a biogeographical province limited to the west and north-west by the Gulf of Bothnia, an arm of the Baltic Sea, and to the east and south-east by the watershed of Suomenselkä, 150—180 m above sea level. It is a plain characterized by numerous rivers, and few lakes. The lake percentage (i.e. the

Table 1. Some features of the lakes studied.

Lake	Size (km^2)	Altitude (m)	Electrolytic conductivity ($\varkappa_{20}$)	Total hardness (°dH)	Colour of water ($mgPtl^{-1}$)
Hirvijärvi	0.96	84.0	57	1.23	280
Jalasjärvi	1.31	82.7	59	1.25	240
Varrasjärvi	0.08	40.0	100	1.81	320
Valkiajärvi	0.03	45.2	233	4.20	90
Kuortaneenjärvi	14.82	75.2	47	0.90	130
Mäenpäänjärvi	0.03	55.6	51	0.95	240
Vähä Vuosjärvi	0.16	58.3	37	0.68	160
Purmojärvi	3.86	64.0	52	0.98	140
Kortesjärvi	0.46	70.0	76	1.40	140
Mustajärvi	0.10	76.0	95	2.03	140
Haapajärvi	1.98	75.0	47	0.77	140
Lappajärvi	147.30	69.4	52	0.96	60
Evijärvi	28.00	61.3	51	0.94	50
Vähäjärvi	0.07	69.0	67	1.53	160
$\bar{x}$	14.23	66.1	73	1.40	160

percentage of the total area occupied by lakes), increases with each river basin from south to north: the Kyrönjoki 1.0 %, the Lapuanjoki 2.8 %, the Purmojoki 3.5 % and the Ähtävänjoki 7.7 % (Sirén 1955).

Altogether 14 lakes were chosen for the study: Hirvijärvi, Jalasjärvi, Varrasjärvi and Valkiajärvi in the drainage basin of the Kyrönjoki; Mäenpäänjärvi, Vähä Vuosjärvi and Kuortaneenjärvi in the drainage basin of the Lapuanjoki; Purmojärvi, Kortesjärvi, Mustajärvi and Haapajärvi in the drainage basin of the Purmojoki; and Lappajärvi, Evijärvi and Vähäjärvi in the drainage basin of the Ähtävänjoki.

All these lakes are situated below the highest shoreline of the ancient Littorina Sea, which nowadays lies about 90 m above sea level in South Bothnia (Mölder & Salmi 1954, Eronen 1974). The lakes studied are on the highest part of the ancient sea bottom, their mean altitude being 66.1 m (range 40.0—84.0 m).

Table 1 lists some features of these lakes. They are, as a rule, shallow, and the lake bottom deepens gradually. Therefore, the littoral plant associations are extensive and well developed. The maximum depth in Lappajärvi is 38 m (Odenwall 1934), in Kuortaneenjärvi 18 m (Levander 1907), and in the other lakes not more than 5 m.

3. Collection technique and material

Snails were collected in 1977 (25—31 July), except in Kuortaneenjärvi, from which they were collected in 1961 by Mutka (1966; see Aho 1978b). The collection technique was identical with that used previously (Aho 1966, 1978c).

Of the total of 75 sample plots, 70 belonged to my own collection and 5 to the collection of Mutka (1966). Nearly all samples, 97 %, originated from the helophyte associations (area of sample plot 4 m^2), and only 3 % from stony bottoms (sampling time 0.5 h). The number of sample plots per lake ranged from 2 to 9, the mean being 5.4. The total area of the helophyte associations sampled with a rod net technique was 292 m^2.

The present collection comprised altogether 5 snail species and 1456 specimens: *Lymnaea stagnalis* (L.) 38 individuals, *L. peregra* (Müller) 307 individuals, *L. palustris* (Müller) 246 individuals, *Bathyomphalus contortus* (L.) 845 individuals, and *Gyraulus albus* (Müller) 20 individuals. *L. stagnalis* was found in Lappajärvi and Evijärvi, *L. peregra* in Lappajärvi, Evijärvi, Haapajärvi and Kuortaneenjärvi, *L. palustris* in Lappajärvi, Evijärvi, Jalasjärvi and Hirvijärvi, *B. contortus* in Lappajärvi, Evijärvi, Purmojärvi and Mäenpäänjärvi, and *G. albus* in Lappajärvi and Purmojärvi. In the remaining 6 lakes I could not find a single gastropod species.

Water chemistry and other abiotic parameters of the lakes have already been described in detail (Aho 1978b).

4. Definition of the problem

The small number of gastropod species in South Bothnia is puzzling (Table 2). The distribution of the gastropod fauna in Finland is fairly well known, thanks to the pioneer work of Nordenskiöld & Nylander (1856) and Luther (1901), and to many subsequent surveys during recent decades (references in Table 2).

In Finland, the snail fauna is richest in the Finnish lake district (Table 2), with 14—21 species, and in the southern and southwestern coastal regions, with about 20 species. North of the lake district the number of species seems to be 10—11, even as far as Kuusamo near the Arctic Circle. In the watershed districts the numbers are smaller; in Suomenselkä 7 and in Southwest Häme 12 species. Only in northernmost Lapland is the number of species as small as in South Bothnia.

Latitude may be partly responsible for the paucity of species in South Bothnia. However, only two of the snail species living in the western half of Finland, *Acroloxus lacustris* (L.) and *Bythinella steini* (Martens), are not found as far north as South Bothnia, according to the literature cited in Table 2 and the collections in the Zoological Museum of the University of Helsinki.

The first evidence for the explanation put forward in this paper was gained from the regression model calculated for the lakes of South Bothnia (Aho 1978b), which indicated that in that region the number of gastropod species was primarily dependent on lake area (A) and lake percentage (I_2) and not, for example, on water quality. The regression model was

$$S = 0.202 + 0.024\, A^{**} + 0.128\, I_2^{*},$$

Table 2. Number of gastropod species in some collections made in Finland.

Area	Number of gastropod species	Mean latitude	Reference
Southern and southwestern coastal region			
Turku district	21	60° 30′	Leppäkoski 1964
Mustionjoki	19	60° 08′	Keynäs 1966
The Finnish lake district			
Lahti district	21	61° 05′	Levanto 1940, Vaittinen 1968
South Saimaa	19	61° 07′	Koli & Turkia 1964
Large lake channels of South Häme	20	61° 16′	Aho 1966, 1978c
Small lakes of the Tampere district	18	61° 25′	Aho 1966
Jyväskylä district	14	62° 15′	Valovirta 1956, 1959, 1962
Kuopio district	15	62° 53′	L. Koli, personal communication
Western coastal region			
South Bothnia	5	62° 58′	Aho 1978b, this paper
North Bothnia	11	65° 00′	Petäjä & Vesanto 1955, Lähdesmäki & Lähdesmäki 1970
Watershed districts of southern Finland			
Southwest Häme	12	60° 50′	Wuorenrinne 1957, Brander & Kantee 1961, Brander 1963
Suomenselkä	7	62° 33′	Mutka 1966
Northern Finland			
Oulunjärvi	10	64° 10′	Leinonen 1950
Kuusamo district	11	66° 09′	L. Koli, personal communication
Lapland, Enontekiö	5	69° 00′	Koli 1955
Lapland, Inari	5	69° 00′	Petäjä & Vesanto 1955, Bagge 1968

which accounted for 76.8 % (A 66.5 %, I_2 10.3 %) of the variation in the number of species (S). Thus, it seems evident that in South Bothnia the diversity of the snail fauna is primarily regulated by the principles of islands biogeography.

Further evidence was afforded by the constant z in the equation $S = CA^z$, or if transformed $\log S = \log C + z \log A$, defining the slope of the area-diversity curve. The theory of island biogeography predicts that z will increase with isolation, both of the islands from each other and of the archipelago as a whole from the nearest archipelago or continent (MacArthur & Wilson 1967). This is regarded as a stringent test of the equilibrial condition. The lakes of South Bothnia were treated as an archipelago for which z was found to be as high as 0.227, whereas for the lakes of the Finnish lake district z clustered in the range 0.061—0.163 (Aho 1978a), and for the extreme oligotrophic lakes of the Suomenselkä watershed it had even a negative value (z = —0.108). In general, the z values for continental habitat islands fall between 0.12 and 0.17 (MacArthur & Wilson 1967). The z for the South Bothnian lakes thus indicates a high degree of isolation.

The third line of evidence concerned the snail species present and their relative abundances. In water bodies where abiotic conditions are extreme, the number of species is small, the dominant species usually being *Lymnaea peregra* and *Gyraulus acronicus* (Férussac) (Koli 1955, Aho 1966, Mutka 1966, Bagge 1968, Lähdesmäki 1970). In South Bothnia the number of freshwater snail species was smaller than in the surrounding areas. However, the paucity of species is not due to severe abiotic conditions. Only five species were found in the fourteen lakes studied; these were *Lymnaea stagnalis* (2.6 % of the total number of specimens), *L. peregra* (21.1 %), *L. palustris* (16.9 %), *Bathyomphalus contortus* (58.0 %) and *Gyraulus albus* (1.4 %). Thus *G. acronicus* was not caught at all during the collection and *L. peregra* was not the commonest species.

The analysis of the present situation suggested that the lakes of South Bothnia are more isolated than the other lakes in southern and western Finland, and that the occurrence of gastropods in them is regulated mainly by the spatial parameters incorporated in the equilibrium model of island biogeography. The crucial factor is the lake area, which emphasizes the danger of extinction of the snail populations in these lakes. The facts presented strongly suggest that the gastropod fauna in the lakes of South Bothnia has not always been so poor as at present.

5. An attempt at explanation

According to the hypothesis, in ancient times the gastropod fauna of the lakes of South Bothnia exceeded the equilibrial number for the modern lake areas and/or distances. From this it follows that the number of species has gradually declined towards the present equilibrium. If so, we must look for some ecological processes that could account for the reduced species diversity. These we find in the postglacial processes described in the following sections.

A. Environmental conditions for gastropods in ancient times

Climate. The higher the latitude the lower is the organic diversity (e.g. FISCHER 1960, HUBENDICK 1962). For example, the freshwater gastropod fauna in Denmark comprises 34 species (LASSEN 1975), in southern Sweden 29 (HUBENDICK 1947), and in the Finnish lake district 21 species (LEVANTO 1950, VALOVIRTA 1956, 1959, 1962, KOLI & TURKIA 1964, AHO 1966, 1978c). The impoverishment is due primarily to unfavourable climatic conditions.

During the Holocene Epoch there have been extensive climatic fluctuations. The Littorina Sea, the early stage of the present Baltic Sea, formed in southern Finland 7400—7300 years ago (= B.P.), and in the northern end of the Gulf of Bothnia about 7000 B.P. (ERONEN 1974, DONNER 1977). Climatically this stage coincided with the Atlantic chron (8000—5000 B.P. according to MANGERUD *et al.* 1974), which was the warmest of the postglacisal period. The climate of South Bothnia was then as favourable as in southern Sweden or Denmark today (MÖLDER & SALMI 1954). At that time many southern plant species extended much farther north than today (KALLIOLA 1973). For example, the waternut (*Trapa natans* L.) grew as far north as the commune of Evijärvi, the northernmost part of my study area (VALOVIRTA 1960, ALHONEN 1964). All the lakes there, except Varrasjärvi and Valkiajärvi, became separated from the Littorina Sea during this warmest phase of the Holocene Epoch.

The next climatic period was the Subboreal chron about 5000—2500 B.P. (MANGERUD *et al.* 1974), during which the climate became a little cooler and more continental. The area of bogs began to expand, and the southern plant species to retreat. The two youngest lakes were formed from the Littorina Sea during the Subboreal chron.

Especially during the warm Atlantic chron the gastropod fauna had good opportunities to disperse into the study area. As such exacting southern aquatic plant species as *Trapa natans* and *Ceratophyllum demersum* L. were then growing in the lakes of South Bothnia (JULIN & LUTHER 1959, VALOVIRTA 1960, KALLIOLA 1973), all the gastropod species living nowadays in Finland probably had a chance to colonize the lakes studied.

Subfossil material of gastropods is not well preserved in Finland. The only papers on these subfossils concern some ancient lakes in northern Finland (SALMI 1963, VASARI *et al.* 1963). In these lakes the number of snail species during the late Preboreal and Boreal chron (9500—8000 B.P.), was already as high as in South Bothnia at present — in Kuusamo probably at least 7 species (VASARI *et al.* 1963), and in Kittilä at least 5 species (SALMI 1963).

Water quality. Gastropods are extremely sensitive to water quality in both brackish-water (KOLI 1961) and freshwater (e.g. AHO 1966) habitats. Nowadays, the water quality of the lakes of South Bothnia does not limit the occurrence of freshwater snails (AHO 1978b), but previously the composition of lake and brackish sea water had a different effect on the distribution of gastropod species in South Bothnia.

The Littorina Sea was preceded by the Mastogloia Sea. When this turned into the Littorina Sea about 7200—7100 B.P., the salinity in South Bothnia rose to a distinctly higher level than in the present Baltic. AARNIO (1927) estimated that the salinity was as high as 8—12 ‰ on the coast of South Bothnia. This means that in the first stage of the Littorina Sea probably the only freshwater gastropod that could live in the coastal waters of South Bothnia was *Lymnaea peregra* (JAECKEL 1950).

The salinity of the Littorina Sea and the subsequent Baltic Sea gradually decreased to the present level, 3.5—5.0 ‰, in the South Bothnia archipelago (SEGERSTRÅLE 1949). The decline in salinity means that the significance of the Gulf of Bothnia as a source area was at first small for the lakes that separated from it. It is not possible to reconstruct the history of the Baltic gastropod fauna, but, as a general trend, the number of freshwater species gradually increased to the present level, which is at least 12 species (VALOVIRTA 1935, SEGERSTRÅLE 1945, 1960, LINDBERG 1948, KOLI 1961, HAAHTELA 1964).

During the recession of the Scandinavian ice sheet, about 10 000—9 000 B.P., nearly the whole country was submerged. When land upheaval started, one lake after another became separated from the ancient stages of the Baltic. The separation process caused drastic changes in the water quality, and so in community structure. The total freshening of the water bodies is estimated to have taken up to 150—200 years in the Finnish southwestern archipelago, where the rate of land uplift is nowadays 5—6 mm per year (BAGGE & TULKKI 1967). On the coast of South Bothnia, this phase of lake succession would have lasted a shorter time because of the more rapid land upheaval.

The separation process led to changes in the number of snail species and the composition of the fauna. The brackish-water species became extinct, and the proportion of freshwater forms increased. In the lakes situated on the large islands of the Finnish southwestern archipelago the number of snail species fell from 8 to 4 during the meromictic phase, whereas in the oldest, totally freshened lake it increased again to 7 species (BAGGE & TULKKI 1967). In the brackish-water of the archipelago there were 10 species.

As a general trend during the Holocene Epoch in Northern and Western Europe, the lakes changed from the earlier alkaline, more or less eutrophic condition, becoming more dystrophic and oligotrophic (IVERSEN 1954, ROUND 1957, VASARI *et al.* 1963, ALHONEN 1967, CRABTREE 1969, KUKKONEN & TYNNI 1970, DIGERFELD 1972, KUKKONEN 1973, HUTTUNEN & TOLONEN 1975, RENBERG 1976). This process was largely independent of the time at which the lake separated from the Baltic. So it is reasonable to assume that in the first phase of their existence the lakes studied provided better conditions for water molluscs than later on, when electrolytes from the surface deposits became less available and extensive bogs developed, rendering the water soft, acid and humous (SEGERSTRÅLE 1958).

RENBERG (1976) has studied the succession in a lake in Sweden, on the opposite shore of the Gulf of Bothnia. The lake is situated 33 m above sea level, and was cut off about 3200 B.P. According to RENBERG, the succession in the lake is probably typical of many of the smaller lakes in the coastal area of the Gulf of Bothnia. In the first stage of the lake history the water was alkaline and relatively nutrient-rich and supported a species-rich flora. This stage was followed by the development of dystrophic conditions with a species-poor flora. Presumably the course of events was similar in the lakes at the same latitude in South Bothnia, the rich flora of the first stage sustaining a correspondengly species-rich fauna of invertebrates, including gastropods.

B. Colonization phases of the lakes studied

Primary colonization. Tilting of the land, a consequence of land uplift, caused many drastic changes in the direction of water flow in the Finnish drainage basins. In the present context the most important point is that during the early stage of the Littorina Sea South Bothnia was biogeographically connected with the Finnish lake district. According to a geomorphological study (TOLVANEN 1924), Näsijärvi, the northern part of the drainage basin of the river Kokemäenjoki, originally discharged into the Gulf of Bothnia through the Lapuanjoki. Tilting of the land caused a transgression through the whole Näsijärvi basin, with the result that a new outlet channel broke through at the southern end of the lake about 5000 B.P. (VIRKKALA

1949, 1962). In addition, Ähtärinjärvi, now part of the northern drainage basin of the Kokemäenjoki, also discharged into the Gulf of Bothnia, but through the Ähtävänjoki. This means that the gastropod fauna that lived in the Finnish lake district during the climatic optimum had excellent opportunities to disperse into South Bothnia during two thousand years (7000—5000 B.P.) via two outlets from the lake district.

Furthermore, during the Atlantic and Subboreal chronozones the lakes of the Suomenselkä watershed district were in all probability in the eutrophic phase of lake succession. Presumably, therefore the watershed district of Suomenselkä, which today acts as an effective filter against immigration of gastropods from the Finnish lake district (Aho 1978b), did not prevent such colonization in those periods when most of the lakes of South Bothnia became separated from the Gulf of Bothnia.

Increase of distances between habitat islands and source areas. The lakes of this study are among the youngest in Finland. They are all situated below the highest shoreline of the Littorina Sea (see p. 166). In South Bothnia the rate of land upheaval is one of the greatest in Finland, which at present means 8—9 mm per year (Lisizin 1963, Kääriäinen 1966). Previously the uplift was even greater, probably 10—13 mm according to the result obtained in the coastal area of Västerbotten in Sweden (Granlund 1943, Renberg 1976). From the data available (Granlund 1943, Mölder & Salmi 1954, Eronen 1974, Renberg 1976, Donner 1977) I estimated that the highest and thus oldest lake (Hirvijärvi) was cut off from the Gulf of Bothnia about 6800 years ago, and the youngest lake (Varrasjärvi) about 3700 years ago.

South Bothnia is a level plain and in consequence the shoreline of the sea receded from the study lakes at a rapid rate. If the values mentioned above are used, the shortest distance between the Gulf of Bothnia and Hirvijärvi increased by about 1100 m per 100 years, and between it and Varrasjärvi by about 1200 m per 100 years. Further, the regression of the shoreline has been continuous, and in this coastal region of Finland there were no transgression phases (Mölder & Salmi 1954, Eronen 1974).

Reduction of stepping-stone habitats. As the ground in South Bothnia is very level, the lakes that separated were mostly shallow. The probability was high that the succession process would soon eliminate them. The life span of a water body depends greatly on its depth. If it is very shallow, the separated water body is called a *flada* lake. Such a lake is, as a rule, transformed into a bog during a few decades (Keynäs 1977). If the separating sea bay is deeper, the water body is called a *glo* lake. At first, the glo is a meromictic lake, which may receive influxes of brackish water from the Gulf of Bothnia. With time, it is usually transformed into a freshwater lake. However, because of succession and because of the levelness of the ground, I believe that in South Bothnia the water bodies that separated tended to become filled up more frequently than in the other coastal regions of Finland. This would explain why the present lake percentage in South Bothnia is so small.

Another reason for the decrease of stepping-stone habitats has been human activity. As most of the lakes were shallow, they were easy to drain for agricultural purpose. Lake drainage reached vast proportions during this century (Luhta & Sevola 1977). Sometimes a lake was not drained totally, but its dimensions were reduced.

The paucity of stepping-stone habitats is illustrated by the mean distance of a lake from its five nearest neighbours. In South Bothnia the mean distance is 4.4. km ($n = 14$), whereas in the Finnish lake district it is only 1.1 km ($n = 43$).

C. Effects on the model of dynamic equilibrium

As shown in previous sections, it is highly probable that in South Bothnia the freshwater gastropod fauna was originally richer in species. Then either the extinction curves became steeper or the immigration curves less strongly concave than elsewhere, because the present number of species is exceptionally small.

Theoretically this study can be regarded as analogous to the ones made on the oceanic or continental land-bridge islands (e.g. Brown 1971, MacArthur *et al.* 1972, Diamond 1973, Simpson 1974, Terborgh 1974), which show that historical factors such as geological changes in island areas and the distances of the islands from sources of propagules must be considered in determining the applicability of the model of island biogeography to the current species diversity.

Immigration rate. Four of the processes described above may have reduced the immigration rate to the lakes studied: 1) the rapid increase of distance between the lakes and the Gulf of Bothnia, 2) the increasing isolation of the lakes from the species-rich Finnish lake district, 3) the decrease in stepping-stone habitats, and 4) the change in the lakes towards dystrophy and oligotrophy. I know of no process that would have raised the immigration rates.

The main source of snail propagules for immigration were in all probability the lake mosaic of the Finnish lake district and the Gulf of Bothnia. Nowadays Lappajärvi, by far the largest lake in South Bothnia, may act as a local dispersal centre. In addition, all the lakes of South Bothnia and the adjacent areas will function as potential stepping-stone habitats for snail immigration. If this hypothesis is valid, the numbers of species should form a decreasing gradient from each source area towards the centre of the study area:

1) According to the hypothesis, the lakes near the coast of South Bothnia should be richer in species than the lakes studied, because the propagules of gastropod populations will have been able to hit the coastal lakes near the source area more frequently than the lakes of this study, which are situated 30—75 km from the coast. At present the Gulf of Bothnia harbours at least 12 species (see p. 169), but the study area only 5. There are, however, no collections from the lakes between those studied and the Gulf of Bothnia. Therefore, it has been necessary to test the hypothesis indirectly by applying it to the northern end of the Gulf of Bothnia, where 9 gastropod species are reported (HAAHTELA 1964, LÄHDESMÄKI 1970). In the *Stratiotes* ponds situated quite near the coast at the same latitude the number of gastropod species is also 9 (LÄHDESMÄKI & LÄHDESMÄKI 1970).

2) The colonization effect of the Finnish lake district was tested by means of the total and mean numbers of gastropod species in four lake groups. The values for the Suomenselkä watershed were calculated from the figures of MUTKA (1966). The lakes of Suomenselkä were divided into two equal groups, those nearer to the lakes of South Bothnia (I in Table 3) and those nearer to the nearest lakes of the Finnish lake district (II). The results are given in Table 3.

Table 3. The total and mean numbers of snail species in four subgroups of lakes from the Finnish lake district to the lakes of this study.

	Lakes of South Bothnia	Lakes of the Suomenselkä watershed I	II	Lakes of the Finnish lake district
Total number of snail species	5	5	6	6
Mean number of snail species	1.1	1.3	2.4	4.5
Electrolytic conductivity ($\varkappa_{20}$)	73	39	34	34
Number of lakes	14	7	7	2

The analysis indicated that although the total numbers of gastropod species was about the same in each subarea, the mean number decreased from the highest large lakes of the Finnish lake district to the lakes of this study, although the trend in electrolytic conductivity runs in the opposite direction, the species being most numerous in the most oligotrophic lakes: I regard this result as strong evidence for the hypothesis that the Finnish lake district acted as an effective source area during the postglacial climatic optimum.

The result presented above is also evidence for the filter effect hypothesis. I believe that today the poor watershed district of Suomenselkä functions as a filter against the immigration of aquatic organisms from the direction of the lake district. The figures in Table 3 suggest that the numbers of species are greater in lakes (II) situated close to the lake district than in those (I) situated farther from that source area.

3) Lappajärvi is regarded as a local source centre because it contains all the species of the study area, and has the highest population densities. If the other lakes of the study area are divided into two equal groups according to distance from Lappajärvi, the total number of species in the nearer lakes was as high as in Lappajärvi (5 species), whereas the more distant lakes together contained only two species. There was a corresponding difference in mean numbers (1.2 /0.5 species).

For gastropods the immigration rate depends on the effectiveness of passive dispersal. The lakes studied are remote from other water bodies, the distances between lakes being about four times those in the Finnish lake district. Moreover, no species-rich dispersal centre exists in the study area or the adjacent areas. The river systems are well developed, but do not provide ecological conditions suitable for gastropod populations. Furthermore, the snail species of the study area are all poorly adapted for life in running waters (KEYNÄS 1966). Thus, the propagules must be supported overland. If the lakes are situated close enough, passive dispersal is quite effective (BOYCOTT 1936, HUBENDICK 1947, REES 1965, LASSEN 1975). The history of the dispersal of *Hydrobia jenkinsi* Smith around the North Sea and in the Baltic is an example of the effectiveness of passive dispersal for small-sized gastropods (HUBENDICK 1950). According to HUBENDICK (1947, 1950), the gastropods are so well adapted for dispersal that the absence of a species from a limited area can only exceptionally be attributed to failure of dispersal. South Bothnia, however, is such an area, where long distances between lakes limit present immigration rates.

In addition, the lakes of South Bothnia have been becoming more dystrophic and oligotrophic since the climatic optimum. As discussed by AHO (1978a), oligotrophy may modify immigration rates, because oligotrophic lakes attract fewer aquatic birds. In South Bothnia this phenomenon is probably of little importance, as the lakes are fairly productive even nowadays.

Extinction rate. According to the regression model, lake area accounts for nearly 70 % of the variation in the number of species, which indicates that extinction has played a dominant role in the dynamic equilibrium in the lakes of South Bothnia. In the larger lakes (n = 7) the mean number of gastropod species was 2.1, but in the smaller ones (n = 7) only 0.1 species. All the 6 lakes without a single gastropod species belonged to the latter group. Thus snail species are almost lacking in the lakes smaller than 50 ha.

Changes in lake size alter extinction rates. As a rule, however, the areas of these lakes have not changed significantly. In natural circumstances tilting of the land due to land uplift may even have increased the lake area slightly. In some cases the lake size has been reduced by draining activity, but this has taken place mainly during the last century. Thus, presumably extinction rates have scarcely been altered by lake size.

In a previous paper (AHO 1978a) I discussed the relation between the extinction rate and the composition of the water. The extinction rate is inversely proportional to water quality. In South Bothnia there has been a general impoverishment of lake water, which has increased the extinction rates.

The point of departure in this research project was the observation (AHO 1966) that a freshwater gastropod species may react differently to total hardness in the lakes of Finland than in the lakes of southern Sweden and Great Britain. MACAN (1963) described the phenomenon as follows:

"HUBENDICK's (1947) findings in Sweden bear out those of BOYCOTT in Britain, but a few species appear to be more and a few to be less exigent in their calcium requirements when the two countries are compared. *Lymnaea stagnalis* is one species which, confined to hard

Table 4. The occurrence of gastropod species in different total hardness classes (according to the collections studied in this paper, in Aho 1966, 1978c and in Mutka 1966). The figures denote the numbers of lakes where the species was found.

	Total hardness (°dH)				
	0.5	1.0	1.5	2.0	≧2.5
Lymnaea stagnalis	3	15	9	9	1
L. peregra	9	25	9	9	1
L. auricularia	1	8	5	7	–
L. palustris	2	15	9	9	1
L. truncatula	–	4	3	1	–
L. glutinosa	3	9	5	3	–
Physa fontinalis	–	4	4	5	–
Planorbarius corneus	–	–	–	1	–
Planorbis carinatus	–	1	2	1	–
Bathyomphalus contortus	2	14	7	9	1
Gyraulus albus	1	12	9	9	1
G. acronicus	3	16	3	5	1
G. crista	1	8	3	8	–
G. riparius	–	6	5	7	–
Hippeutis complanatus	–	3	2	5	–
Acroloxus lacustris	–	4	5	8	–
Bithynia tentaculata	–	3	2	7	–
Bythinella steini	–	–	1	1	–
Valvata cristata	–	2	5	6	–
V. piscinalis	2	6	5	5	–
Number of species	10	18	19	20	6
Number of lakes	19	27	12	11	2

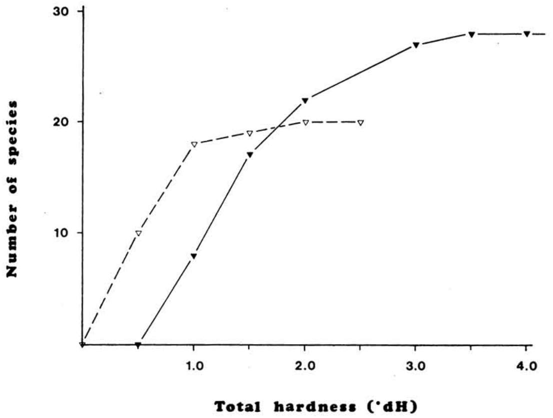

Fig. 1. The cumulative increase in the number of gastropod species in the lakes of southern and western Finland (broken line) and in the lakes of southern Sweden (solid line; according to Hubendick 1947:495).

water in Britain, occurs in soft water in Sweden, and I can testify to my own surprise when I took it in a peaty lake in the north of Finland, and a Finn assured me that the water was as poor in lime as it looked".

The difference in reaction to water quality requirements was confirmed (AHO 1966). The difference is further borne out by results of this study and by the material collected from the large lakes of the Finnish lake district (AHO 1978c) as well as from the lakes of the Suomenselkä watershed (MUTKA 1966), and a comparison was made between the Finnish lakes and the lakes of southern Sweden (Table 4, Fig. 1).

The number of gastropod species in Finland increases with total hardness (describing the calcium content; 1 °dH = 7.1 mg Ca l^{-1}) in parallel with the gastropod fauna of southern Sweden (Fig. 1), but in Finland the gastropods as a whole are better able to tolerate extremely poor water quality. I believe that the difference is due primarily to genetic adaption, but the adaptation process and the mechanisms influencing it are not discussed here. Over a long period of time, genetic adaptation can result in lowered rates of extinction and so in a higher evolutionary equilibrium (SEPKOSKI & REX 1974). Thus, the adaptation process would reduce the effect of the extreme water quality on the extinction rates. Adaptation is the only known process which can increase the value of S in the model of dynamic equilibrium. These observations mean that a gastropod species is not confined to a single universal niche but the niche spectrum may differ in different areas, as in *Lymnaea stagnalis* in Great Britain, southern Sweden and Finland.

Most freshwater gastropods must be regarded as fugitive species (LASSEN 1975), which have a good ability for dispersal and a high reproductive potential allowing them to build up a population whenever conditions are favourable, although later they may be ousted by other species (HUTCHINSON 1951, MACARTHUR 1962, LEVINS & CULVER 1971, HORN & MACARTHUR 1972, SLATKIN 1974). MACAN (1950) found that most extinctions occur among snails with a high rate of dispersal. The fugitive nature of freshwater gastropods together with the palaeoecological processes, will explain the regional paucity of species on South Bothnia.

Alterations in the species pools. Reduction of the species pool of potential immigrants will reduce the number of species on the island, i.e. the immigration curve will be lower and will intersect the extinction curve at a new equilibrium with a smaller number of species (MACARTHUR & WILSON 1963). At the beginning of the history of the lakes of South Bothnia the Finnish lake district was probably the main source of species, although colonization of the lake communities must have proceeded via stepping-stone habitat islands. When, with increasing land uplift, the watercourses of Näsijärvi and Ähtärinjärvi ceased to discharge through the rivers of South Bothnia and the filter effect of the Suomenselkä watershed increased, the direction of immigration probably shifted and the source area became the Gulf of Bothnia. In any case, the value of P in the equilibrium model decreased. Today it seems that the primary source of species is Lappajärvi, and so P is only 5 species in the equilibrium system of South Bothnia. This will be a further reason for assuming that the lakes studied have very low immigration rates. Therefore I conclude that during the history of the lakes their species pool (P) has been reduced and the values of S have decreased. However, the main reason for the low immigration rates in South Bothnia must be the long distances between the habitat islands.

Changes in the number of species at equilibrium. All the processes of natural succession described in the previous sections will primarily have reduced the immigration rates and the species pools, but will also to some extent have increased the extinction rates. The main cause for this trend is regarded as the increase in the degree of isolation of the lakes studied. The only process opposing the downward trend will have been the adaptation of the gastropod populations, probably simultaneously with the change in lake water from eutrophy towards greater oligotrophy and dystrophy. Therefore, the very small number of gastropod species in the lakes of South Bothnia today is probably due to a gradual decrease in the number of species from a higher ancient equilibrium to the present low equilibrium. The extinction rate has exceeded the immigration rate, and the equilibrium point has moved slowly towards smaller numbers of species. Nowadays the immigration rate in the study area is probably very near zero, and the further history of the local snail populations will depend almost wholly on their ability to avoid extinction.

SIMPSON (1974) has succeeded in finding concrete evidence for the role of palaeo-ecological events in the determination of modern species diversity in the island situation. This study, in contrast, has led to a hypothetical explanation invoking palaeo-ecological events as causal factors, as in most studies made on land-bridge islands (e.g. BROWN 1971, DIAMOND 1973). Furthermore, it is pointed out that not only palaeo-ecological processes, but also adaptive processes will influence species diversity via the functional principles of the equilibrium model of island biogeography.

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