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The distribution of the gastropods *Theodoxus fluviatilis* (L.) and *Potamopyrgus antipodarum* (Gray) in lakes on the Åland Islands, southwestern Finland

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On the Åland Islands, surrounded by the brackish Baltic Sea, the two species *Theodoxus fluviatilis* (L.) and *Potamopyrgus antipodarum* (Gray) are common and widespread. *T. fluviatilis* was found in lakes where the hardness values were below 3 °dH. *P. antipodarum* was found in four lakes at sea level and in two additional lakes of older age (higher elevation). On the Åland Islands the short distances from the lakes to the sea are advantageous for the transportation of snails, provided the lakes are connected to the sea through open ditches where fish wander or active colonization is possible. *T. fluviatilis* appears to be absent in Finnish lakes and *P. antipodarum* has previously not been encountered in Finnish lakes. The absence of the species in Finnish mainland lakes may be due to too high contents of humic substances and too low calcium values.

Introduction

In order to be present in lakes, snails must be transported there. This transport may be carried out by birds (Russell-Hunter 1978), deer and moose (Pip 1986), fishes (Haynes *et al.* 1985) and possibly by fishing tools. In lakes, snails are subjected to abiotic and biotic conditions. Biotic interactions may be very complex, including trophic interactions such as trophic cascades. For example, the removal of a predator will affect a species two steps down the food chain, by reducing the number of individuals (Brönmark *et al.* 1997, Brönmark and Vermaat 1998). Interspecific competition is considered less important for snails (Lodge *et al.* 1987). However, it has been noted that some animal species ("supertramps") occur in species-poor communities and will be out-competed in more species-rich communities, some occur in communities of any number of species ("tramps") and a third group of species ("high-S species"), possibly depending on a high competitive ability, only occur in species-rich communities (Diamond 1975). The same seems to be true for snails (Jokinen 1987). If conditions are not suitable, the species will locally go extinct.

Lodge *et al*. (1987) claimed that water chemistry variables screen potential colonists only on a biogeographical scale, and as soon as calcium values are above 5 mg l^{-1}, other factors such as food selectivity, predation and physical disturbance (e.g. winterkill, oxygen deficiency, drought and waves) come into play. The two freshwater snail species *Theodoxus fluviatilis* (L.) and *Potamopyrgus antipodarum* (Gray) have, on the mainland Finland, only been found in the coastal brackish waters of the Baltic Sea (Valovirta 1987). *T. fluviatilis* has been recorded in recently isolated lakes on the southwestern Finnish mainland (Bagge and Tulkki 1967). During an investigation on the Åland Islands performed during the summers of 1994–1996 both species were found in several freshwater lakes (R. Carlsson unpubl.). The reason for *T. fluviatilis*, with the above mentioned exceptions, being absent in lakes on the Finnish mainland has been explained by calcium deficiency (Segerstråle 1945) as the lakes are situated on the Baltic shield, mostly built up by acidic granites, gneisses and similar types of rocks. In the Pyhäjärvi area in the vicinity of Tampere, for instance, the hardness values are lower than 2 °dH, conductivity values are low, and humus values are high as in general in the Finnish lakes (Aho 1966). Calcium is needed for several vital life processes in snails, the most obvious being the formation of shells (Skoog 1978).

T. fluviatilis has been found in deposits from the Litorina age (about 6000 years B.P.) on the Åland Islands (Hausen 1964) and so may be regarded as an indigenous species to the Baltic area. *P. antipodarum*, on the other hand is native to New Zealand and has come to Europe in ballast water and was first observed in the Thames estuary in 1859. In 1887, the species was reported from the Baltic Sea for the first time in the Wismar Bight and in 1898 in the Kiel Canal (Lassen 1978).

The first observation of *P. antipodarum* in Finland is from the Åland archipelago in 1926. This species is now found everywhere along the Finnish coasts (Valovirta 1987). Until now it is not known from the Finnish lakes, but it is reported from many other European lakes, e.g. Norway (23 localities) (Økland and Økland 1992) and Sweden where the species was first found in freshwater in Lake Mälaren 1950 (Aijmer 1951), and has recently been reported from some coastal lakes in the province of Småland (Nilsson *et al.* 1998), from running water at the Öland Island (J. Grudemo pers. comm.) and from the Ekopark area, Stockholm (von Proschwitz 1995). For the distribution in other European countries, *see* Lassen (1978) and Økland (1990).

The two species also have different kinds of reproduction. In *T. fluviatilis* the sexes are separate and egg capsules containing 70–100 eggs may be found on stones in all seasons. From each capsule only one juvenile hatches while the other eggs will serve as nourishment (Hubendick 1949, Skoog 1978). In *P. antipodarum,* on the other hand, sexes are also separate, but in Europe very few males have been found and the reproduction is mainly parthenogenetic, thus offering a very efficient propagation and dispersal potential (Jacobsen and Forbes 1997): one specimen may start a new population.

The aim of this paper is to discuss possible reasons for the two species being present in lakes on Åland and absent in lakes on the Finnish mainland.

Study area

The Åland Islands, located in the southwestern part of Finland (Fig. 1) have a bedrock consisting of acidic rapakivi granites on the mainland and older acidic granites, gneisses and related kinds of rocks in the archipelago (Bergman 1986). However, the soils covering the bedrock are rich in ground limestone originating from limestone beds on the bottom of the Gulf of Bothnia (Hausen 1964). The lakes on the Åland Islands have hardness values reaching as high as 9.6 °dH with an average of 3.7 °dH in the 51 lakes investigated. On the Finnish mainland, also with an acidic bedrock, the soils are poor in calcium and so are the lakes.

All the lakes in this investigation are located

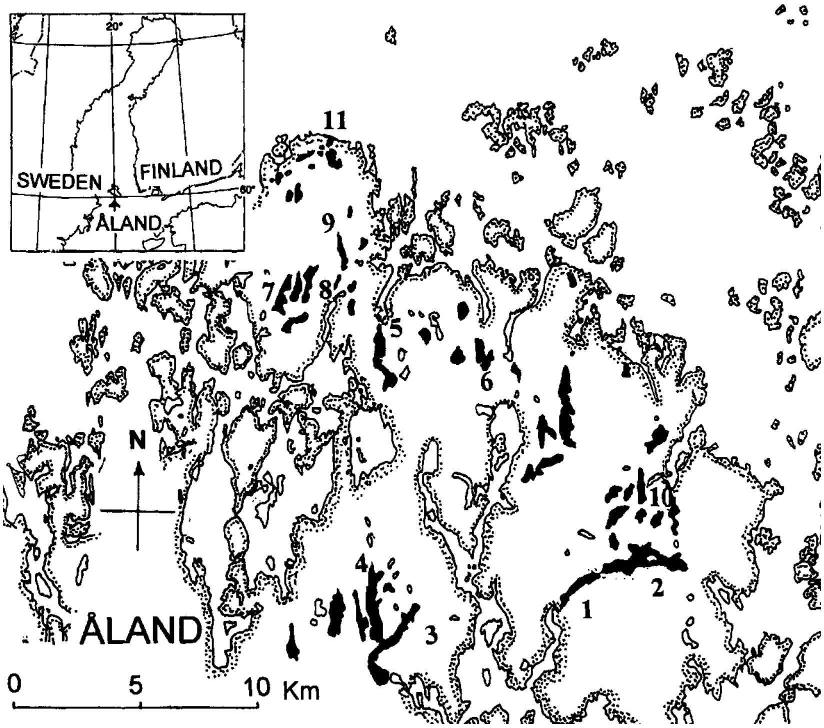

Fig. 1. Map of the study area with investigated lakes in black. Lakes in which *Theodoxus fluviatilis* and *Potamopyrgus antipodarum* have been found together are numbered 1–6. In lakes 7–9 *T. fluviatilis* is permanent and in lakes 10–11 it has been encountered but is not regarded as permanent. Elevation above sea level in brackets. 1 = Västra Kyrksundet (0.15 m), 2 = Östra Kyrksundet (0.15 m), 3 = Långsjön (0.15 m), 4 = Markusbölefjärden (0.15 m), 5 = Tjudö träsk (3.1 m), 6 = Toböle träsk (8.3 m), 7 = Olofsnäs träsk (1.1 m), 8 = Byträsk (1.4 m), 9 = Norsträsk (4 m), 10 = Borgsjön (13.4 m), 11 = Potten (0.9 m)

on the Åland mainland rapakivi massif, with hills in the northern and northeastern parts of the landscape, in the municipalities of Geta, Saltvik and Sund while the rest consists mainly of lowland. The massif is highly dissected with deep bays stretching far inland, consequently none of the lakes are located far from the brackish water of the archipelago.

The lakes are located at elevations ranging from sea water level to the highest lake, Svartträsk, in the municipality of Geta, at 40.5 metres above sea level.

The Åland Islands are, after the last ice age, subjected to land upheaval, at a rate of approximately 4–5 millimetres per year (Lindholm 1991). Therefore ages of the lakes differ, as they were formed successionally when bays were isolated from the sea.

Thus lakes at different elevations have different histories of colonization. "Relict populations" of species, trapped in the lake when it was isolated from the sea, occur in some lakes and the youngest lakes may contain plant species indigenous to the waters of the archipelago (Lindholm 1991).

Material and methods

Each of the 51 lakes studied was visited two to fifteen times in June–September 1994–1996. From each lake, one water sample was taken during the last week of July 1994, after a longish dry period with a stable high pressure. Analyses were made on total hardness (Ca + Mg) with a Hach test kit (EDTA titration), and alkalinity by titration with 0.01 M HCl. Conductivity and pH were recorded and water colour (mg Pt l^{-1}) was measured with a Shimadzu UV 160 spectrophotometer. Hardness values can be transformed to mg Ca l^{-1}, assuming that 1 °dH equals 0.178 mmol $CaCO_3$ l^{-1} or 7.1 mg Ca l^{-1} (Aho 1978). Elevation above sea level, lake area, shore length and shortest distance to the sea. were obtained from scale 1:20000 maps.

Snails were collected by hand-picking and with a rod sieve which was swept through the shore-vegetation. Collecting was considered finished when no further species were found. In some lakes 5–10 visits were needed to encounter all the species present.

The statistical analysis of water chemistry and topographic parameters was made with a programme package, SYSTAT by SPSS, Version 5.05, and included tests of normal distribution (Kolmogorov-Smirnov, Lilliefors test), average ± standard deviations for all lakes, and for lakes in which *T. fluviatilis* respectively *P. antipodarum* were found. To test for differences in the characters of the lakes, Kruskal-Wallis one way analyses of variance were performed.

Results

Water chemistry parameters as well as topographic parameters show large variations (Table 1). Low values for pH, alkalinity, hardness and conductivity are generally from lakes higher above the sea level, while higher values are from lakes at lower elevation.

The Kolmogorov-Smirnov (Lilliefors) test showed that none of the topographic parameters followed normal distributions. Of the water chemistry parameters, only pH may be regarded as normally distributed. Therefore the non-parametric Kruskal-Wallis test was used when testing for differences between lakes.

P. antipodarum and *T. fluviatilis* were jointly found in six lakes (Lakes 1–6) and *T. fluviatilis* alone in five additional lakes (Lakes 7–11) of the 51 lakes investigated. A total of eighteen species of gastropods were found (Table 2), and of these, fourteen occurred in the same lakes as *P. antipodarum* and *T. fluviatilis.* Other invertebrate taxa encountered were Hirudinea, Oligochaeta, Crustacea, Trichoptera, Ephemeroptera, Odonata and Bivalvia. The six lakes in which the two species were found together show high values for water chemistry parameters (pH, alkalinity, hardness and conductivity) and are well developed with zones of helophytes and submersal vegetation. This also applies to three (Lakes 7–9) of the remaining lakes in which only *T. fluviatilis* is present. For ten of the eleven lakes (Lakes 1–10), the number of fish species is known (Helminen 1979, Storberg 1981 and K.-E. Storberg unpubl.). However, the eleventh lake probably only houses a few species (at a guess perch, crucian carp and some other carp fish) and in that lake *T. fluviatilis* was encountered only once.

P. antipodarum was encountered in four lakes (Lakes 1–4) recently isolated from the Baltic Sea during the 20th century, and at first I considered these populations to be "relict populations", trapped in the lakes when they were isolated from the sea. This species was also found in two more lakes, located 3 (Lake 5) and 8 (Lake 6) m a.s.l. and thus isolated from the sea some 600 and 1600 years B.P.

P. antipodarum was found on coarse sand and gravel and sometimes under stones or boulders while *T. fluviatilis* preferred hard rocky substrata. In one lake (Lake 7), it was also found under the leaves of water lilies.

Table 1. Average values and standard deviations for water chemistry and environmental parameters in all investigated lakes and for the lakes in which *P. antipodarum* and *T. fluviatilis* occurred. Minimum and maximum values within brackets. The asterisks indicate values differing from corresponding "all lakes"-values and level of significance after Kruskal-Wallis-test. Note that statistics have been calculated only for the nine lakes in which *T. fluviatilis* may be regarded permanent.

	All lakes (n = 51)		*P. antipodarum* (n = 6)		*T. fluviatilis* (n = 9)	
Lake area, ha	33.2 ± 39.4	(2–200)	115 ± 54	(52–200)***	87 ± 63	(25–200)***
Shorelength, km	3.6 ± 2.9	(0.6–14.5)	9.5 ± 3	(5.9–14.5)***	7.8 ± 3.7	(4.1–14.5)***
Altitude, m	8 ± 9.4	(0.15–40.5)	2 ± 3	(0.15–8.3)*	2.1 ± 2.7	(0.15–8.3)*
Distance to the sea, km	0.94 ± 0.74	(0.03–3.1)	0.93 ± 0.87	(0.18–2.5)	0.96 ± 0.7	(0.18–2.5)
pH	7.6 ± 0.8	(5.6–9)	8.4 ± 0.2	(8.2–8.9)**	8.3 ± 0.3	(7.8–8.9)*
Alkalinity, meqv^{-1}	0.87 ± 0.49	(0.14–2.48)	1.35 ± 0.14	(1–1.56)*	1.20 ± 0.28	(0.67–1.56)*
Hardness, °dH	3.72 ± 2.27	(0.83–9.6)	5.78 ± 1.5	(4.08–8.16)*	5.35 ± 1.64	(2.88–8.16)*
Conductivity, µS cm^{-1}	160 ± 85	(33–375)	260 ± 64	(196–375)**	232 ± 74	(120–375)*
Water colour, mg Pt^{-1}	55 ± 21	(20–115)	56 ± 28	(25–115)	51 ± 26	(25–115)
Number of snail species	6.7 ± 3.9	(0–13)	12.2 ± 1	(11–13)***	11.7 ± 1.7	(8–13)***
Number of fish species	5.9 ± 2.9	(n = 36)	10 ± 1.7	(8–12)	9.3 ± 2	(6–12)

Discussion

P. antipodarum appears to be a species that requires water chemistry values that are higher than the average for the 51 lakes surveyed (Table 1). Boycott (1936) and Macan (1977) refered to *P. antipodarum* as a softwater species and to *T. fluviatilis* as a hard water species. The borderline between soft and hard water is a calcium concentration of 20 mg l^{-1} (Boycott 1936, Macan 1977) and the soft water species may occur in waters of higher calcium values. It is possible that 20 mg Ca l^{-1} is a critical limit for some snail species. *Lymnaea stagnalis* (L.), for example, requires small amounts of energy for calcium absorbtion in waters with a calcium concentration above 20 mg l^{-1}, though uptake is possible at values as low as 2.5 mg l^{-1} (Greenaway 1971). Greenaway (1971) discussed the possibility that snails may be genetically adapted to the lower calcium values of the Scandinavian lakes. For *P. antipodarum*, it is known that, two different genetical strains (A-strain and B-strain) exist in Denmark, one of them more adapted to freshwater environments than the other (Jacobsen and Forbes 1997). So, the *P. antipodarum* individuals found in Danish lakes may belong to the A-strain, while individuals from brackish waters may belong to the B-strain according to Jacobsen *et al*. (1996).

In semi-isolated bays of the Baltic Sea, *T. fluviatilis* and *P. antipodarum* coexist in communities of only five to six snail species (R. Carlsson unpubl.). The low number of freshwater snail species is probably due to the high salinity (2‰–5‰ S). In two of the lakes, *T. fluviatilis* was represented by chance individuals. One of the lakes (Lake 11) is very small and rather humic and located some thirty metres from the sea shore. In the other lake (Lake 10), located 13.4 m a.s.l., about half a kilometer from the sea and surrounded by forests, the occurrence is harder to explain, as this lake is considered one of the most oligotrophic lakes in the Åland Islands with a hardness value of only 1.68 °dH. In lake 10, there were only four individuals at one spot on one occasion and the species has not been seen there since. The occurrence of *P. antipodarum* in lake 5 and 6 implies that the species must have been transported to these lakes by birds or other agents, possibly by fish, some time before the 1970s. In unpublished field records, from the beginning of the 1970s, it is recorded as *Hydrobia* sp. in Lake Toböle träsk (Husö Biological Station, unpubl.). *P. antipodarum* is capable of surviving passage through the alimentary canal of fresh water fish (Haynes *et al.* 1985). Hydrobiids of the related genus *Hydrobia* are also reported to pass the gut of juvenile flounder alive (Aarnio and Bonsdorff 1997). The simplest explanation, for the species being present in lakes of the Åland Islands and absent on the Finnish mainland, may be that the Åland Islands are located in the middle of the Baltic Sea, in the spreading centre of the two species. The lakes are located at short distances from the sea, and snails may colonize the lakes by active dispersal of adults, or perhaps by birds (or more seldom fish or fishing tools) acting as transportation agents. In Denmark, colonization is known to have occurred through river systems (Lassen 1978). In Norway the species so far has a distribution limited to coastal lakes (Økland 1990). The outlets of most lakes on the Åland Islands are ditches,

Table 2. Species in snail assemblages in lakes on the Åland Islands. Total = total number of lakes where the species occur, P. ant. = number of lakes where *P. antipodarum* is present, T. flu = number of lakes where *T. fluviatilis* is permanent. Number within bracket = number of lakes where *T. fluviatilis* has been found but not regarded permanent. Note that *Radix peregra* and *R. auricularia* are treated as a single species.

Snail species	Total	P. ant.	T. flu.
L. stagnalis (L.)	29	6	9
Radix ovata (Drap.) /*R. auricularia* (L.)	43	6	9 (2)
Stagnicola palustris (Müll.)	35	6	9 (1)
Myxas glutinosa (Müll.)	4	–	–
Galba truncatula (Müll.)	1	–	–
Physa fontinalis (L.)	30	6	9 (1)
Planorbis planorbis (L.)	7	3	3
Gyraulus albus (Müll.)	37	6	9 (1)
Armiger crista (L.)	36	6	9 (1)
Bathyomphalus contortus (L.)	22	6	8
Hippeutis complanatus (L.)	10	1	1
Acroloxus lacustris (L.)	31	5	9 (1)
Valvata cristata (Müll.)	13	4	6
V. piscinalis (Müll.)	5	–	2
V. macrostoma (Steenbuch)	1	–	1
Bithynia tentaculata (L.)	23	5	8
P. antipodarum (Gray)	6	6	6
T. fluviatilis (L.)	11	6	9 (2)

overgrown with weeds or periodically even dry, making them unsuitable for fish wandering or active colonization by snails. This could also be the reason why *P. antipodarum* in Sweden only has colonized coastal lakes so far. Also, the lakes in Scotland were colonized more slowly by *P. antipodarum* than the lakes of southern England. The cause is the extensive system of canals, promoting dispersal in the southern parts of England (Lassen 1978). The average values for shortest distances from the studied lakes, on Åland, to the open sea (Table 1) are rather high for colonization to take place. Lakes 1–2 and 3–4 respectively are closely interconnected and were isolated from the sea by man-made dams during the 1970s (Lindholm 1975, Bonsdorff and Storberg 1990). If a snail colonizes the lake closest to the sea, further dispersal to the more distant lake takes place easily. From the points of isolation (man-made dams) these two lake systems have contact with the sea through canals and bays with a rising salinity gradient.

On mainland Finland, the postglacial history of, for example, Länsi-Uusimaa in southern Finland can be compared to that of the Åland Islands, since there are recently cut off bays which gradually form lakes due to land uplift. In this area, the older lakes show low conductivity values as compared with the lakes in this paper (Helminen 1984). No studies have been made concerning the occurrence of *P. antipodarum* in that area. Perhaps it could be found along the coasts of Finland in recently cut off bays or "flads". In such places, the water is a mixture of freshwater and calcium rich sea water, due to intermittent influxes of sea water during autumn storms or other events with high sea level. At least in the Åland Islands this species is encountered in almost every "coastal lake" which still has a water exchange with the sea through, for example, a man-made channel (R. Carlsson unpubl.). *T. fluviatilis* has been recorded in recently isolated lakes in southwestern Finland (Bagge and Tulkki 1967). That the species remains within, and also colonizes, totally isolated lakes on the Åland Islands may be due to the fact that the moraine of the islands contains large quantities of lime, from which calcium seeps into the lakes with influxes of groundwater and thus the high conductivity and calcium values are maintained.

Jacobsen and Forbes (1997) showed that the optimal salinity for *P. antipodarum* is 5‰ S, a salinity often found in bays of the Åland archipelago, but it also grows and propagates at higher and lower concentrations (Jacobsen and Forbes 1997). However, the artificial fresh water, used in the experiment by Jacobsen and Forbes (1997) had a calcium concentration of approximately 28 mg l^{-1}, which is higher than in the lakes studied by Aho (1966).

Most studies have so far been on the effects of calcium. However, Pip (1978) and Dussart (1979) showed that different snail species are affected by different elements (e.g. potassium, sodium, magnesium, phosphate, chloride) or other environmental factors (e.g. dissolved organic solids, dissolved oxygen, type of substratum). Jokinen (1987) reported that snail species diversity was negatively affected by high Na:Ca ratios. Aho (1966) found a strong negative correlation between humic substances and the number of gastropod species present. This factor may act alone or be combined with calcium deficiency as in the eastern Gulf of Bothnia, where *T. fluviatilis* is absent in humic water, poor in calcium (Kangas and Skoog 1978).

Furthermore, and disregarding the differences in water chemistry between the lakes on the Åland Islands and those of the Finnish mainland, the size of the lakes may also be of importance for colonization and long term survival. Theoretically, the shores of a smaller lake will be silted faster than those of a larger lake where waves will build up and wash the silt and mud to deeper areas, thus offering a suitable habitat for *P. antipodarum*, explaining the absence in most of the smaller lakes. This statement finds support in Boycott (1936) who discussed the importance of water movement.

Another reason for finding the two species in larger water bodies is that both of them are prosobranchs and so show life history tactics and adaptations to stable environments, less susceptible to e.g. drought or hypoxia (Brown 1983, 1991, Gallardo *et al.* 1994). Lakes of smaller size are more susceptible to short-time environmental variations than are larger lakes (Lodge *et al.* 1987).

The impact of biotic interactions may also be important. There are strong reasons to believe that snail communities are structured by for example molluscivorous fish (e.g. Brönmark *et al.* 1997, Brönmark and Vermaat 1998).

Also, both species may, in freshwater lakes, be regarded as "high-S species" as they appear in the most species-rich snail assemblages. However, very little is known about the competitive capacities and other relationships between the species. Brown (1991) poined out that more work is needed to determine whether nonoverlapping distributions of pulmonates and prosobranchs are due to competition. Four of the lakes are inter-connected, and in these, *T. fluviatilis* occurs in two lakes (7 and 8) and the pulmonate *Myxas glutinosa* (Müller) in two adjacent lakes. On the Åland Islands, these 2 species were not found together. The water chemistry of the four lakes is similar and *M. glutinosa* also, like *T. fluviatilis*, mostly occurs on solid rocks (Whitfield *et al.* 1998) and under leaves of water lilies (R. Carlsson unpubl.).

T. fluviatilis and *P. antipodarum* are found on the same kind of substrata as in the waters of the surrounding archipelago. The occurrence of *T. fluviatilis* under leaves of water lilies may be explained by the fact that the plants are offering the same kind of substrata as stands of bladder-wrack (*Fucus vesiculosus* (L.)) and eelgrass (*Zostera marina* (L.)) on which it is often found in the Baltic Sea (Skoog 1978, Boström and Bonsdorff 1997). Hubendick (1949) regarded *T. fluviatilis* as a brackish water species, rather than a freshwater species. If so, the leaves of water lilies may be regarded as a kind of substitute for bladder-wrack and eelgrass in freshwater lakes.

Conclusions

P. antipodarum and *T. fluviatilis* do well in freshwater environments, provided the water bodies are large enough, suitable habitats are available and calcium values are not too low. In the Åland Islands, the soils, rich in ground limestone, make the lakes calcium rich. This, combined with the neighbouring brackish sea, promotes the dispersal of the species from the brackish water surrounding the islands. Along the coasts of the Finnish mainland, and also along the Swedish coasts, it should be possible to find the species in recently isolated lakes even though calcium values are in general low. Finally, it would be important to test whether snails on the Finnish mainland generally comprise a genetic variety, adapted to lower calcium values than snails elsewhere.

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