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Freshwater Snail Communities and Lake Classification. An Example from the Åland Islands, Southwestern Finland

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With 4 Figures and 6 Tables

Key words: Freshwater snails, calcium, hardness, lake types, Åland Islands

Abstract

The freshwater snail fauna in 51 lakes on the Åland Islands was investigated. By means of cluster analysis it appears that lakes may be divided into four groups on the basis of snail species composition. The lakes of the four groups show a spatial distribution which is related to topographical differences, terrestrial vegetation and land use. Snails may be divided on the basis of water hardness into hard water species and calcium indifferent species or into demanding and modest/indifferent species when clustering is based on presence/absence.

Introduction

MACAN (1977) summarised the work of BOYCOTT (1936) on British freshwater snails in the following way: "The optimum conditions in a habitat are much the same for all the species, with few exceptions. Good conditions are a large volume of moderately warm calcareous water, free from inorganic matter in suspension and from organic pollution, flowing not too rapidly over a shallow bottom, with a moderate but not excessive growth of plants". Do different types of lakes offer different environments to which some species are adapted and some are not? Do particular snail communities develop in the different lake types or are the snail species distributed at random? Many earlier investigations have dealt with these problems (e.g. CALOW 1973; AHO et al. 1981; LODGE 1985; PIP 1986a, 1986b, 1987, 1988; COSTIL 1994). In this paper, the division of lakes into lake types is based on the assumption that the presence of a particular snail species reflects the environmental needs of that species, or its ecological niche. The Åland land uplift area with its many lakes (CEDERCREUTZ 1934, 1937; LINDHOLM 1991) offers an excellent opportunity to study lakes of different age and thus different water chemistry properties.

The Finnish botanist CARL CEDERCREUTZ classified lakes on the Åland Islands on the basis of their planktonic algae and vascular plants (CEDERCREUTZ 1934, 1937, 1947), following the ideas of SAMUELSSON (1925) and ALMQVIST (1929). CEDERCREUTZ classified lakes into "Weissmoor"-lakes (dystrophic lakes), *Lobelia*-lakes (oligotrophic lakes) and *Potamogeton*-lakes (eutrophic lakes). The *Potamogeton*-lakes were further subdivided into *Chara*-lakes (relatively shallow lakes, usually recently isolated from the sea), *Anabaena*-lakes (relatively deep and large lakes with open surfaces), "Algengyttja"-lakes (shallow lakes, deteriorating because of sedimentation, and therefore they often partly or completely dry up during summer) and "Braunmoor"-lakes (shallow lakes, overgrowing from the shores). "Zwischen"-lakes (mixed lakes), do not fit well into any category but show traits from two or more of them.

Landscape ecology is an emerging discipline and the ecological organisation of lake districts has recently paid much attention (e.g. KRATZ et al. 2000; LEWIS & MAGNUSON 2000). In a study of species-area relationships CARLSSON (2001a) found that water hardness and aquatic vegetation were the two most import factors determining the number of snail species in lakes on the Åland Islands, while lake area was of minor (and not even statistically significant) importance. This lead to the belief that there was a general pattern with a higher species richness in some lakes than in others and that this pattern is perceivable in the landscape. This paper may be seen as a continuation of the above mentioned paper.

Study area

The Åland Islands are located in southwestern Finland, approximately at Lat. 60° N, Long. 20° E, about halfway between Sweden and the Finnish mainland (Fig. 1). Between

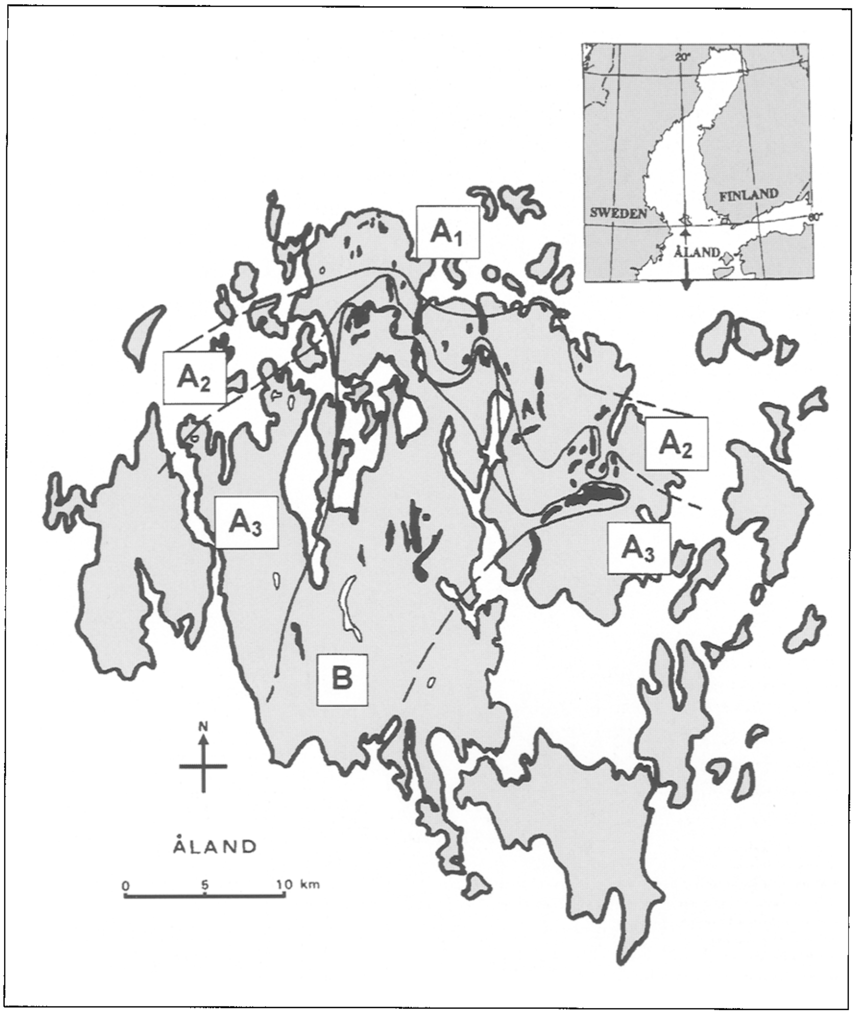

Fig. 1. The Åland Islands with lines separating different types of lakes. Dashed lines indicate uncertain limits. The 51 investigated lakes in black, other visited lakes, more extensively surveyed, in white. One of the A_1-lakes (Mönträsk) is in the A_3-area, its location is depending on the south-westerly extension of the northern hill area.

the central island of Åland and Finland is a vast archipelago and the Sea of Åland separates the Åland Islands from Sweden in the west. The bedrock of the main island of Åland is composed of different kinds of acidic rapakivi granites while the archipelago is built up of older bedrock consisting mainly of gneisses, migmatites and related kinds of rocks (BERGMAN 1986). Despite the acidic bedrock, many lakes on the Åland Islands are rich in calcium due to lime in the moraine, which covers the bedrock (HAUSEN 1964). However, in the northern part of the province, in the municipalities of Geta, Saltvik and Sund, there are bare rock outcrops and only a very thin moraine cover. The hills gradually descend into a more flat landscape with till and clay deposits between residual rocky hills. The lakes in the northern area are more oligotrophic and poor in calcium than are the lakes in the lowland areas, which also are affected by farming. The landscape is dissected by faults running in different directions, making a mosaic of bays and firths alternating with smaller and larger islands. New lakes are still being formed in the area due to land uplift, the rate of it is currently about 4–5 mm per year (LINDHOLM 1991).

Materials and Methods

Snails were collected 2–15 times, depending on size and complexity of the lakes, in 51 lakes by hand picking and with a rod sieve during 1994–1996. The species have been identified according to HUBENDICK (1949), MANDAHL-BARTH (1970) and MACAN (1977). The two species *Radix ovata* (DRAPARNAUD) and *R. peregra* L. were treated as one species together with *Radix auricularia* L. from which they with certainty can be told only by examination of their internal genitalia (MACAN 1977). Also *Stagnicola palustris* (MÜLLER) [Syn. *Lymnaea palustris* (MÜLLER)] is treated as one species though it is nowadays regarded as a complex of several species (JACKIEWICZ & VON PROSCHWITZ 1991; VON PROSCHWITZ, pers. comm.).

Water samples were taken at a depth of about 20 cm in the littoral zone of each lake during one week in July 1994. Hardness (°dH) was analysed by EDTA titration (Hach test kit), conductivity ($\mu S\ cm^{-1}$) with a Metrohm 660 conductometer, pH with a Metrohm 691 pH meter and water colour with a Shimadzu UV 160 spectrophotometer. Alkalinity was analysed by titration with 0.01 M HCl.

Areas of lakes and cultivated fields and circumferences of the lakes were measured from 1:20000 topographical maps.

Statistical analysis was performed with a SYSTAT by SPSS, Version 5.05 programme package and included Kolmogorov-Smirnov and Lilliefors test for testing of normality and average ± standard deviations. Cluster analyses on both lake and snail data (Euclidean distance, average linkage) were performed with SYSTAT 9. The cluster analysis of the lakes was based solely on the occurrences of snails. The status of a snail species in each lake was designated by the number 1 (present) or 0 (absent). The presence of a snail species in a particular lake is assumed to reflect the total ecological niche of that particular species (AHO et al. 1981). Kruskal-Wallis one way ANOVA was used to find out differences in the characters of the lakes.

For comparison, the same clustering technique was also applied on data on Finnish lakes (AHO 1966) to show possible regional differences. For clustering of snails two methods were used; one based on the presence/absence in lakes and one based on average ± S.D. values for water hardness of the lakes where the species occurred.

Results

The results from the water sampling are in agreement with earlier results from similar investigations (e.g. HELMINEN 1977; ÖSTMAN 1988; unpubl. data on Husö Biological Station), and may be regarded as representative (Table 1). Altogether, 18 species of snails were encountered in the 51 Åland lakes. As each lake was visited more than once, there is a large probability that most occurring species were encountered. Other investigations (e.g. ØKLAND 1990) are based on sampling limited to half an hour, and then some species may have been missed. Some species were present in most lakes while others were found only in a few lakes (Table 2). In three lakes snails were

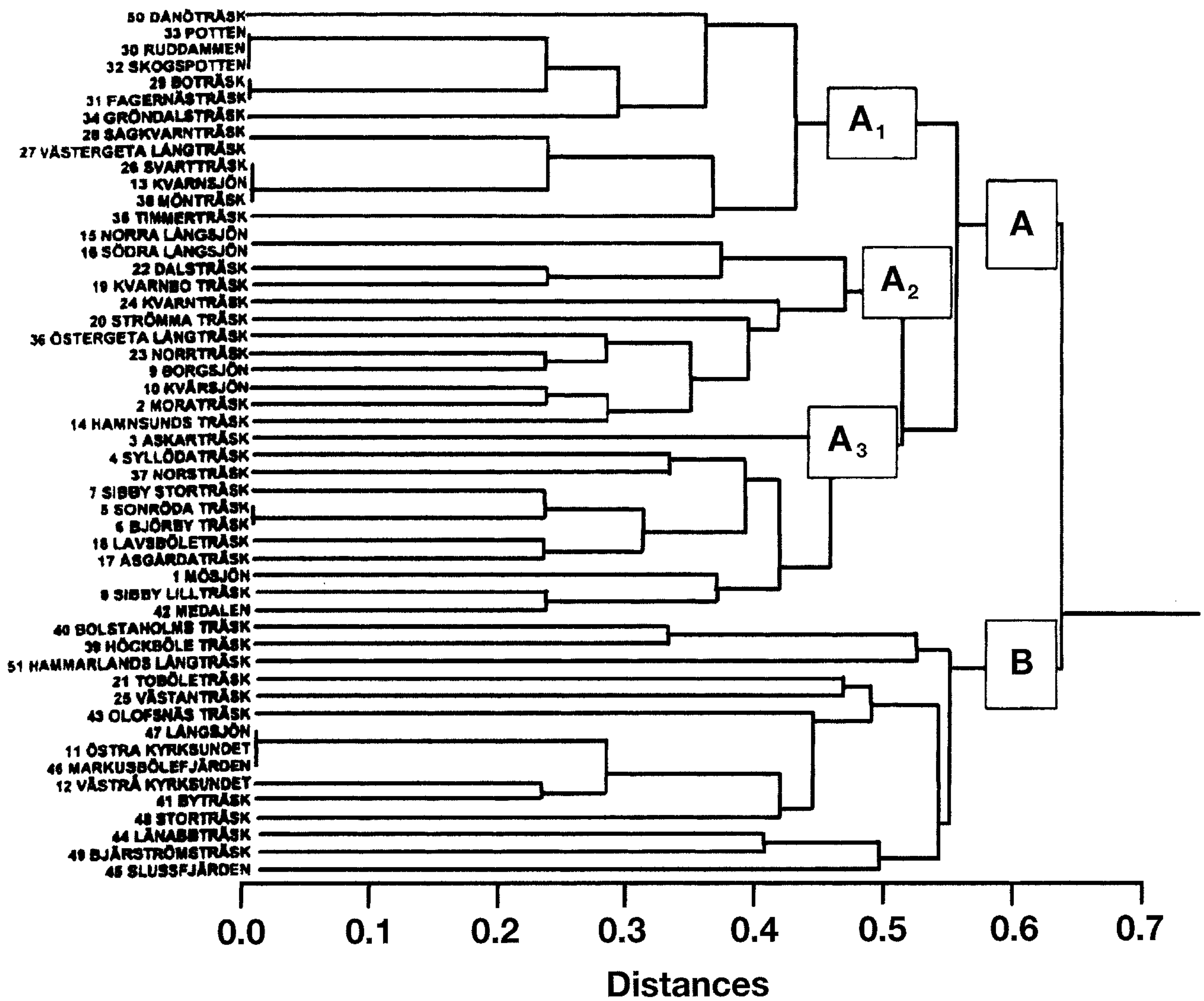

Fig. 2. Lake cluster based on presence/absence of snails. Note that subclusters $A_1 - A_3$ emanate from the same cluster, while the lowland lakes of cluster B form a separate group. Clustering was performed with average linkage, and distances are Euclidean.

Table 1. Some topographical and water chemistry parameters for the investigated lakes. [1]) = Acidified lakes subjected to liming in order to raise the pH value.

Lake	Area, hectares	Elevation, m.a.s.l.	pH	Alkalinity, meq l^{-1}	Hardness, ° dH	Conductivity, × µS cm^{-1}
1. Mösjön	26	6.8	7.5	1.19	4.08	152
2. Moraträsk	41	3.8	7.5	0.65	2.88	130
3. Askarträsk	12	3.1	9.0	1.31	3.36	159
4. Syllödaträsk	22	3.6	8.9	1.33	5.28	236
5. Sonröda träsk	43	2.1	8	0.81	4.08	169
6. Björby träsk	15	2.1	7.2	0.8	3.9	165
7. Sibby Storträsk	19	3	8	0.6	2.64	107
8. Sibby Lillträsk	6	3	7.1	0.48	1.92	108
9. Borgsjön	18	13.4	8.3	0.44	1.68	89
10. Kvärsjön	15	20.1	7.6	0.35	1.44	73
11. Östra Kyrksundet	200	0.15	8.5	1.1	4.08	196
12. Västra Kyrksundet	59	0.15	8.2	1.0	4.56	212
13. Kvarnsjön	13	22.9	6.8	0.14	0.84	53
14. Hamnsunds träsk	8	11.7	6.4	0.2	0.84	65
15. Norra Långsjön	46	22.7	7.7	0.43	1.68	92
16. Södra Långsjön	66	22.7	7.8	0.69	1.92	85
17. Åsgårdaträsk	36	17.8	8	0.9	2.88	132
18. Lavsböleträsk	31	17.7	8.1	0.63	2.88	108
19. Kvarnbo träsk	18	17.7	6.9	0.61	3.12	117
20. Strömma träsk	12	1.9	7.2	1	4.08	157
21. Toböleträsk	52	8.3	8.4	1.31	5.28	216
22. Dalsträsk	26	19.6	7.8	0.46	3.02	138
23. Norrträsk	25	12.2	8.3	1.02	3.6	151
24. Kvarnträsk	18	13.5	7.9	0.89	3.36	165
25. Västanträsk	82	3.1	8.9	1.28	5.04	245
26. Svartträsk[1]	7	40.5	5.6	0.28	0.36	33
27. Västergeta Långträsk[1]	15	38	6.4	0.18	1.08	55
28. Sågkvarnträsk[1]	8.8	8.5	5.7	0.88	0.84	50
29. Boträsk	4.5	7.5	6.7	0.28	1.68	66
30. Ruddammen	2.5	4	6.7	0.28	1.2	75
31. Fagernästräsk	9	2.6	6.7	0.29	1.44	79
32. Skogspotten	2	2.2	7.4	0.61	1.92	155
33. Potten	2	0.9	7.3	0.6	2.64	136
34. Gröndalsträsk	30	1	7.4	0.5	2.16	114
35. Timmerträsk	6	7.3	7.5	0.64	1.92	102
36. Östergeta Långträsk	8.5	6.5	7.5	0.72	2.88	113
37. Norsträsk	25	4	7.9	0.67	2.88	120
38. Mönträsk	13	9.2	6.5	0.35	1.92	70
39. Höckböle	6.5	1.2	8	2	9.6	260
40. Bolstaholm	33	1.5	8	1.51	6.24	230
41. Byträsk	32	1.4	8.2	1.01	4.68	180
42. Medalen	16.5	1.3	7.3	1.09	5.52	210
43. Olofsnästräsk	40	1.1	7.8	1.44	6	235
44. Länabbträsk	34	0.2	8	1.13	7.92	330
45. Slussfjärden	10	0.3	7.3	1.33	4.8	243
46. Markusbölefjärden	156	0.15	8.3	1.45	8.16	375
47. Långsjön	140	0.15	8.2	1.56	7.44	313
48. Storträsk	92	3.1	8	2.48	7.44	352
49. Bjärströmsträsk	26	1.8	8.9	1.17	6.96	258
50. Dånöträsk	10.5	1.8	8.3	1.1	5.04	162
51. Hammarlands Långträsk	56	10.9	7.7	1.4	8.4	345

lacking. By cluster analysis the lakes may be divided into two main groups, A and B, of which A is further subdivided into three sub-groups, A_1–A_3 (Fig. 2 and Table 3). The lakes of group B are vegetation-rich lowland lakes with high values for most water chemistry parameters, while those of group A are located at higher elevations, having more sparse vegetation and showing lower water chemistry values. The Kruskal-Wallis test shows significant differences between the clusters obtained (Table 4). The number of snail species increases from A_1 to B just like the water chemistry values (Table 5). Lakes of group A_1 are poor in species (three of the lakes with no snails at all), with *Radix ovata* and/or *Stagnicola palustris* and *Armiger crista* as dominant species . In one of the A_1-lakes, with a pH of 5.7, only *R. ovata* was present. The individuals of

Table 2. Species composition in lake clusters on the Åland Islands. The letters A_1–B indicate lake clusters, cf. Fig. 2. The number of lakes in which each species was recorded is given for lake clusters and for the total number of lakes. Species regarded as common (occurring in 30 lakes or more) are marked with an asterisk.

Snail species	A_1 (n = 13)	A_2 (n = 12)	A_3 (n = 11)	B (n = 15)	Total (n = 51)
L. stagnalis (L.)	1	7	8	13	29
Radix ovata /R. auricularia coll.*	7	12	10	14	43
Stagnicola palustris coll.*	5	8	8	15	36
Myxas glutinosa (MÜLL.)	–	–	1	3	4
Galba truncatula (MÜLL.)	–	–	1	–	1
Physa fontinalis (L.)*	7	–	8	15	30
Planorbis planorbis (L.)	–	–	–	7	7
Gyraulus albus (MÜLL.)*	2	13	10	12	37
Armiger crista (L.)*	7	4	10	15	36
Bathyomphalus contortus (L.)	–	4	3	15	22
Hippeutis complanatus (L.)	–	3	3	4	10
Acroloxus lacustris (L.)*	–	10	10	11	31
Valvata cristata (MÜLL.)	–	–	1	12	13
V. piscinalis (MÜLL.)	–	1	–	4	5
V. macrostoma (STEENBUCH)	–	–	–	1	1
Bithynia tentaculata (L.)	–	1	10	12	23
P. antipodarum (GRAY)	–	–	–	6	6
T. fluviatilis (L.)	–	–	–	9	9
% Prosobranchs	0	3.2	13.2	25.7	16.6

Table 3. Comparison of clusters concerning lake type according to CEDERCREUTZ (1937, 1947), water hardness, vegetation, water properties and trophic status. In each group may be some lakes which deviate from the rest in some aspects. However, CEDERCREUTZ (1947) claimed that these lakes were difficult to readily fit into any lake category, since they showed traits from more than just one.

	A_1	A_2	A_3	B
Lake type according to CEDERCREUTZ	Weissmoor- and *Lobelia*-lakes	*Lobelia*- and Zwischen-lakes	Mainly Zwischen- and a few *Anabaena*-lakes	Mainly *Chara*- and *Anabaena*- lakes
Size and surroundings	Generally small (< 10 ha), in areas with bare rocks or thin soils and coniferous trees	Medium size, mostly surrounded by forests. Some cultivated fields, pastures	Medium size, parts of catchment areas cultivated fields or pasture	Generally large lakes in areas with deciduous trees, cultivated fields and pastures
Water	Soft, humic water, low alkalinity and pH	Soft to medium hard, slightly humic to clear water	Medium hard to somewhat soft water with some tendencies for being humic	Medium hard to hard water, often slightly greenish. Plankton turbidity, high alkalinity and pH
Vegetation	Sparse vegetation	Sparse vegetation	Intermediate to rich vegetation	Rich vegetation
Trophic status	Dystrophic	Oligotrophic to mesotrophic	Mesotrophic to eutrophic	Eutrophic

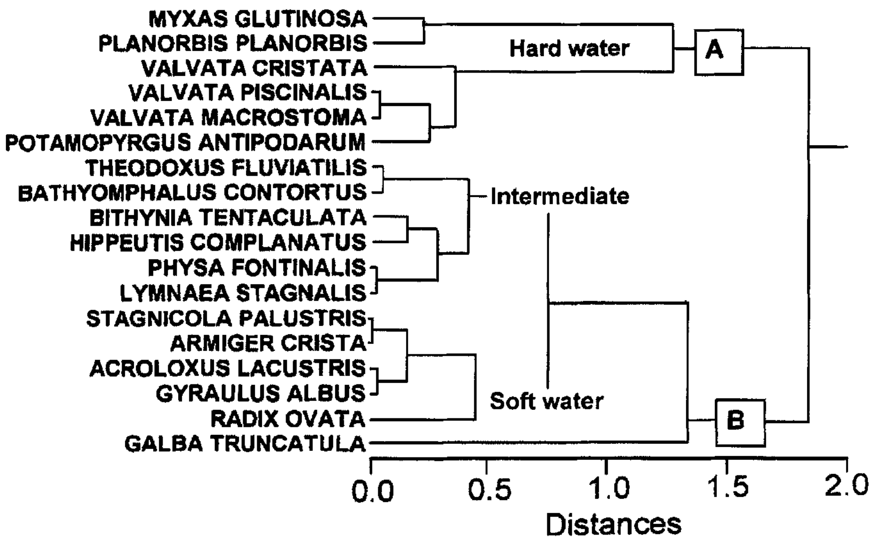

Fig. 3. Snails clustered according to hardness (average and standard deviations of water) in lakes were recorded. Clustering was performed with average linkage, and distances are Euclidean.

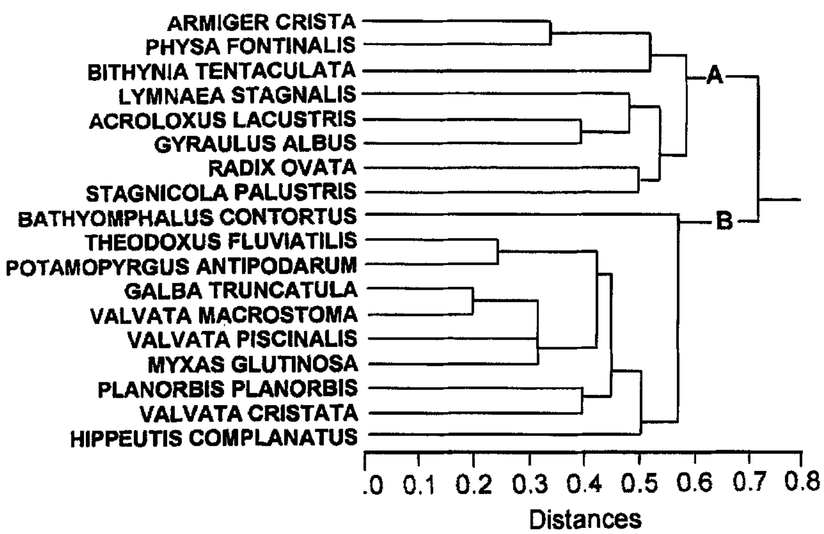

Fig. 4. Snails clustered according to presence/absence in lakes. Clustering was performed with average linkage, and distances are Euclidean.

Table 4. Probability values for differences in water chemistry and environmental parameters between clusters after Kruskal-Wallis test. [1]) = $P \leq 0.05$; [2]) = $P \leq 0.01$; [3]) = $P \leq 0.001$.

	A_1/A_2	A_1/A_3	A_1/B	A_2/A_3	A_2/B	A_3/B
Lake area, ha	0.004 [2]	0.002 [2]	0.000 [3]	0.902	0.016 [1]	0.007 [2]
Shorelength, km	0.011 [1]	0.003 [2]	0.000 [3]	0.242	0.008 [2]	0.012 [1]
Altitude, m.a.s.l.	0.157	0.487	0.006 [2]	0.005 [2]	0.000 [3]	0.009 [2]
pH	0.008 [2]	0.003 [2]	0.000 [3]	0.384	0.006 [2]	0.156
Alkalinity, meqv^{-1}	0.102	0.004 [2]	0.000 [3]	0.042 [1]	0.000 [3]	0.001 [3]
Hardness, °dH	0.053	0.001 [3]	0.000 [3]	0.072	0.000 [3]	0.000 [3]
Conductivity, µS cm^{-1}	0.082	0.003 [2]	0.000 [3]	0.045 [1]	0.000 [3]	0.000 [3]
Water colour, mg Pt^{-1}	0.397	0.560	0.745	0.496	0.492	0.464
Cultivated fields, %	0.008 [2]	0.000 [3]	0.000 [3]	0.009 [2]	0.000 [3]	0.253
Number of species	0.001 [3]	0.000 [3]	0.000 [3]	0.000 [3]	0.000 [3]	0.001 [3]

Table 5. Average values and standard deviations for water chemistry and environmental parameters in all investigated lakes and clusters A_1–B. Range values within brackets.

	All lakes (n = 51)	A_1 (n = 13)	A_2 (n = 12)	A_3 (n = 11)	B (n = 15)
Lake area, ha	33.2 ± 39.4 (2–200)	9.5 ± 7.2 (2–30)	26 ± 17 (8–66)	22.9 ± 10.9 (6–43)	67.9 ± 54.8 (6.5–200)
Shorelength, km	3.6 ± 2.9 (0.6–14.5)	1.7 ± 0.9 (0.6–4.1)	2.8 ± 1.6 (1.6–6.8)	3.1 ± 1.2 (1.8–3.7)	6.4 ± 3.5 (1.4–11.6)
Elevation, m.a.s.l.	8 ± 9.4 (0.15–40.5)	11.3 ± 13.1 (0.9–40.5)	13.8 ± 7.1 (1.9–22.7)	5.9 ± 6.0 (1.3–17.7)	2.2 ± 3.1 (0.15–10.9)
% cultivated fields	8.9 ± 9 (0–32)	0.8 ± 2.4 (0–8.8)	3.2 ± 2.8 (0–6.6)	13.4 ± 10.4 (1–32)	17.3 ± 4.3 (9.6–21.7)
pH	7.6 ± 0.8 (5.6–9)	6.8 ± 0.7 (5.6–8.3)	7.6 ± 0.5 (6.4–8.3)	7.9 ± 0.6 (7.1–9.0)	8.2 ± 0.4 (7.3–8.9)
Alkalinity, meqv^{-1}	0.87 ± 0.49 (0.14–2.48)	0.47 ± 0.27 (0.14–1.1)	0.62 ± 0.26 (0.2–1.0)	0.89 ± 0.3 (0.48–1.33)	1.41 ± 0.38 (1.0–2.4)
Hardness, °dH	3.72 ± 2.27 (0.36–9.6)	1.77 ± 1.12 (0.36–5.04)	2.54 ± 1.0 (0.84–4.08)	3.58 ± 1.11 (1.92–5.28)	6.44 ± 1.63 (4.08–9.6)
Conductivity, µS cm^{-1}	160 ± 85 (33–375)	88 ± 40 (33–162)	115 ± 34 (65–165)	151 ± 43 (107–236)	266 ± 59 (180–375)
Water colour, mg Pt^{-1}	55 ± 21 (20–115)	57 ± 20 (25–95)	49 ± 22 (20–95)	52 ± 19 (35–95)	57 ± 21 (25–115)
Number of species	6.7 ± 3.9 (0–13)	2.2 ± 1.7 (0–5)	4.8 ± 1.3 (3–7)	8.2 ± 1.7 (6–11)	11.2 ± 1.6 (7–13)

Table 6. Probability values for differences in presence of snail species between lake clusters after Kruskal-Wallis test.
^{1}) = P ≤ 0.05; ^{2}) = P ≤ 0.01; ^{3}) = P ≤ 0.001.

	A_1/ A_2	A_1/ A_3	A_1/B	A_2/ A_3	A_2/B	A_3/B
L. stagnalis	0.021 ^{1}	0.000 ^{3}	0.000 ^{3}	0.118	0.042 ^{1}	0.392
R. ovata coll.	0.039 ^{1}	0.011 ^{1}	0.018 ^{1}	0.338	0.872	0.740
S. palustris	0.330	0.100	0.000 ^{3}	0.479	0.007 ^{2}	0.035 ^{1}
M. glutinosa	1.000	0.277	0.094	0.296	0.107	0.455
P. fontinalis	0.003 ^{2}	0.351	0.004 ^{2}	0.000 ^{3}	0.000 ^{3}	0.035 ^{1}
A. lacustris	0.000 ^{3}	0.000 ^{3}	0.000 ^{3}	0.082	0.923	0.068
P. planorbis	1.000	1.0000	0.005 ^{2}	1.000	0.007 ^{2}	0.009 ^{2}
G. albus	0.000 ^{3}	0.000 ^{3}	0.000 ^{3}	1.000	0.197	0.216
A. crista	0.312	0.051	0.004 ^{2}	0.006 ^{2}	0.000 ^{3}	0.243
B. contortus	0.026 ^{1}	0.049 ^{1}	0.000 ^{3}	0.758	0.000 ^{3}	0.000 ^{3}
H. complanatus	0.060	0.049 ^{1}	0.048 ^{1}	0.903	0.923	0.973
B. tentaculata	1.000	0.000 ^{3}	0.000 ^{3}	0.000 ^{3}	0.000 ^{3}	0.122
P. antipodarum	1.000	1.000	0.012 ^{1}	1.000	0.015 ^{1}	0.019 ^{1}
V. cristata	1.000	0.277	0.000 ^{3}	0.296	0.000 ^{3}	0.000 ^{3}
V. piscinalis	0.298	1.000	0.048 ^{1}	0.338	0.232	0.068
T. fluviatilis	1.000	0.277	0.002 ^{2}	0.296	0.003 ^{2}	0.022 ^{1}

this lake had very soft and paper-thin shells. Occasionally *Physa fontinalis* and some other species may be found in A_1. A_2 is a cluster of transition with an increasing number of species present. In group A_3 there are generally 5–11 species, and *Bithynia tentaculata* is present in all of the lakes. *Planorbis planorbis* and *Potamopyrgus antipodarum* (GRAY) are only found in group B and, with a few exceptions, also *Myxas glutinosa, Valvata cristata, V. piscinalis* and *Theodoxus fluviatilis.* In the lakes of group A_1 and A_2 none of the species mentioned in group B occur. *M. glutinosa* lakes are described elsewhere (WHITFIELD et al. 1998; CARLSSON 2001b). There are significant differences between occurrences of snail species in the different lake clusters, the most obvious between cluster A_1 and B (Table 6). The Finnish lakes (AHO 1966) formed two distinct clusters, one with the polyhumous dys-oligotrophic lakes in a separate subcluster surrounded by dys-oligotrophic lakes. The dys-eutrophic lakes were found in both of the clusters. The snails of AHO (1966) formed an unusual pattern, with *L. peregra* (MÜLLER) and *Gyraulus acronicus* FERUSSAC isolated from the other snails. The rest of the snails, with the exception of *M. glutinosa* formed one cluster. Cluster analysis based on average hardness gives two clusters, where A represents calcium demanding species and B calcium indifferent species (Fig. 3). Clustering on the basis of presence/absence also gives two groups of snails (Fig. 4).

Discussion

The number of snail species increases from group A_1 to B, probably due to a simultaneous increase in water chemistry values and lake area. Lake chemistry is related to geological features. Consequently the lakes of group A_1 are located in the calcium-poor northern part of the area. These lakes are mostly dystrophic and are often surrounded by a mat of *Sphagnum*-bog. A considerable part of the catchment areas is bare rock or rocky pine forest. The lakes of cluster B are located on lowland, where deciduous forests, fields and pastures surround the lakes. The lakes of clusters A_2 are located on the footslopes of the hills to the north and A_3 adjacent to clay areas (farmlands) at lower elevation between isolated rock outcrops. To sum it up, the lake clusters clearly reflect the properties of the landscape, concerning elevation, vegetation and land use. In general, the percentage of cultivated fields increases, when going from A_1 to B (Table 5). The same probably also concerns pastures, though this cannot be measured from maps with the same accuracy. In A_1 there are no pastures at all, in A_2 just a few, while grazing cattle is a common sight in A_3 and B. This tendency is also in agreement with Norwegian results (ØKLAND 1990). Eight different clusters were found in Norway, where the geology is more complex than on the Åland Islands.

The "Weissmoor"-lakes and some of the *Lobelia*-lakes of CEDERCREUTZ (1947) belong to group A_1, while the rest of the *Lobelia*-lakes as well as the lakes of "Zwischen"-type belong to group A_2. The lakes of group A_3 represent a mix of "Zwischen"-lakes and *Anabaena*-lakes and group B, finally, are *Anabaena*- and *Chara*-lakes. It is however, difficult to judge exactly where the differences in species composition between the lake clusters are to be found, though the Kruskal-Wallis analyses give significant differences for particular species. *R. ovata* occurs in a very wide environmental range (HUBENDICK 1947) and was found in most of the lakes, also in those with low water chemistry values. The occurrence of *R. ovata* individuals with paper-thin shells in one of the lakes is most likely an indication of low pH and soft water (ØKLAND & ØKLAND 1986). On the other hand, *M. glutinosa, Planorbis planorbis, V. piscinalis, B. tentaculata, Potamopyrgus antipodarum* and *T. fluviatilis* seem to prefer richer lakes. Some of the observed species probably represent chance individuals (CARLSSON 2000). Concerning *Stagnicola palustris*, the distribution across all clusters may be a consequence of the fact that it is a species complex with species adapted to both lower and higher water chemistry values. The distribution of *Physa fontinalis* is also unexpected as it occurs in almost all of the lakes in clusters A_3 and B, not in cluster A_2 and then in cluster A_1. Should the findings of *P. fontinalis* be regarded as two species, do the findings represent locally adapted subspecies or is the observed distribution just a random phenomenon reflecting the colonization history?

Prosobranch snails with a few exceptions (chance individuals) are found mainly in clusters A_3 and B while pulmonate snails can be found in all clusters. The percentage of prosobranchs increases from cluster A_1 to B. Prosobranchs do not occur in ponds and smaller lakes which dry up during summer or in lakes with poor oxygen conditions (LODGE et at. 1987). Also in Canada prosobranchs were lacking in small ponds though they were water-filled during summer (PIP 1986a). None of the lakes in my investigation falls into this category, however, and it is possible that biotic factors are involved. It is possible that prosobranchs are out-competed by pulmonates in lakes of clusters A_1 and A_2, where predation pressure is probably low, due to the absence or low abundance of fish predators. Where predators are abundant, prosobranchs with thick shells survive while pulmonates with thin shells are eaten (LODGE et al. 1987).

From the papers of BROWNE (1981) and PIP (1986a) it appears that the composition of snail communities may differ much between lakes which are located close to each other. This is not the case in the Åland lakes. Apart from the lakes of group A_1, there are some common species which are likely to be found in most lakes (Table 2). From evidence given above, it seems likely that the most prominent factor determining species composition is water chemistry and especially hardness and dissolved minerals.

The snails on the Åland Islands seem to have about the same calcium needs as British and Swedish snails, whereas snails in Norway and on the Finnish mainland seem to tolerate lower values (BOYCOTT 1936; HUBENDICK 1947; AHO 1978; ØKLAND 1990). This may seem contradictory, but similar observations have been made in Canada where the granitic bedrock of the Canadian Shield in the east meets the Ordovician dolomite in the west. In that area, species regarded as soft water species in the west, may behave as hard water species in the east and vice versa (MCKILLOP & HARRISON 1972; MCKILLOP 1984). The reason for this is unclear, but PIP (1985) suggests that regional adaptation to the poorer conditions in the shield region has taken place. GREENAWAY (1971) discusses the possibility that Scandinavian snails are genetically adapted to lower calcium concentrations.

From a reinvestigation of the lakes of HUBENDICK (1947) in the Småland highlands (NILSSON et al. 1998) it appears that most species common to the Åland Islands show adaptations to lower water chemistry values in southern Sweden. Exceptions from this are *R. ovata, G. albus, A. crista* and *A. lacustris* which are found at slightly lower pH- and/or hardness values in the Åland Islands. For many species the minimum values for hardness, conductivity and alkalinity on the Åland Islands are much higher. *M. glutinosa* and *P. planorbis*, for example, do not occur on the Åland Islands unless hardness values are about six times higher than minimum values in southern Sweden (NILSSON et al. 1998). BOYCOTT (1936) made a division in hard water and soft water species where the borderline between soft and hard water was a calcium concentration of about 20 mg $\cdot$ l^{-1}. According to this, all of the species regarded as hard water species by BOYCOTT (1936) may be so even in my investigation, although *L. stagnalis* and *B. tentaculata* are borderline cases. *V. piscinalis, V. cristata* and *Potamopyrgus antipodarum* were regarded as soft water species by BOYCOTT (1936), but at least the last two mentioned species seem to be hard water species. When clustering the species according to average hardness, 6 species are hard water species, 5 soft water species and 6 are intermediate (Fig. 3). The cluster emanating from the presence/absence of snails gives two groups of snails, where the upper group largely, but with some exceptions, coincides with the soft water species of BOYCOTT (1936), while the lower group is more mixed (Fig. 4). This in turn, may also be due to the fact that some of the species prefer larger lakes or to some unknown factors. Prosobranch snails are mainly found in the lower cluster, encompassing more demanding species. The fact that the snails of AHO (1966) do not form clearly distinguishable clusters may be due to their adaptation to the poor waters in the lakes of the Finnish mainland. Finnish lakes differ from those on the Åland Islands in being generally richer in humic substances, poorer in dissolved substances, e.g. calcium. Also, most Finnish lakes lie higher above the sea and are much older than the Åland lakes, thus offering the snails a long time for adaptation to the prevailing conditions.

However, data from AHO et al. (1981) give a somewhat different picture of the Finnish snail communities.

Why do some species in the Åland lakes require higher water chemical values than snails on the mainlands of Finland and Sweden? This may be a result of the colonization history of each species. The colonization of the Åland lakes has probably taken place gradually via islands in the archipelago (CARLSSON 2001a). This could easily be tested by modern DNA-techniques. It is unlikely that snails have travelled non-stop, for example on birds, from a lake on the Finnish mainland to a lake on the Åland Islands.

Unfortunately, no "Algengyttja"-lake was examined in this investigation. From scattered observations it seems that this type of lake is in such a far developed state of deterioration that the environment is hostile to snails. As this type of lake frequently dries up during summer, only a few species of pulmonates, e.g. *Stagnicola palustris* and *R. ovata* are likely to be found.

Conclusions

The Alandian lakes are classified on the basis of freshwater snail communities. Although the results may represent a snapshot picture from a limited geographical region, it is here suggested that the lakes of cluster A_1 should be named *Radix ovata/Armiger crista*-lakes, cluster A_2 mixed lakes, cluster A_3 *Bithynia*-lakes and cluster B *Valvata*-lakes. Lakes gradually shift from type B to type A_1 and change due to land uplift from low elevation to higher elevations. CEDERCREUTZ (1937) claimed that lakes go through a series of successional stages. *Anabaena*-lakes arise when deep inlets are cut off from the sea while *Chara*-lakes are formed from shallow bays. *Chara*-lakes as well as shallow parts of *Anabaena*-lakes develop into "Braunmoor"-lakes and further to "Weissmoor"-lakes. Inlets in poor environments develop into *Lobelia*-lakes and gradually turn into "Weissmoor"-lakes.

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