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Freshwater snail assemblages of semi-isolated brackish water bays on the Åland Islands, SW Finland

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The aim of the study was to relate the distribution of freshwater snails in 21 semi-isolated bays (within a salinity range of 0.7–7.4 practical salinity units, PSU) to environmental variables of the Åland Islands, SW Finland. Altogether 16 species of freshwater snails were found when the bays were investigated by hand-picking and a rod sieve. Of these, six or seven species may be regarded as almost ubiquitous. The salinity limiting most freshwater snails is approximately 4–5 PSU. The marine snail *Hydrobia ventrosa* was found in only two of the bays. The highest number of snail species occurred in bays with large catchment areas, especially where there were freshwater lakes in the local area. The number of species increased with decreasing salinity (Spearman's $\varrho = -0.513$). The maximum number of species was found in a bay with almost freshwater-like conditions, inferring that tolerance to higher salinities in some species is restricted.

Introduction

Around the coastal areas of the northern Baltic Sea, new lakes are continuously born as bays are cut off from the sea due to the land-uplift process (Lindholm 1996, Brunberg *et al*. 2002). The archipelagos of Finland and Sweden comprise a unique land-uplift area, with small lakes and lagoon-like bays of different age and a range of salinities (Munsterhjelm 2005). With a few exceptions (e.g. Bagge and Tulkki 1967, Munsterhjelm 1997, 2005), the bays have been little studied (Lindholm 1996). The few investigations which were made, mostly concern the vegetation of these bays (Munsterhjelm 1997, 2005 and references therein).

Because the bays are at different stages of isolation, some of them have almost the same salinity as the open sea, while others are less saline. The first stage of lake formation is the juvenile flad. A juvenile flad may have several contacts with the open sea, but as land uplift continues, it will gradually turn into an archipelago flad, usually with only one opening. In the last flad stage, the gloflad, the opening is shallow and often overgrown with reeds and other plants. When there is no longer any contact with the sea, the flad is called a glo (Munsterhjelm 1997, 2005). In order to maintain navigable channels, on the Åland Islands many gloes or gloflads have been reconnected to the sea by dredging. Some of the flads are too shallow and will never become gloes because of enhanced sedimentation (Munsterhjelm 1997). Similar conditions, with varying salinities, occur in tidal marshes and estuaries elsewhere (Rundle *et al*. 1998, Costil *et al*. 2001, Attrill and Rundle 2002). All these environments may be regarded as ecotones between freshwater

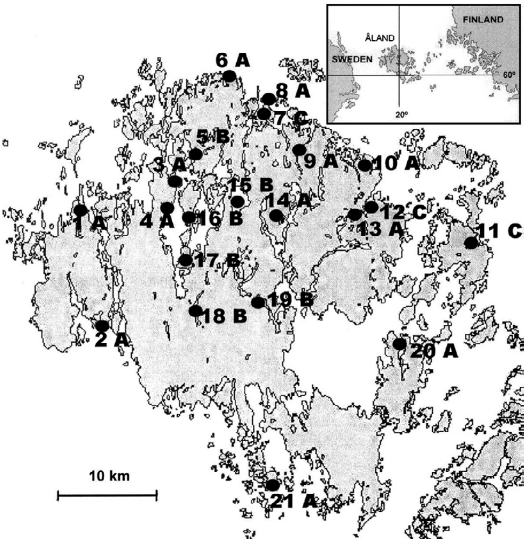

Fig. 1. Map of the Åland Islands. The locations of the investigated bays' areas are indicated by numbers 1–21. The accompanying letters refer to the clusters presented in Fig. 4.

and marine conditions. Some species of freshwater snails have been recorded at the Finnish and Swedish archipelagos, in places where the water is diluted with freshwater from adjacent land areas (Wallström *et al*. 2000).

Although most present species of freshwater snails are known from shell gravel deposits of the *Littorina* age from Sweden (Hubendick 1949) and some of them from Åland (Segerstråle 1927, Carlsson 2002), snails may later have colonised the lakes of the Alandian mainland via small lakes in the archipelago before they reached mainland Åland, where they first colonised semi-isolated bays (Carlsson 2001a). This transport is probably carried out by birds (e.g. Boag 1986) nesting on islands or resting in shallow lakes or bays on the islands. Another possibility might be transport on drifting logs, branches or plants. In this paper, I describe the gastropod species composition of bays in different stages of isolation and attempt to determine the upper level of salinity that limits the distributions of freshwater snails in the archipelago. My assumption is that the distribution of freshwater snails in the archipelago is limited by too high salinity.

Study area

The Åland Islands (approx. 60°N, 20°E) are located in the northern Baltic Sea, about halfway between the Swedish and Finnish mainlands (Fig. 1). The bedrock (rapakivi granite) has been subject to faulting. The fault lines, and depressions carved by the latest continental ice sheet, are now water-filled, forming some 120 lakes on mainland Åland. The archipelago between Åland and Finland consists of tens of thousands of islands and skerries, many of which have small lakes and rock pools (Lindholm 1996). In addition, in the whole area there is a large number of bays in various stages of isolation, which because of vertical post-glacial shoreline displacement, currently ca. 5 mm/year (Ekman 1996), will in the future turn into lakes. The bays investigated in this study have different degrees of exposure. Some are linked to or close to the sea, while others have more interior positions (Fig. 1). Many of them are in the gloflad stage. Only three of the bays (Mönsviksfladan (8), Lillsundet (2) and Gloet (10)) are in a natural stage. The inlets of the other bays have been dredged and are connected to the sea by ditches of varying lengths. One of the bays, Vargsundet (18), was isolated at the beginning of the last century but in the 1930s a ditch was dug and the salinity of the surface water is now about 1 PSU or lower. However, because of influxes of saline water, a halocline has formed at a depth of about 10–15 m. Below the halocline, the salinity is 3–4 PSU, i.e. the same as most of the waters of the innermost archipelago. The salinity of the water in the Åland archipelago is 6–7 PSU (Lindholm and Öhman 1995). Some of the bays are deep while others are shallow. Some of the catchment areas are rather small with mostly pine forest heath on rocky ground. Others are large and include cultivated fields and farmlands.

Like the waters of the Baltic Sea, the waters of the Åland archipelago are not tidal. Despite this, there may be significant variations in water level. These are caused by wind-generated seiches and partly by differences in air pressure between the Baltic Sea and the North Sea, forcing saline water into the Baltic Sea and finally into the semi-isolated bays. Influxes of saline water into the Baltic Sea occurred frequently until the middle of the 1970s, but have been more irregular and rare during recent years (Nausch *et al*. 2003). Long term predictions, based on computer models, suggest that the salinity may in future be lower (e.g. Omstedt *et al*. 2000).

In shallow bays and in shallow areas of deeper bays, the bottom is covered by *Chara* spp., *Najas marina* and other plants characteristic of shallow bays (Wallström *et al*. 2000). In some of the outer bays, marine algae like *Monostroma* sp., *Enteromorpha* sp., *Chorda filum* and *Fucus vesiculosus* occur. Most of the bays are fringed by reed, *Phragmites australis*, which in some bays may be the dominant vegetation.

Marine and brackish water animal species, e.g. *Macoma balthica*, *Mytilus edulis*, *Cerastoderma glaucum*, *Mya arenaria*, *Balanus improvisus*, *Gammarus* spp. and *Membranipora crustulenta* occur in some of the more exposed bays, while inner bays have a more freshwater-like species composition with species of e.g. Hirudinea, *Anodonta* sp., Odonata, Ephemeroptera, Trichoptera and Coleoptera.

Material and methods

The objective of the sampling was to obtain presence/absence data for different freshwater snail species and to study their distribution in relation to salinity and other environmental variables. I visited each of the 21 bays repeatedly — 4–10 times depending on the size and complexity of the bays — from June to September in 1999–2003 until I could find no further species. I collected snails in the littoral zone of the bays, by hand-picking from stones, branches and other firm substrata. In addition, I used a rod sieve (household sieve, mesh size ~ 1.5 mm) to catch snails in the vegetation and the soft sediments of the bays. On each visit, sampling lasted for about 0.5–1 h. I used a magnifying glass in order to detect the smallest (< 2 mm) snails. *Galba truncatula* was not included in the investigation since it is not a true aquatic species, but is amphibious (Boycott 1936, Macan 1977). Here I treat the two lymnaeid species complexes, formerly called *Lymnaea peregra* and *Lymnaea palustris* (*see* e.g. Hubendick 1949, Macan, 1977) as two taxa, *Radix* spp. and *Stagnicola palustris*, respectively (Glöer and Meier-Brook 1998, Jackiewicz and von Proschwitz 1991). Because it was necessary to use internal examination of the genitalia to distinguish *R. auricularia* from *R. ovata*, these two species were not separated and were therefore recorded as *Radix* spp.

I took water samples from the shores at a depth of 20 cm in all of the bays, after a long, dry period, representing maximum values of salinity. I recorded conductivity (μS) with a Metrohm 660 conductometer (Herisau, Switzerland) corrected for 25 °C, and transformed the values to salinity according to the formula PSU = 0.6701 μS – 0.3723, derived from Lewis (1980) and adapted to local conditions. I measured pH with a Metrohm 691 pH meter (Herisau, Switzerland).

Areas of bays and their catchments were obtained from digital maps using GIS (ArcView). I assessed distances from the mouths of the bays via the inlets, to the open (~1 km from nearest land on mainland Åland) sea on a Map Source (Garmin) digital map.

Presence or absence of each snail species in each of the bays was designated as 1 or 0, respectively, and compared using cluster analysis (group average method based on the Bray-Curtis similarity index) and non-parametric multidimensional scaling (nMDS) procedures in PRIMER 5.2.2. for Windows® (Plymouth Marine Laboratory; Clarke 1993). The SYSTAT 11 programme was used for general statistical analyses. The Kolmogorov-Smirnov test of normality indicated that neither snails nor environmental variables showed a normal distribution. Thus I calculated Spearman rank correlations between the different parameters and numbers of snail species. A BIO-ENV analysis was run in order to match the snail distribution patterns to environmental variables.

I calculated equations of species–area relationship (SAR), $S = C \times A^z$ (MacArthur and Wilson 1967), in order to find out if there were any area effects on the number of snail species. In the formula, S is the number of species, C is a constant, denoting the y intercept giving the number of species in one unit of area (Jok-

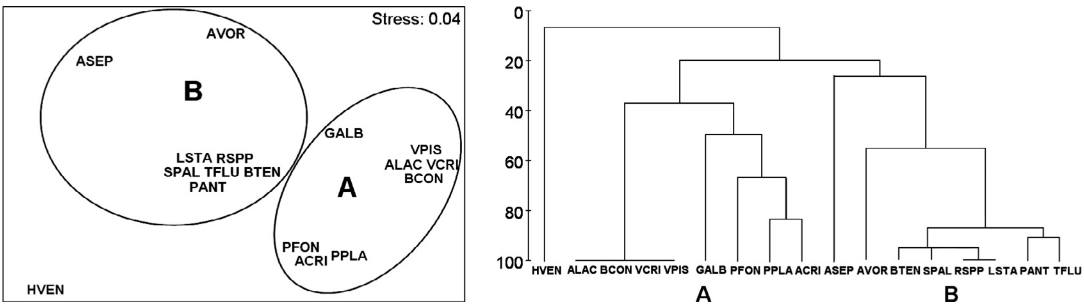

Fig. 2. nMDS and cluster diagram (Bray-Curtis similarity) on snails based on presence/absence in the studied bays. Name codes according to first letter of generic name and three first letters of species name; LSTA = *Lymnaea stagnalis,* RSPP = *Radix* spp., SPAL = *Stagnicola palustris,* PFON = *Physa fontinalis*, PPLA = *Planorbis planorbis*, AVOR = *Anisus vortex*, ASEP = *A. septemgyratus*, GALB = *Gyraulus albus*, ACRI = *Armiger crista*, BCON = *Bathyomphalus contortus*, ALAC = *Acroloxus lacustris*, VCRI = *Valvata cristata*, VPIS = *V. piscinalis*, BTEN = *Bithynia tentaculata*, HVEN = *Hydrobia ventrosa*, PANT = *Potamopyrgus antipodarum*, TFLU = *Theodoxus fluviatilis.*

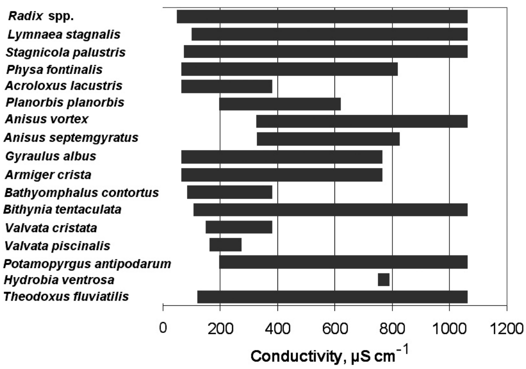

Fig. 3. Salinity ranges for the different gastropod species according to this investigation (highest values) and Carlsson (2001b; lowest values). A conductivity of about 350 µS cm^{-1} corresponds to a salinity of 2 PSU.

inen 1987), z is the slope of the species–area regression line and is theoretically about 0.25 (MacArthur and Wilson 1967).

Results

Altogether 17 species of snails appeared in my samples (Table 1). *Lymnaea stagnalis* and *Radix* spp. were found in all bays. *Stagnicola palustris*, *Bithynia tentaculata*, *Potamopyrgus antipodarum* and *Theodoxus fluviatilis* were almost as common. When I clustered snails (Fig. 2) these six species formed a group which was found in most of the bays (cf. Table 1). Two other species, associated with this group within 25% Bray-Curtis similarity, *Anisus vortex* and *Anisus septemgyratus*, were found in nine and three of the bays, respectively. *Anisus septemgyratus* is possibly a new record for brackish water in the Åland Islands. I found the marine snail *Hydrobia ventrosa* in only two bays. Of the remaining species, I found *Valvata cristata*, *V. piscinalis*, *Acroloxus lacustris* and *Bathyomphalus contortus* only in the most dilute, almost freshwater-like bay, Vargsundet (Table 2). The rest, i.e. *Physa fontinalis*, *Planorbis planorbis*, *Gyraulus albus* and *Armiger crista* were found with scattered occurrences in intermediate salinities (Table 3). It appears that cluster B of the snail cluster (Fig. 2) consists of species which are well adapted to a life in brackish water, while the snails of group A seem to prefer less saline water. *Myxas glutinosa*, *Hippeutis complanatus* and *Valvata macrostoma*, which I have previously found in freshwater lakes (Carlsson 2001a, 2001b), were not found in this survey.

The distribution of the different species in relation to salinity (conductivity) is given in Fig. 3, where the low conductivity (summer) values are from Carlsson (2001b).

The properties of the bays and their catchment areas are diverse (Table 2). When I clustered the bays according to presence/absence of snails, they formed three bigger groups; I, II and III at 77% Bray-Curtis similarity (Fig. 4). Two of the bays, the freshwater-like Vargsundet (18) and the very small and deep Gröndalsviken (6), were isolated from these three groups. Group I of the cluster contains four bays which are small

Table 1. Bays and their snail species. + = present, − = absent. Species: 1 = *Radix* spp., 2 = *Lymnaea stagnalis*, 3 = *Stagnicola palustris*, 4 = *Physa fontinalis*, 5 = *Acroloxus lacustris*, 6 = *Planorbis planorbis*, 7 = *Anisus vortex*, 8 = *Anisus septemgyratus*, 9 = *Gyraulus albus*, 10 = *Armiger crista*, 11 = *Bathyomphalus contortus*, 12 = *Bithynia tentaculata*, 13 = *Valvata cristata*, 14 = *Valvata piscinalis*, 15 = *Potamopyrgus antipodarum*, 16 = *Theodoxus fluviatilis*, 17 = *Hydrobia ventrosa*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Kråkskärsfjärden	+	+	+	−	−	−	−	−	−	+	−	+	−	−	+	+	−
2. Lillsundet	+	+	+	−	−	−	−	−	−	−	−	+	−	−	+	+	+
3. Norrviken	+	+	+	−	−	−	−	+	−	−	−	+	−	−	+	+	−
4. Korrvik	+	+	+	−	−	−	+	+	+	−	−	+	−	−	+	+	−
5. Ramsvik	+	+	+	+	−	−	+	−	+	+	−	+	−	−	+	+	−
6. Gröndal	+	+	−	−	−	−	+	−	−	−	−	−	−	−	+	+	−
7. Mönsviksfladan	+	+	+	−	−	−	+	−	−	−	−	+	−	−	−	+	−
8. Nordanmellan	+	+	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−
9. Inre Verkviken	+	+	−	−	−	−	−	−	−	−	−	+	−	−	+	+	+
10. Gloet, Saltvik	+	+	+	−	−	−	+	−	−	−	−	+	−	−	+	+	−
11. Lövösundet	+	+	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−
12. Hästholms sund	+	+	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−
13. Inre viken	+	+	+	−	−	−	+	−	−	−	−	+	−	−	+	+	−
14. Tällviken	+	+	+	−	−	−	−	+	−	−	−	+	−	−	+	+	−
15. Vandöfjärden	+	+	+	+	−	+	−	−	−	+	−	+	−	−	+	+	−
16. Gloet, Finström	+	+	+	+	−	−	−	−	−	−	−	+	−	−	+	+	−
17. Holmsjön	+	+	+	+	−	−	−	−	+	+	−	+	−	−	−	+	−
18. Vargsundet	+	+	+	+	+	+	−	−	+	+	+	+	+	+	+	+	−
19. Ämnäsviken	+	+	+	+	−	+	−	−	−	+	−	+	−	−	+	+	−
20. Bölsvik	+	+	+	−	−	−	+	−	−	−	−	+	−	−	+	−	−
21. Söderfjärden	+	+	+	−	−	−	+	−	−	−	−	+	−	−	+	+	−

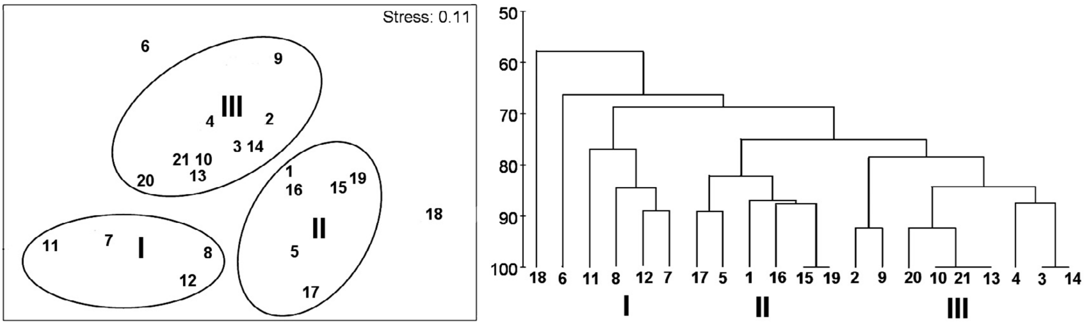

Fig. 4. nMDS and cluster diagram (Bray-Curtis similarity) of the investigated bays based on the presence/absence of snails.

and shallow. The Holmsjön-Ämnäsviken (group II) bays are mainly located in more interior positions of the Åland mainland and the remaining group (group III) is composed of a mix of bays with varying properties. The bays of group II have lower salinity than those of group III. The means ± S.D. of the clusters imply a large variation in environmental conditions (Table 4).

In pair-wise correlation analyses I obtained the highest correlation between number of species and depth of the bay, followed by salinity and area of catchment. Also, there was a negative but non-significant correlation between catchment area and salinity (Table 5). The BIO-ENV analysis shows that pH and depth are the variables determining species composition most, with a correlation value of 0.203 (Spearman's ϱ), followed by salinity, pH and depth (0.179). The fifth important variable is area of catchment.

When applying the equation of species–area relationship (SAR), $S = C \times A^z$ to examine area effects on the number of snail species, I obtained

Table 2. Some characteristics of the investigated bays. The depths marked with an asterisk are assessments based on general topography of the area.

	Distance to the sea (km)	Area (ha)	Catchment (ha)	Salinity (‰)	pH	Depth (m)	Number of snail species
1. Kråkskärsfjärden	6	25	727	3.1	9.73	2*	7
2. Lillsundet	2	4	37	5.38	9.26	3*	7
3. Norrviken	10	8.5	66.5	5.73	8.83	4	7
4. Korrvik	15	8.5	60	2.09	8.79	4.5	9
5. Ramsvik	12	12	1544	4.71	8.83	4*	10
6. Gröndal	1	0.2	19.4	5.26	8.72	4*	5
7. Mönsviksfladan	2	30	120	5.28	9.52	2.8	5
8. Nordanmellan	2	3.5	40.5	5.28	9.47	1	5
9. Inre Verkviken	8	50	500	5.16	9.28	17	6
10. Gloet, Saltvik	6	38	164	5.49	9.10	3	7
11. Lövösundet	15	29	529	5.82	9.35	0.8	4
12. Hästholms sund	1	4	29	4.02	7.49	1	4
13. Inre viken	13	14	212	6.03	8.10	8	7
14.Tällviken	38	38	385	4.87	8.71	4	7
15. Vandöfjärden	16	651	2413	3.83	8.27	8	9
16. Gloet, Finström	16	7	50	5.29	8.87	3	7
17. Holmsjön	19	6	50	3.41	8.46	4.5	8
18. Vargsundet	19	129	2491	0.7	8.52	30	14
19. Ämnäsviken	35	60	3640	2.41	7.60	2	9
20. Bölsvik	34	5	74	6.66	9.64	3*	6
21. Söderfjärden	2	5	52	7.39	9.53	1.5*	7

Table 3. Average ± S.D. for the investigated variables and snail species (range in parentheses). Some species were found only in one bay and thus no variation measures are given for these species.

	Distance to open sea (km)	Area (ha)	Catchment, (ha)	Salinity (PSU)	pH	Number of snail species	Depth of bay (m)
CLUSTER A							
P. fontinalis	20 ± 8 (12–35)	144 ± 253 (6–651)	1698 ± 1440 (50–3640)	3.4 ± 1.7 (0.7–5.3)	8.4 ± 0.5 (7.6–8.9)	9.5 ± 2.4 (7–14)	9 ± 11 (2–30)
A. lacustris	19	129	2491	0.7	8.5	14	30
P. planorbis	23 ± 10 (16–35)	280 ± 323 (60–651)	2848 ± 687 (2413–3640)	2.3 ± 1.6 (0.7–3.8)	8.1 ± 0.5 (7.6–8.5)	10.7 ± 2.9 (9–14)	13 ± 8 (2–30)
A. septemgyratus	21 ± 15 (10–38)	18 ± 17 (9–38)	171 ± 186 (60–385)	4.2 ± 1.9 (2.1–5.7)	8.8 ± 0.1 (8.7–8.8)	7.7 ± 1.2 (7–8)	4 ± 0 (4–5)
G. albus	16 ± 4 (12–19)	39 ± 60 (6–129)	1036 ± 1197 (50–2491)	2.7 ± 1.7 (0.7–4.7)	8.7 ± 0.2 (8.5–8.8)	10.3 ± 2.6 (8–14)	11 ±13 (4–30)
A. crista	18 ± 10 (6–35)	147 ± 251 (6–651)	1811 ± 1305 (50–3640)	3.0 ± 1.4 (0.7–4.7)	8.6 ± 0.7 (7.6–9.7)	9.5 ± 2.4 (7–14)	8 ± 11 (2–30)
B. contortus	25	129	2491	0.7	8.5	14	30
V. cristata	25	129	2491	0.7	8.5	14	30
V. piscinalis	25	129	2491	0.7	8.5	14	30
H. ventrosa	5 ± 4 (2–8)	27 ± 33 (4–50)	269 ± 327 (37–500)	5.3 ± 0.2 (5.2–5.4)	9.3 ± 0 (9.3)	6.5 ± 0.7 (6–7)	10 ± 10 (3–17)
CLUSTER B							
Radix spp.	13 ± 11 (1–38)	53 ± 140 (0.2–651)	629 ± 1017 (19–3640)	4.7 ± 1.6 (0.7–7.4)	8.9 ± 0.6 (7.5–9.7)	7 ± 2.3 (4–14)	5 ± 7 (1–30)
L. stagnalis	13 ± 11 (1–38)	53 ± 140 (0.2–651)	629 ± 1017 (19–3640)	4.7 ± 1.6 (0.7–7.4)	8.9 ± 0.6 (7.5–9.7)	7 ± 2.3 (4–14)	5 ± 7 (1–30)
S. palustris	14 ± 11 (2–38)	53 ± 144 (1–651)	668 ± 1061 (29–3640)	4.6 ± 1.7 (0.7–7.4)	8.8 ± 0.7 (7.5–9.7)	7 ± 2.3 (4–14)	5 ± 6 (1–30)
A. vortex	8 ± 6 (1–15)	15 ± 11 (0.2–30)	307 ± 489 (19–1544)	5.3 ± 1.4 (2.1–7.4)	9.0 ± 0.5 (8.1–9.5)	6.8 ± 1.9 (4–10)	4 ± 2 (1–8)
B. tentaculata	14 ± 11 (2–38)	57 ± 147 (4–651)	666 ± 1061) (29–3640)	4.6 ± 1.7 (0.7–7.4)	8.8 ± 0.7 (7.5–9.7)	7.4 ± 2.2 (4–14)	6 ±7 (1–30)
P. antipodarum	15 ± 12 (1–38)	65 ± 160 (0.2–651)	777 ± 1126 (19–3640)	4.6 ± 1.8 (0.7–7.4)	8.9 ± 0.6 (7.6–9.7)	7.7 ± 2.1 (5–14)	6 ± 7 (2–30)
T. fluviatilis	11 ± 13 (1–38)	62 ± 155 (0.2–651)	732 ± 1106 (19–3640)	4.5 ± 1.7 (0.7–7.4)	8.8 ± 0.5 (7.6–9.7)	7.7 ± 2.1 (5–14)	6 ± 7 (2–30)

Table 4. Average ± S.D. (range in parentheses) for the investigated variables of the different clusters in Fig. 4.

	Distance to open sea (km)	Area (ha)	Catchment, (ha)	Salinity (PSU)	pH	Species number	Depth (m)
Cluster I (*n* = 4)	8 ± 7 (2–15)	17 ± 15 (4–30)	180 ± 236 (29–529)	5.1 ± 0.8 (4.0–5.8)	9.0 ± 1.0 (7.5–9.5)	4.5 ± 0.6 (4–5)	1.7 ± 0.9 (0.8–2.8)
Cluster II (*n* = 6)	17 ± 10 (6–35)	127 ± 258 (6–651)	1404 ±1426 (50–3640)	3.8 ± 1.1 (2.4–5.3)	8.6 ± 0.7 (7.6–9.7)	8.3 ± 1.2 (7–10)	3.9 ± 2.2 (1.5–17)
Cluster III (*n* = 9)	14 ± 13 (2–38)	17 ± 17 (4–50)	172 ± 166 (37–500)	5.4 ± 1.5 (2.1–7.4)	9.0 ± 0.5 (8.1–9.6)	7.0 ± 0.9 (6–9)	5.3 ± 4.7 (2–17)

the formula $S = 5.49A^{0.084}$ ($P = 0.039$, $r^2 = 0.206$). When I applied the SAR equation only to the species of group A (Fig. 2) I obtained the following formula; $S = 1.51A^{0.164}$ ($P = 0.025$, $r^2 = 0.238$). A corresponding treatment of group B gives the same result as for the total number of species. The corresponding equations for the species–catchment area relationships are $S = 4.05A^{0.101}$ ($P = 0.011$, $r^2 = 0.296$) and $S + 1 = 0.668A^{0.217}$ ($P = 0.002$, $r^2 = 0.415$), respectively.

Discussion

A salinity of about 4–5 PSU seems to be a threshold value, above which true freshwater species are not found, except for some species adapted to higher salinities (Macan 1977). This is also in agreement with Cognetti and Maltagliati (2000) who suggested that there is a drop in species number in the salinity range 5–8 PSU. At a salinity of about 2 PSU there is a dramatic shift in the ionic relations between Ca^{++}/Na^{+} and K^{+}/Na^{+} (Cognetti and Maltagliati 2000). The six species — *L. stagnalis*, *R. ovata*, *S. palustris*, *B. tentaculata*, *P. antipodarum* and *T. fluviatilis* — are found also at high salinities in the waters of the archipelago. For example *S. palustris* can be found up to 6–7 PSU (Cognetti and Maltagliati 2000) and *R. ovata* 10–11 PSU (Skoog 1978) though it is also known as a generalist, doing well even at low salinities (Hubendick 1949, Skoog 1973). *P. antipodarum* and *T. fluviatilis* seem to be better adapted to brackish water than the others (Carlsson 2000) and according to Skoog (1978) *T. fluviatilis* may be found up to 18 PSU in the southern parts of the Baltic Sea. Jacobsen and Forbes (1997) showed that the optimal salinity of *P. antipodarum* is 5 PSU, a salinity common in the semi-isolated bays, but it also propagates at lower and higher salinities. Helminen (1975) found four of the above mentioned species in his investigation of the benthos of the Alandian archipelago, if *P. antipodarum* is included in his "*Hydrobia* spp". He did not find *L. stagnalis* and *S. palustris* but on the other hand, *Gyraulus* sp., *Planorbis* sp. (= *P. planorbis*) and *Physa fontinalis* were found in some of the innermost bays.

The findings of *A. septemgyratus* from brackish water may possibly be regarded as a parallel of *A. vortex* (L.), which was for several years only noted from brackish water bays, as noted by Luther (1901) and Carlsson (2001a). The first observation of *A. vortex* in an isolated water body on the Åland Islands was in June 2003, when it was found in a large (0.17 ha) rock pool, about 2 m above sea level some 20 m from the sea shore of northern Geta (R. Carlsson unpubl. data). Bagge and Tulkki (1967) found *A. vortex* in both pure archipelago waters and in a lake with low salinity.

It has often been said (*see* e.g. Glöer and Meier-Brook 1998) that *T. fluviatilis* comprises two different species, adapted to fresh and brackish water. However, Zettler *et al*. (2004) recently investigated populations from both types of environments and found no morphological differences, other than that individuals from freshwater were, on average, a little larger than those from brackish waters. There are no genetic differences between fresh and brackish water individuals. In fact, all *T. fluviatilis* of northern Europe seem to be closely related, as a result of post-Pleistocene range expansion (Bunje 2005). *T. fluviatilis* populations from the Åland Islands include two haplotypes which are closely related to some populations in northern Germany and eastern Sweden. However, they are all morphologically similar and there is no apparent difference between populations from different habitats (Bunje 2005).

It is possible that *H. ventrosa* is present in more of the outer bays, as it often lives in sand and gravel and other soft sediments (Hylleberg 1978) and may have been missed. It could possibly be found with a bottom grab or a core sampler in more of the investigated bays. The same may apply for *Peringia ulvae* (Pennant), which was not found in any of the studied bays, but which has been found in many other semi-isolated bays in the area (Wallström *et al*. 2000). On the other hand, Hylleberg (1978) noted that *Potamopyrgus antipodarum* is the only small hydrobiid present in the most freshwater bay systems.

It is difficult to draw any further conclusions from the bay clusters (Fig. 4), although cluster I seems to differ from cluster II and III in number of species and depth. The four bays forming cluster I are shallow and/or have rather soft bottoms, making them unsuitable for *T. fluviatilis*. This conclusion is supported by the fact that just outside the recently dredged inlet of the shallow but rocky bay Nordanmellan (8), *T. fluviatilis* was found on the rocky shore. It is possible that these shallow bays will never become lakes but will instead turn to swamps or shore meadows as land uplift continues.

The innermost bays (Ramsvik, Holmsjön, Vandöfjärden, Ämnäsviken, Gloet (Finström) and Vargsundet) have low salinities and form a group (II) with a higher number of species, within the bay cluster (Fig. 4). This group of bays have, on average, a longer distance to the open sea, and larger catchments than those of the other clusters. The rather high number of species in Ramsvik (5) is not surprising, as the bay forms the outlet of a species rich lake system with a large drainage area, as well as being in the innermost location of a bay system. Ämnäsviken (19) is a similar bay, where a big lake system has its outlet and would for that reason be expected to contain many species. Despite this, I found only

Table 5. Spearman's rank correlations ($n = 21$) between the investigated variables. P values in parentheses.

	Distance to open sea	Area	Catchment	Salinity	pH	Depth	Species number
Distance to open sea	1						
Area	0.462 (0.035)	1					
Catchment	0.476 (0.029)	0.901 (0.000)	1				
Salinity	–0.331 (0.143)	–0.376 (0.093)	–0.326 (0.149)	1			
pH	–0.461 (0.036)	–0.185 (0.422)	–0.094 (0.687)	0.468 (0.032)	1		
Depth	0. 300 (0.187)	0.355 (0.115)	0.256 (0.263)	–0.315 (0.165)	–0.417 (0.060)	1	
Species number	0.461 (0.035)	0.412 (0.063)	0.496 (0.022)	–0.513 (0.017)	–0.383 (0.086)	0.557 (0.009)	1

nine species here, possibly because the bay is highly eutrophic, with algal blooms and a resulting oxygen deficiency in late summer.

Vargsundet (18) is an outlier which is more freshwater-like than the other bays and its conductivity/salinity values above the halocline are comparable to, or even lower than, those of many Alandian lakes (Carlsson 2001b).

The result of the BIO-ENV analysis should be interpreted with caution. For example, pH fluctuates strongly and some of the depth data are based on assessments. The low correlation may result from the use of presence/absence data and use of abundance data would probably have ended up with other results.

The high correlation between species number and depth of the bays (Table 5) should also be taken with some caution. It is possible, however, that many snail taxa prefer deeper water and larger water bodies (Carlsson 2001b), while the most shallow bays are in a stage where they become even shallower due to sedimentation (Munsterhjelm 2005). The correlation between species number and both salinity and catchment area is not surprising, however, as this concerns freshwater snails that are poorly adapted to saline conditions. It may reflect an indirect species-area relationship (Carlsson 2001a and references therein). The bays and their catchments may be regarded as freshwater islands in an infinitely large sea, since the open inlets are connected to the Baltic and the Atlantic, and the freshwater snails are trapped in the diluted bays. Species with a limnic origin have, with few exceptions, a lower adaptability range and are restricted to areas close to freshwater inputs (Cognetti and Maltagliati 2000). The high value of C and the low value of z in the SAR equation imply a high frequency of dispersal between islands with saturated snail communities. Corresponding values, obtained by Aho (1978), Brönmark (1985), Carlsson (2001a), Jokinen (1987) and Lassen (1975), range between about 0.114–0.370. This is not surprising, since in most of the bays all the species of group B of the snail cluster (Fig. 2) are found. For the rest of the snails, i.e. those of group A (Fig. 2), the sea surrounding the bays is a true obstacle to dispersal and accordingly the z value of these species is higher. The correlation between species number and catchment area would possibly be even higher if the inlets of the bays were of equal size, thereby permitting influxes of saline water. Also, one must take into consideration the effect of winds and degree of exposure. Theoretically, a sheltered bay with a large catchment, i.e. a high surface runoff with freshwater, and a small inlet would have the most diluted water and the highest number of freshwater snail species.

The notion of a lower salinity in the future should be taken with some caution, as it is based on simple computer models. Long term studies indicated that salinity changes are common on a time scale of several decades and that the salinity showed no trend during the last century (Winsor *et al*. 2001).

From the discussion above I draw the conclusion that my assumption, that the distribution of freshwater snails in the archipelago is limited by too high salinity, is supported by this investigation.

Comparing my results with those of Costil *et al*. (2001) from a tidal area, nine species are common to both areas. The values of maximum salinity tolerance differ, however. This may be taken as an indication that populations of different geographic areas have local adaptations (Cognetti and Maltagliati 2000). A similar phenomenon was reported by Aho (1966), who noted that Finnish freshwater snails tolerate lower hardness values than snails in Britain and Sweden, where hardness levels are often higher than in the Finnish lakes. Most of the species encountered in this study were found at salinities above 5 PSU and this is in agreement with Bagge and Tulkki (1967) who found several freshwater species in the water of the archipelago between the Åland Islands and the Finnish mainland.

Another factor, which I have not investigated, is the habitat structure of the bays. The general rule is that a larger and deeper bay may offer more habitats than a smaller and shallower one. Some of the smaller bays are also shallow, with soft bottoms, and the shores are dominated by reeds. These contrast with the larger bays which are more freshwater-like with a high habitat complexity.

Finally, since this is an uplift area which is also affected by increasing human activities, there may be a large element of chance concerning which snails that may be found. Some snails may be able to survive in a locality, but have just not arrived there yet. An example of this is the distribution of *S. palustris*, which is mostly confined to the area of the interior bays, where it is also found in most of the lakes, contrary to the absence of the species in, for example, the north-eastern marginal areas (Carlsson 2001b). Also, the lakes most rich in snails seem to be located in areas affected by cultivation and grazing cattle (Carlsson 2001b), an observation which may also apply to bays. The lack of clarity might be because this is a particularly dynamic ecological situation.

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References

Aho J. 1966. Ecological basis of the distribution of the littoral freshwater molluscs in the vicinity of Tampere, South Finland. *Ann. Zool. Fennici* 3: 287–322.

Aho J. 1978. Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland. *Ann. Zool. Fennici* 15: 146–154.

Attrill M.J. & Rundle S.D. 2002. Ecotone or ecocline: Ecological boundaries in estuaries. *Estuar. Coast. Shelf Sci.* 55: 929–936.

Bagge P. & Tulkki P. 1967. Studies of the hydrography and biota of recently isolated lakes. *Merentutkimuslait. Julk./Havforskningsinst. Skr.* 223: 13–33.

Boag D.A. 1986. Dispersal in pond snails: potential role of waterfowl. *Can. J. Zool.* 64: 904–909.

Boycott A.E. 1936. The habitats of fresh-water Mollusca in Britain. *J. Anim. Ecol.* 5: 116–186.

Brönmark C. 1985. Freshwater snail diversity: effects of pond area, habitat heterogeneity and isolation. *Oecologia (Berlin)* 67: 127–131.

Brunberg A., Nilsson E. & Blomqvist P. 2002. Characteristics of oligotrophic hardwater lakes in a postglacial land-rise area in mid-Sweden. *Freshwater Biology* 47: 1451–1462.

Bunje P.M.E. 2005. Pan-European phylogeography of the aquatic snail *Theodoxus fluviatilis* (Gastropoda: Neritidae). *Molecular Ecology* 14: 4323–4340.

Carlsson R. 2000. The distribution of the gastropods *Theodoxus fluviatilis* (L.) and *Potamopyrgus antipodarum* (Gray) in lakes on the Åland Islands, southwestern Finland. *Boreal Env. Res.* 5: 187–195.

Carlsson R. 2001a. Species-area relationships, water chemistry and species turnover of freshwater snails on the Åland Islands, southwestern Finland. *J. Moll. Stud.* 67: 17–26.

Carlsson R. 2001b. Freshwater snail communities and lake classification. An example from the Åland Islands, southwestern Finland. *Limnologica* 31: 129–138.

Carlsson R. 2002. Shell gravel deposits on the Åland Islands, southwestern Finland, with special reference to the molluscan assemblages. *Boreas* 31: 203–211.

Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Austr. J. Ecol.* 18: 117–143.

Cognetti G. & Maltagliati F. 2000. Biodiversity and adaptive mechanisms in brackish water fauna. *Mar. Poll. Bull.* 40: 7–14.

Costil K., Dussart G.B.J. & Daguzan J. 2001. Biodiversity of aquatic gastropods in the Mont St-Michel basin (France) in relation to salinity and drying of habitats. *Biodiversity and Conservation* 10: 1–18.

Ekman M. 1996. A consistent map of the postglacial uplift of Fennoscandia. *Terra Nova* 8: 158–165.

Glöer P. & Meier-Brook C. 1998. *Süsswassermollusken. Ein Bestimmungsschlüssel für die Bundesrepublik Deutschland*, 12th ed. Deutscher Jugendbund für Naturbeobachtung.

Helminen O. 1975. Bottenfaunan i den åländska skärgården. [Bottom fauna in the Åland archipelago]. *Husö biol. stat. Medd.* 17: 43–71. [In Swedish with English summary].

Hubendick B. 1949. *Våra snäckor. Snäckor i sött och bräckt vatten*. Bonniers bokförlag, Stockholm.

Hylleberg J. 1978. Tusensnäckor på Åland II: Storlek och utbredning som ett mått på mellanartskonkurrens. [Mud snails on Åland II: A study of potential competition in terms of snail sizes and spatial segregation.] *Husö biol. stat. Medd.* 20: 32–49. [In Swedish with English summary].

Jackiewicz M. & von Proscwitz T. 1991. *Stagnicola (Stagnicola) occulta* (JACK.), *Lymnaea (Stagnicola) vulnerata* KÜST und *Lymnaea (Lymnaea) corvus* (GMEL.) — drei für Schweden neue Schlammschneckenarten (Gastropoda: Basommatophora: Lymnaeidae). *Malakol. Abh. Staatl. Mus. für Tierkunde Dresden* 15: 125–132.

Jacobsen R. & Forbes V. 1997. Clonal variation in life-history traits and feeding rates in the gastropod *Potamopyrgus antipodarum*: performance across a salinity gradient. *Functional Ecology* 11: 260–267.

Jokinen E.H. 1987. Structure of freshwater snail communities: species-area relationships and incidence categories. *Amer. Malacol. Bull.* 5: 9–19.

Lassen H.H. 1975. The diversity of freshwater snails in view of the equilibrium theory of island biogeography. *Oecologia* 19: 1–8.

Lewis E.L. 1980. The practical salinity scale 1978 and its antecedents. *IEEE, J. Ocean. Eng.* 5: 3–8.

Lindholm T. 1996. A survey of small lakes in the archipelago of NW Åland (SW Finland). *Mem. Soc. F.F.F.* 72: 31–36.

Lindholm T. & Öhman P. 1995. Occurrence of bloom-forming and potentially harmful phytoplankton in the Åland archipelago in the summer of 1993. *Memoranda S.F.F. F.* 71: 10–18.

Luther A. 1901. Bidrag till kännedomen om land- och sötvattengastropodernas utbredning i Finland. *Acta Soc. F.F.F.* 20: 1–125.

Macan T. T. 1977. *A key to British fresh- and brackish-water gastropods*, 4th ed. Freshwater Biological Association Scientific Publications 13.

MacArthur R.H. & Wilson E.O. 1967. *The theory of island biogeography.* Princeton University Press. Princeton N.J.

Munsterhjelm R. 1997. The aquatic vegetation of flads and gloes, S coast of Finland. *Acta Bot. Fennica* 157: 1–68.

Munsterhjelm R. 2005. Natural succession and human-induced changes in the soft-bottom macrovegetation of shallow brackish bays on the southern coast of Finland. *Walter and Andrée de Nottbeck Foundation Scientific Reports* 26: 1–53.

Nausch G., Matthäus W. & Feistel R. 2003. Hydrographical and hydrochemical conditions in the Gotland deep area between 2002 and 2003. *Oceanologia* 45: 557–569.

Omstedt A., Gustafsson B., Rodhe B. & Walin G. 2000. Use of Baltic Sea modelling to investigate the water and heat cycles in GCM and regional climate models. *Climate Research* 15: 95–108.

Rundle S.D., Attrill M.J. & Arshad A. 1998. Seasonality in macroinvertebrate community composition across a neglected ecological boundary, the freshwater-estuarine transition zone. *Aquatic Ecology* 32: 211–216.

Segerstråle S.G. 1927. Skalmärgelfyndigheterna i Finland. [Die der Litorinazeit entstammenden Schalenablagerungen i Finnland]. *Fennia* 47: 1–52. [In Swedish with German summary].

Skoog G. 1973. Salinity reactions of two fresh water snails from brackish water. *Oikos* (*Supplement*) 15: 253–260.

Skoog G. 1978. *Aspects on the biology and ecology of Theodoxus fluviatilis (L.) and Lymnaea peregra (O.F. Müller) (Gastropoda) in the northern Baltic*. Ph.D. dissertation, University of Stockholm.

Wallström K., Mattila J., Sandberg-Kilpi E., Appelgren K., Henricsson C., Liljekvist J., Munsterhjelm R., Odelström T., Ojala P., Persson J. & Schreiber H. 2000. Miljötillstånd i grunda havsvikar. Beskrivning av vikar i regionen. Uppland-Åland-sydvästra Finland samt utvärdering av inventeringsmetoder. *Upplandsstiftelsen, Naturvård & Friluftsliv* 18: 1–141.

Winsor P., Rodhe J. & Omstedt A. 2001. Baltic Sea ocean climate: an analysis of 100 yr of hydrographic data with focus on the freshwater budget. *Climate Research* 18: 5–15.

Zettler M.L., Frankowski J., Bochert R. & Röhner M. 2004. Morphological and ecological features of *Theodoxus fluviatilis* (Linnaeus, 1758) from Baltic brackish water and German freshwater populations. *Journal of Conchology* 38: 305–316.