

Long-term changes in distribution and frequency of aquatic vascular plants and charophytes in an estuary in the Baltic Sea

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The long-term impact of natural and human-induced large-scale changes on aquatic phanerogams and charophytes has remained mostly unstudied in the Baltic Sea, largely because of a lack of historical data. A vegetation data set based on transects in an estuary in the western part of the Gulf of Finland studied in the 1930s–1940s, however, exists. We re-surveyed 91 of these transects in 2005 and 2007. The historical data set included 60 species and the contemporary 52 species. The species were classified into increasing, decreasing or unchanged according to the change in their occurrence frequencies. A significant frequency change was found for 31 of the 50 (62%) species which were present in both surveys. The proportion of species/growth forms with high-nitrogen and low-light preferences increased, whereas that of species/growth forms preferring oligotrophic conditions and species of shallow waters decreased. In the area, the species expanded their distribution ranges mainly towards the open sea. Eutrophication, reduced grazing pressure and shore overgrowth by *Phragmites australis* are suggested as the main reasons for the observed changes. In addition, increased boating and shore-construction activities contributed to the long-term floristic changes.

Introduction

Decreasing distribution of species is a serious problem. As natural systems are hierarchically connected to each other (Levin 1992, Alahuhta *et*

al. 2011), finding reasons for changes in species distribution on a lower ecosystem level is challenging. For example, environmental conditions (especially salinity) within an archipelago or estuary reflect those of the Baltic Sea in general,

but also there is a set of conditions (e.g. eutrophication) generated within these formations. The aquatic-species composition and distribution in the northern Baltic Sea have changed over the decades (e.g. Kautsky *et al.* 1986, Lehtonen *et al.* 2009, Olli *et al.* 2011). Some of these changes are natural, caused mainly by gradual land uplift and long-term salinity fluctuations (Luther 1951a, Munsterhjelm 1997). Several studies suggest, however, that the most dramatic alterations have been caused by human activities, such as excessive nutrient runoff, leading to eutrophication (Eriksson *et al.* 1998, Vahteri *et al.* 2000), and mechanical alterations in the littoral environments by dredging, boating and building near shores (Eriksson *et al.* 2004, Vaalgamaa 2004, Munsterhjelm 2005). Additionally, introduction of exotic species (Packalén *et al.* 2008, Järv *et al.* 2011) and overfishing (Eriksson *et al.* 2009, Eriksson *et al.* 2011) have contributed to changes in community composition of the biota in the Baltic Sea.

Eutrophication causing increased turbidity and decreased light penetration, increased sedimentation, and sediment oxygen deficiency, has had documented effects on the composition of the species and distribution of different aquatic taxa on different trophic levels in the Baltic Sea (Bonsdorff *et al.* 1997, Elmgren 2001, Rönnerberg & Bonsdorff 2004). An eutrophication-related increase in opportunistic filamentous algae negatively affects both perennial brown algae and vascular plants (Kangas *et al.* 1982, Valiela *et al.* 1997). There are also recent records showing that the distribution of charophyte (Charophyta ssp.) species decreased in the Baltic Sea during the 20th century (Blindow 2000, Schubert & Blindow 2003, Munsterhjelm *et al.* 2008). These reductions and community changes in vegetation are potentially far reaching, as aquatic vegetation has an important ecosystem function, e.g. by serving as habitat and food resources for both aquatic and terrestrial species, reducing water turbidity and buffering against erosion and sediment transport (Costanza *et al.* 1997, Duarte 2002, Rosqvist *et al.* 2010, Hansen *et al.* 2011).

In the beginning of the 20th century, the impact of human activities on aquatic vegetation of the northern Baltic Sea was decisively smaller than at present. Eutrophication was first observed

mainly near point sources, like Ekenäs and Helsinki, from which untreated sewage waters were released into the sea (Häyrén 1944, Luther 1951a, Vaalgamaa 2004). Eutrophication has reached its present levels in the Baltic Sea during the last 50 years, and affects both the open sea and coastal areas (Elmgren 2001, Rönnerberg & Bonsdorff 2004, Savage *et al.* 2010). The effects of local nutrient loading are amplified in complex archipelago landscapes (Cederwall & Elmgren 1990). Near-shore building and dredging were more delimited especially in the archipelago area in the early decades of the 20th century than at present (Luther 1951a). Also agriculture has changed by, for instance, cessation of cattle grazing on the shores affecting the distribution of plant species (Pykälä & Bonn 2000).

Historical data provide a baseline for determining long-term changes in species composition and help address questions regarding changes in community, species decline or even species loss. Although there is ample evidence of large-scale changes in the Baltic Sea ecosystem, a long-term distribution study on vascular plants and charophytes over a wide geographical area is lacking. This is partly explained by the absence of reliable historical baseline information about the former status of the aquatic vegetation. Also methodological changes concerning the survey practices contribute to the problem in relating past and present survey data (Tingley & Beissinger 2009, Magurran *et al.* 2010).

A unique, comprehensive, pre-eutrophication baseline set of data collected during the 1930s–1940s from the estuarine area of the Pojo-viken–Ekenäs archipelago (western Gulf of Finland), however, exists (Luther 1951a, 1951b). In order to compare these spatially-extensive aquatic-plant distribution data with the recent data and to detect possible long-term floristic changes in the aquatic vascular-plant and charophyte vegetation, during 2005 and 2007 we re-surveyed a subset of the 1930s–1940s vegetation transects using the same methods. The present study aims at characterizing spatiotemporal changes in vascular-plant and charophyte distributions and occurrence frequencies. Our specific goals are (1) to identify the ‘winners’ and ‘losers’ among the vascular-plant and charophyte species in a changing Baltic Sea, and (2) to relate the changes

to environmental factors such as eutrophication and shore grazing. This is important for assessing the status of the macrophyte vegetation and the ecological state of this estuary area.

We use the Swedish names of the localities, because they were also used in most of the previous studies referred to in the present article.

Study area

The study area — Pojoviken–Ekenäs archipelago — is situated at the southern coast of Finland, in the northern Baltic proper (Fig. 1). The area belongs to the hemiboreal vegetation zone (Ahti *et al.* 1968). Ice normally covers Pojoviken and the archipelago area from December/January to April. The vegetation period continues from May to October (Luther 1951a). Water temperature is highest in July–August (15–20 °C, Munsterhjelm 1997).

Geologically, the area is located on a pre-glacial peneplane sloping gently southwards (Hausen 1931). A deep canyon penetrating in a north-easterly direction from the open sea towards the fjord-like Pojoviken gives the outer area a brackish-marine character. Because of the favourable bottom topography, the archipelago is prone to reflect environmental (e.g. salinity) fluctuations from the open sea (Kangas *et al.* 1982, Holmberg *et al.* 2003). Due to more restricted water exchange with the open sea, the brackish-limnic inner parts of the area, Stadsfjärden off Ekenäs (Fig. 1) and Pojoviken are affected mainly by natural and anthropogenic factors deriving from the surrounding land or from the water areas themselves (Holmberg *et al.* 2003), and are especially vulnerable to eutrophication.

Pojoviken and the island area outside it, form a unique series of archipelago zones with different morphological and environmental characteristics. The zones are divided into (Fig. 1): sea zone (henceforth SZ), outer archipelago zone (OZ), outer mainland zone (OMZ), inner archipelago zone (IZ), mainland zone (MZ) and Pojoviken (PZ); (Häyrén 1900, Luther 1951a, Munsterhjelm 1997, 2005). This division is based on the changes in the morphological, hydrographical and biological factors from the open sea towards Pojoviken. The zonation of the archi-

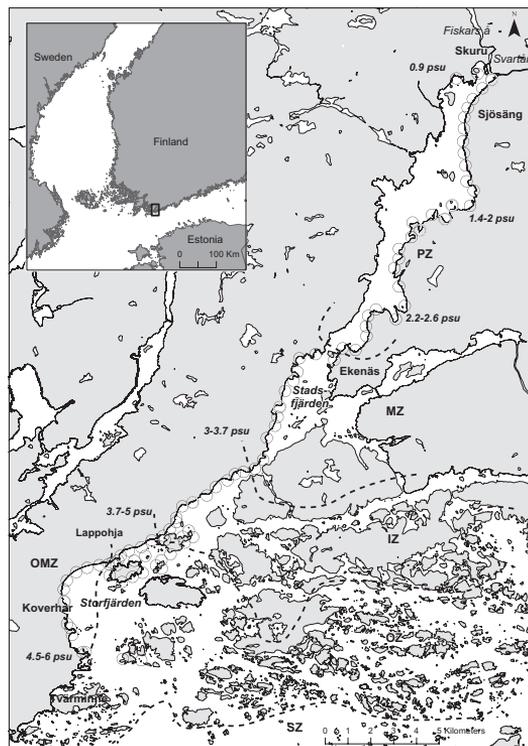


Fig. 1. The Pojoviken–Ekenäs archipelago area, in the western part of the Gulf of Finland. Circles depict the 91 transect lines. The archipelago zones are indicated with dashed lines: SZ = sea zone, OZ = outer archipelago zone, OMZ = outer mainland zone, IZ = inner archipelago zone, MZ = mainland zone, PZ = Pojoviken.

pelago results from a long-term process driven by both post-glacial land uplift and deposition of organic matter causing a positive shore-level displacement (Häyrén 1900, Munsterhjelm 1997). Besides gradients in geomorphology, there are also a number of influential environmental gradients running across the area. The salinity of the brackish seawater decreases from 5–6 psu in the outer archipelago to < 1 psu in the northernmost part of Pojoviken, where the rivers Svartån and Fiskars å enter the bay. The portion of shallow and sheltered shores increases towards the inner parts of the area. With decreasing wind and wave exposure, sandy and rocky bottoms slowly turn to finely granulated sedimentary bottoms (organic gyttja and clay). Along with these environmental gradients, the composition of aquatic communities also changes, e.g. the marine and brackish-water species are gradually replaced by freshwater species.

The Pojoviken–Ekenäs archipelago is considered an especially vulnerable area under the Habitat Directive of the European Union (Natura 2000 network), the Helsinki Commission (Baltic Sea Protected Area, BSPA) and the Ramsar Convention (Ramsar wetlands site). According to the Finnish Environment Institute (2009), the present ecological status of the water in the area is poor (Pojoviken) or moderate (archipelago) based on assessments of phytoplankton, bottom fauna and the maximum depth of *Fucus vesiculosus*.

In the 1930s–1940s, the human impact on aquatic environments increased inwards in the study area (Luther 1951a). The Pojoviken and mainland zones, as well as the two major rivers reaching the area, were surrounded by largely inhabited and cultivated land (Halme 1944), but the effect of pollution from these scattered sources on aquatic vegetation was considered to be low (Luther 1951a). The nutrient load entering the watershed originated mainly from point sources, for example from the town of Ekenäs (Häyrén 1944, Luther 1951a). The effects of the town waste waters were somewhat emphasized in the shallow and restricted sea area surrounding it (Luther 1951a). During the time of the historical surveys (Anonymous 1944, Luther 1951a), the main area subjected to dredging, and most affected by regular boating and ship traffic, was the fairway into Pojoviken, crossing the shallow Stadsfjärden off Ekenäs. The impact of small harbours (e.g. Skuru in the northernmost end of Pojoviken and Lappohja) was very local, as was the influence of the few sites for gathering floated timber (Luther 1951a). According to the field notes of Luther, sheltered gyttja shores with luxuriant vegetation were grazed by cows and horses on altogether 17 of the 44 transects situated in the Pojoviken and mainland zones. In addition, reeds were harvested for household use from three of these inner transects. The archipelago was largely unaffected by human activities, as the occasional weak pollution from scattered fishing and farming settlements was compensated by good water exchange with the open sea (Luther 1951a).

Between the surveys, former permanent settlements were replaced by the extensive modern-day summer cottages. This develop-

ment is especially evident in the archipelago, where only eight permanent residents live today (Saaristoasiain neuvottelukunta 2007), while in 2005 there were over 5000 summer cottages in Ekenäs, the largest municipality within the study area (Suomen virallinen tilasto 2005). In 2005, the total population of the municipality of Ekenäs and the village of Lappohja together was over 15 000 inhabitants (Statistical Yearbook of Finland 2006). In 1938, the population was over 14 000 inhabitants, 3420 living within the actual town area (Suomen tilastollinen vuosikirja 1940). Currently, the municipal waste water treatment plants are still the main point sources of nutrients leaking into the watershed (Holmberg *et al.* 2003). According to Holmberg *et al.* (2003, 2008), the gradual reduction of phosphorus (1990: 11 kg d⁻¹, 2006: 2–3 kg d⁻¹) and oxygen-consuming material in the treated waste waters has been more successful than the reducing of nitrogen (1990: 290 kg d⁻¹, 2006: 250 kg d⁻¹). In the archipelago, point sources for waste waters, including the village of Lappohja and a smelter in Koverhar, are fewer (Fig. 1) (Holmberg *et al.* 2003). However, diffuse nutrient loading originating from intensified agriculture, forestry, scattered settlements and traffic is nowadays the main source especially of nitrogen entering into the Baltic Sea (HELCOM 2009).

Intensification of agriculture in the study area since the 1960s has contributed to almost complete cessation of shore pasturing (Luther & Munsterhjelm 1983, Pykälä & Bonn 2000). Reed harvesting (Storå 1981) or timber floating (H. Pitkänen unpubl. data) is not practiced anymore. Some industrial plants were built in the area between the surveys, mainly in the 1960s (Vuorio 2011). Due to improved water protection, their influence as local pollution sources has declined since the 1980s, although heavy-metal levels in sediments still reveal the impact of industry on the aquatic biota (Holmberg *et al.* 2003). The extension of existing industrial harbours and construction of new ones have caused local shore alterations and intensified ship traffic. The level of motorization and vessel sizes have increased gradually since the first half of the 20th century (Riimala 1994). High number of cottages, as well as increasing standard of living during the last half of the 20th century led

to enhanced recreational boating in the northern Baltic Sea (Norrby 2001), also in the shallower and narrower coastal areas where its impact is most intense (cf. Rönnberg & Östman 2001). Varying-sized marinas have been built especially in the mainland and archipelago zones (H. Pitkänen unpubl. data). As the size and number of motor boats has increased, additional small-scale construction and dredging of the shores and bays is being carried out throughout the area (Munsterhjelm 1997, 2005; H. Pitkänen unpubl. data).

Material and methods

Aquatic vegetation (submerged and emergent vascular plants, charophytes, aquatic bryophytes) on adjacent transects covering the entire Pojoviken–Ekenäs archipelago area was investigated by Luther (1951a, 1951b) in the years 1936–1939 and 1945–1948. For the current vegetation research, we selected 91 transects from those studied earlier by Luther. Field works were carried out in Pojoviken in 2005 and in the Ekenäs archipelago in 2007.

Historical data (1930s–1940s)

In the 1930s–1940s, Hans Luther surveyed the entire mainland shoreline from Pojoviken to the southern side of the Hanko peninsula, as well as the shorelines of some islands in the archipelago area. In the first paper (Luther 1951a), he described the methodology, the characteristics of the study area and the impact of abiotic and biotic factors on the occurrence of aquatic plants in the area, and presented distribution maps of the species. In the second paper (Luther 1951b), he presented the ecology of the species found in the area.

The historical data for the 91 transects were derived from Luther's authentic, transcribed field notes kept in the Floristic archives at the Botanical Museum of the University of Helsinki. Owing to the lack of historical coordinates, very careful effort was put into locating the historical transects from Luther's notes on the basis of landmarks and directions mentioned. The dis-

tribution maps of the species in Luther (1951a), provided an additional geographical aid in locating the transects, but Luther's original field notes were the primary source for georeferencing the historical data.

To ensure the census efficiency at the individual-species level (which must be the same in the historical and contemporary surveys), a set of species included in the historical survey were excluded from the current comparisons. Besides three species occurring mainly as shore plants (*Acorus calamus*, *Glyceria maxima* and *Juncus bulbosus*), these include *Callitriche cophocarpa*, *C. palustris*, *Chara braunii*, *Crassula aquatica*, *Limosella aquatica* and *Subularia aquatica*, whose occurrences were restricted to the vicinity of the shoreline (Luther 1951a, 1951b, Luther & Munsterhjelm 1983). The reason for these exclusions was that in 2005/2007 we could visit only the shorelines which were free or sparsely covered by reeds. We also surveyed a set of transects with moderate–dense reeds to the shoreline, and found no occurrences of these species. This, however, could not be confirmed for the transects with dense reed growth where surveys were impossible to carry out.

Field methods

Fieldwork was conducted in July–September both in 1936–1939 and 1945–1948, and in the years 2005 and 2007, when aquatic vegetation is fully developed (Luther 1951a). To ensure comparability of the surveys, in our survey we applied the same collection methods (e.g. Luther-dredge) and field procedures as those presented in Luther (1951a). In the 1930s–1940s, the entire shoreline of the study area was divided into transect lines situated next to each other (Luther 1951a). In 2005/2007, we selected 91 transects situated approximately every 500 meters in the study area starting from the NW end of Pojoviken. In some cases their positions were slightly adjusted because of obstacles on the shores, e.g. houses and piers. The distances between the transect lines were measured and the coordinates of the transects were taken using dGPS (Garmin®). In addition, some transects were placed at sites where since the 1970s aquatic

vegetation data have been sporadically collected by the local water protection association for water quality monitoring purposes. Also these transects correspond to the transects studied by Luther.

The transect lines were perpendicular to the shore and vegetation was investigated from the shoreline to the depth where no living higher vegetation was found. Open areas inside dense reed stands covering the shallowest shorelines were investigated when these openings could be seen from the outer edge of the reeds. The shallowest part of the shore (0–1 m), free from the reed, was studied by observing vegetation with an aquascope, which was occasionally also used at greater depths (from a boat), when water transparency allowed for visual surveys. Plant samples for species identification were collected in shallow waters by hand. Where water turbidity did not allow for visual methods, a long-spiked garden rake was used to 1.5-m depth. According to e.g. Munsterhjelm (1997), sampling with rakes is a relevant way of surveying aquatic vegetation on soft bottoms. The deepest parts of the transects were sampled with a Luther dredge (Luther 1951a). Every depth along the transects was investigated until no new species were found after approximately ten samplings per depth. Water depth was measured with scales marked on handles or ropes of the dredges or with a separate plummet cord.

Environmental variables

The information about the long-term salinity variation at 10-m depth was acquired from Westerbom (2006). This salinity information is based on the monitoring data of the Tvärminne Zoological Station, and covers the period from the 1920s to the beginning of the 21st century. The data originate from a sampling station in Storfjärden, situated in the outer archipelago zone (see Fig. 1) and are gathered every 10th day. The historical transparency values measured by Halme (1944) were obtained from Luther (1951a). The contemporary transparency values are from the monitoring data of the Water Protection Association of Western Uusimaa (R. Holmberg pers. comm.). They are from May and

September, and were measured at seven stations situated across the study area.

Nomenclature

The nomenclature for vascular plants follows Hämet-Ahti *et al.* (1998), for charophytes Schubert and Blindow (2003) and for bryophytes Koponen *et al.* (1995). Some taxa that are very difficult to identify to species level were treated as species groups. These include the vascular plants *Sparganium* sp., *Schoenoplectus* sp., and aquatic bryophytes *Fontinalis* sp. and *Drepanocladus* sp. Two very similar *Myriophyllum* species (*M. sibiricum* and *M. spicatum*) occurring side by side in the inner parts of the study area had been regarded as *M. spicatum* in the 1930s–1940s. They were taxonomically separated in the beginning of the 1980s (Faegri 1982). Because of the possibility that *M. sibiricum* was present on the transect lines in the 1930s–1940s, here they were regarded as *M. spicatum s. lato*. *Nymphaea alba s. lato* includes the subspecies *N. alba ssp. alba* and *N. alba ssp. candida*. *Ruppia maritima* coll. consists of two variations of the species, *R. maritima* var. *maritima* and var. *brevirostris*. *Zannichellia palustris* coll. includes the variations *Z. palustris* var. *palustris* and *Z. palustris* var. *pedicellata*.

Distribution maps

Distribution maps of the species for the 1930s–1940s and 2005/2007 were prepared with ArcGIS (ArcMAP 10). Transects are marked on the presence–absence maps with circles.

Occurrence frequencies

Occurrence frequencies of the species were calculated for both 1930s–1940s and 2005/2007 by dividing the number of transect lines where a species was present by the total number of investigated transects (91). The relative change in the species frequencies was calculated as:

$$\Delta F_{\text{rel}} = [(F_1 - F_2)/F] \times 100\%$$

where F_1 is the species frequency in 2005/2007, F_2 is the species frequency in 1930s–1940s, and $F = F_1$ or F_2 if $F_1 > F_2$ or $F_2 > F_1$, respectively. A positive value (+) means an increase in the species frequency, and a negative value (–) a decrease in occurrence frequency.

Turnover rates

Species turnover indicates the amount of change in the species composition over time. It has been widely used for detecting species composition changes for example on islands (Nilsson & Nilsson 1985). Absolute turnover rates per transect were calculated as:

$$T_{\text{abs}} = (E + I)/2t$$

where E is the number of extinctions and I the number of colonisations on the transects during t years (Herwitz *et al.* 1996, Hannus & von Numers 2010). In this study, $t = 70$ because the first inventory (starting 1936) took place 70 years before the second one (starting 2005).

Ellenberg indicator values

Ellenberg *et al.* (1991) related the ecological responses of plant species to conditions of their environment, e.g. to light and nitrogen. This has facilitated the use of plants as bioindicators reflecting environmental changes indirectly (*see* Diekmann 1995). The values from one to nine describe the intensity of the species' preference for a certain factor. For every transect, we calculated a mean indicator value for light and nitrogen preference on the basis of the Ellenberg values of the vascular plants. The mean light indicator values were calculated both with and without emergent species, but only values without them were used. This enabled us to detect the change in the underwater light conditions using solely the submerged plants. Nitrogen indicator values were available for 44, and light indicator values for 40 (excluding emergent species) vascular plant species. The nitrogen values for two species (*Stuckenia pectinata*, *Zannichellia major*) were considered unusually high for our study area, and

thus they were excluded from the calculations. Changes in the indicator values for nitrogen can be linked to the amount of nutrient leakage from the land and to the elevated production in aquatic environments. The light indicator values can be indirectly related to eutrophication via changes in the water turbidity. Recently, the Ellenberg indicator values have been successfully used in Sweden and Finland to detect various environmental changes in terrestrial vegetation (Diekmann 1995, von Numers & Korvenpää 2007).

Statistical analyses

Before performing statistical tests, the data were tested for normality (Kolmogorov-Smirnov) and homogeneity of variances (Levene's test). A paired t -test was used to compare the historical and contemporary sets of transect species numbers, mean indicator values (light indicator values square-root-transformed) and water transparencies (May 1930s–1940s and 2005 values log-transformed). Transparency values for May 1930s–1940s and 2007 were compared with a non-parametric Wilcoxon test, as their distributions were not normal, even after transformations. The difference between the nitrogen/light indicator values of different zones was analyzed using one-way ANOVA and Tukey's *post-hoc* test on raw (nitrogen) and log-transformed (light) data. For the analysis, the zones were joined into three groups: PZ ($n = 32$), MZ + IZ ($n = 28$) and OZ + OMZ ($n = 31$). All statistical tests were performed using SPSS ver. 20.

Results

The overall species number in the study area did not change significantly between the surveys. Altogether 50 vascular plant, eight charophyte and two bryophyte taxa (species/species groups) were present on the transects in the 1930s–1940s. In 2005/2007, 42 vascular plant, seven charophyte and three bryophyte taxa (species/species groups) were found. Nine vascular plant species and one charophyte were exclusive to the 1930s–1940s surveys, and one vascular plant and one bryophyte species for the 2005/2007

surveys. The majority of the exclusive species were rare (< 12 occurrences). One of the species found only in the 2005/2007 surveys was new to the area, the lemnid *Spirodela polyrhiza*. It has sparsely colonized sheltered sites in Pojoviken since the late 1970s when it was first noticed (Luther & Munsterhjelm 1983). To the contemporary survey exclusive *Fissidens fontanus* was found in the study area in the 1930s–1940s, but was so rare that it did not occur on the historical transects. Some species in Luther's data were very sparsely distributed in certain zones and, hence, did not occur on the historical nor the present transects (e.g. in the outer zones *Zostera marina*, *Chara tomentosa*; inner zones *Stuckenia filiformis*, *Tolypella nidifica*).

In both surveys, the species numbers were greatest on the transects situated in the inner parts of the area (PZ and MZ), and they gradually decreased towards the outer archipelago zone with increasing salinity, exposure, and transition from fine to coarser sediments. However, there was no significant difference in the total species numbers between the 1930s–1940s and 2005/2007 (t -test: $t_{90} = -0.282$, $p = 0.778$).

The Storfjärden salinity values for the 1930s–1940s were similar to those for the 21st century. The September transparency values were significantly higher in the 1930s–1940s than in 2005 (t -test: $t_6 = 2.980$, $p = 0.025$) and in 2007 (t -test: $t_6 = 6.870$, $p < 0.0001$). May transparencies showed no significant difference between the 1930s–1940s and 2005 (t -test*: $t_6 = 2.043$, $p = 0.087$) or 2007 (Wilcoxon test: $z = -1.581$, $p = 0.114$). In PZ, the September median transparency decreased from 3.2 (1930s–1940s) to 2.9/2.3 m (2005/2007), in MZ from 3.8 to 2.2/2.3 m, and in IZ from 4.1 to 3.1/2.2 m. In OZ, the September transparencies were 4.8 m (1930s–1940s) and 5.1/3.0 m (2005/2007). In PZ, the May median transparencies were 1.5 m (1930s–1940s) and 1.5/1.4 m (2005/2007), in MZ 1.3 m (1930s–1940s) and 1.1/1.1 m (2005/2007), in IZ 2.5 m (1930s–1940s) and 2.0/1.8 m (2005/2007), and in OZ 5.5 m (1930s–1940s) and 2.5/5.7 m (2005/2007).

Changes in species frequencies

Species were categorized according to whether

* data log-transformed

between the 1930s–1940s and 2005/2007 their occurrence frequencies increased (13 species), decreased (18 species), or remained unchanged (17 species). ΔF_{rel} values for the species whose frequencies increased/decreased were $> \pm 30\%$, and differences between the 1930s–1940s and 2005/2007 transect numbers $\geq \pm 4$. *Phragmites australis* was classified as a species whose frequency increased based on the increase in the volume of its stands throughout the study area. Ten species were found exclusively in the 1930s–1940s surveys and two in the 2005/2007 surveys. Two annual charophyte species with considerable inter-annual occurrence-frequency fluctuations (Luther 1951b) were not categorized because of the difficulties in making conclusions about possible distribution changes from one re-survey only. Categorization of the species was based on their occurrence frequency changes in the entire study area (Fig. 2). There were, however, some species whose overall occurrence frequencies remained unchanged, but local values changed considerably; e.g. *Potamogeton pusillus* decreased in PZ and MZ and increased in IZ and OZ, or *Callitriche hermaphroditica* increased in PZ and MZ, but was not found in the outer parts of the area in 2005/2007.

Species whose occurrence frequencies increased

Ceratophyllum demersum (Fig. 3)

As a non-rooted species, *Ceratophyllum* was often found as recumbent on sheltered bottoms. On soft substrates, its shoots could be lightly anchored in sediments. The species tolerates turbid conditions (Luther 1951b). Its frequency increased throughout the study area, the most in PZ (from 14 to 27 occurrences) and MZ (from 2 to 11 occurrences). Especially noteworthy is the increase in the sheltered parts of the archipelago, where this species did not occur in the 1930s–1940s.

Drepanocladus sp. (Fig. 4)

This bryophyte group consisted of loose-floating species occurring on the bottoms of PZ and

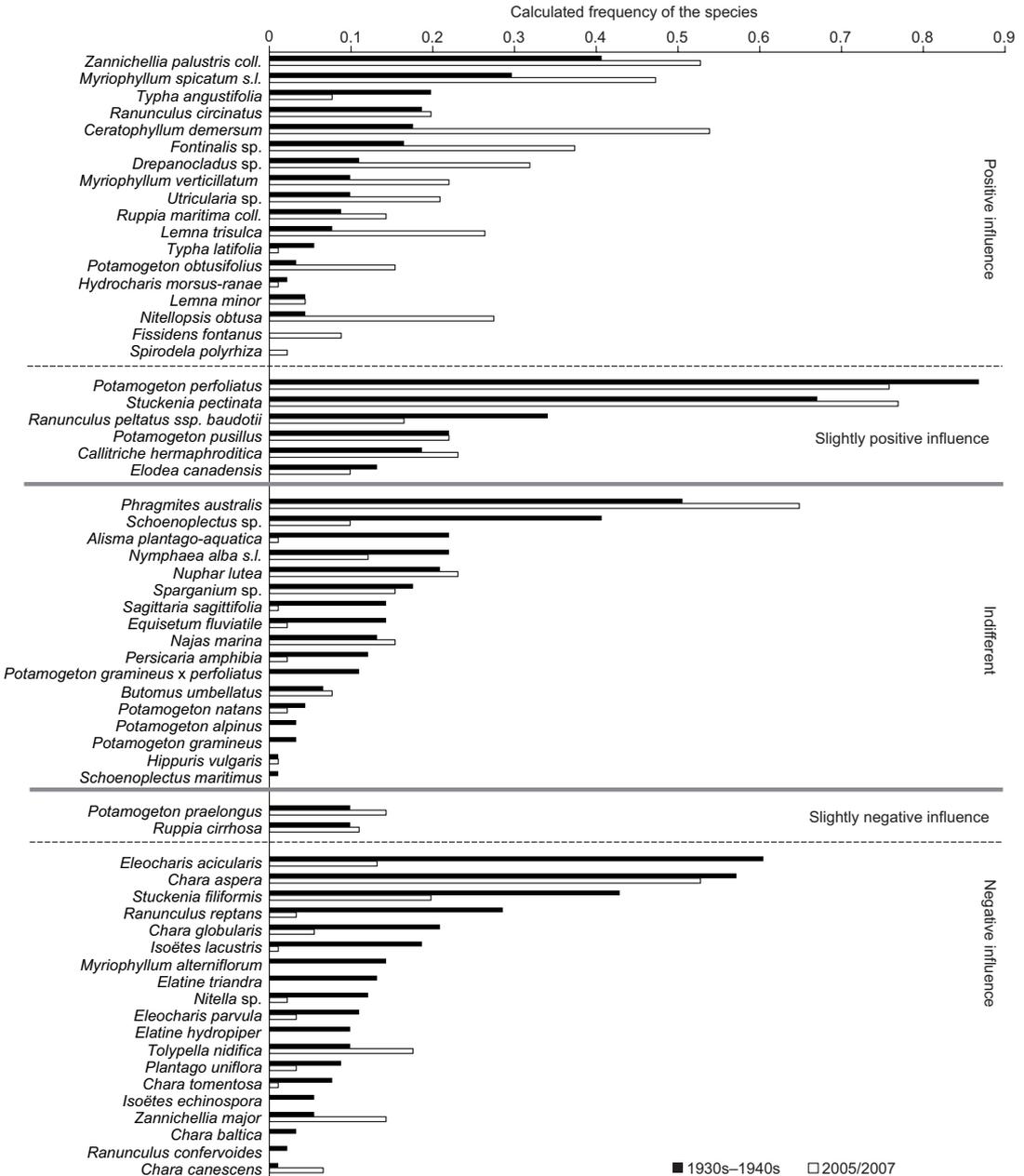


Fig. 2. Occurrence frequencies of all the species found in the study area. The species are arranged according to their reaction to eutrophication (positive, negative or indifferent). Sources for the classification: Luther 1951a, 1951b, Kurimo 1970, Wallentinus 1979, Toivonen 1984, Toivonen & Huttunen 1995, Munsterhjelm 1997, Penning *et al.* 2008.

MZ. They became nearly three times more frequent as compared with the situation in the 1930s–1940s (increase from 10 to 29 occurrences). *Drepanocladus* species had preferred sheltered sites in the 1930s–1940s, but then spread to more exposed sites. The most common

species in the group, *D. aduncus*, occurred very seldom beyond MZ (Luther 1951b).

Fontinalis sp. (Fig. 5)

This species group of loosely bottom-dwelling

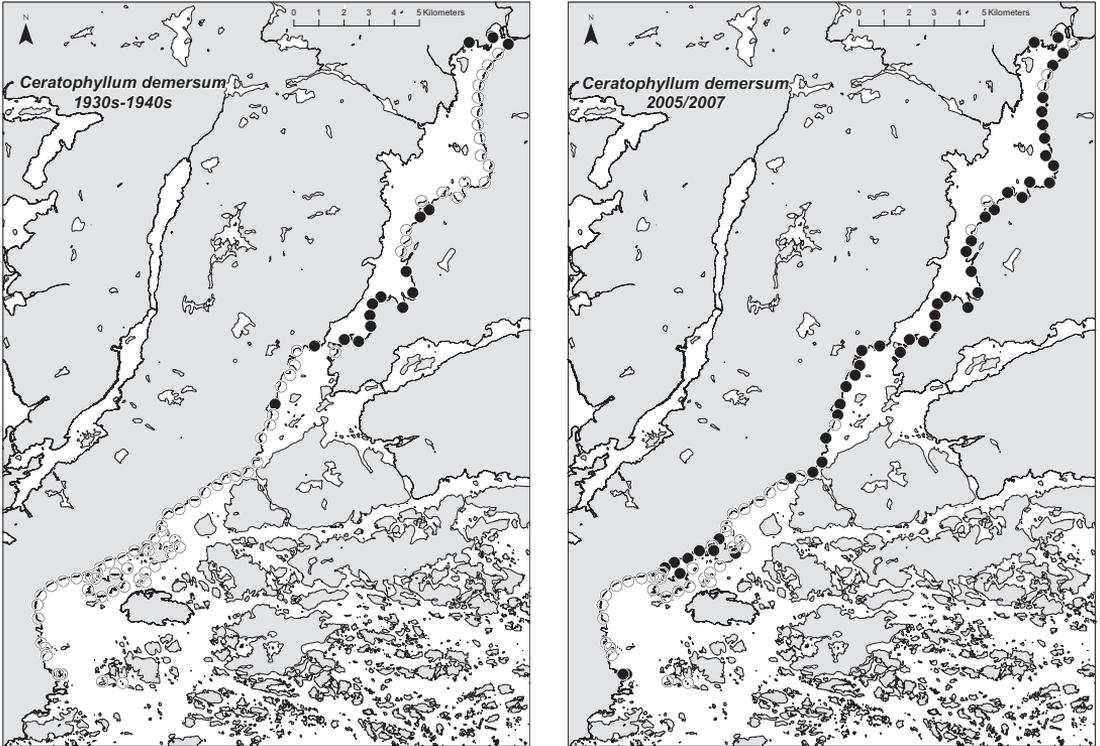


Fig. 3. Distribution of *Ceratophyllum demersum*. ● presence, ○ absence. [Shoreline maps in Figs. 3–64 ©National Land Survey of Finland licence number 49/MML/12].

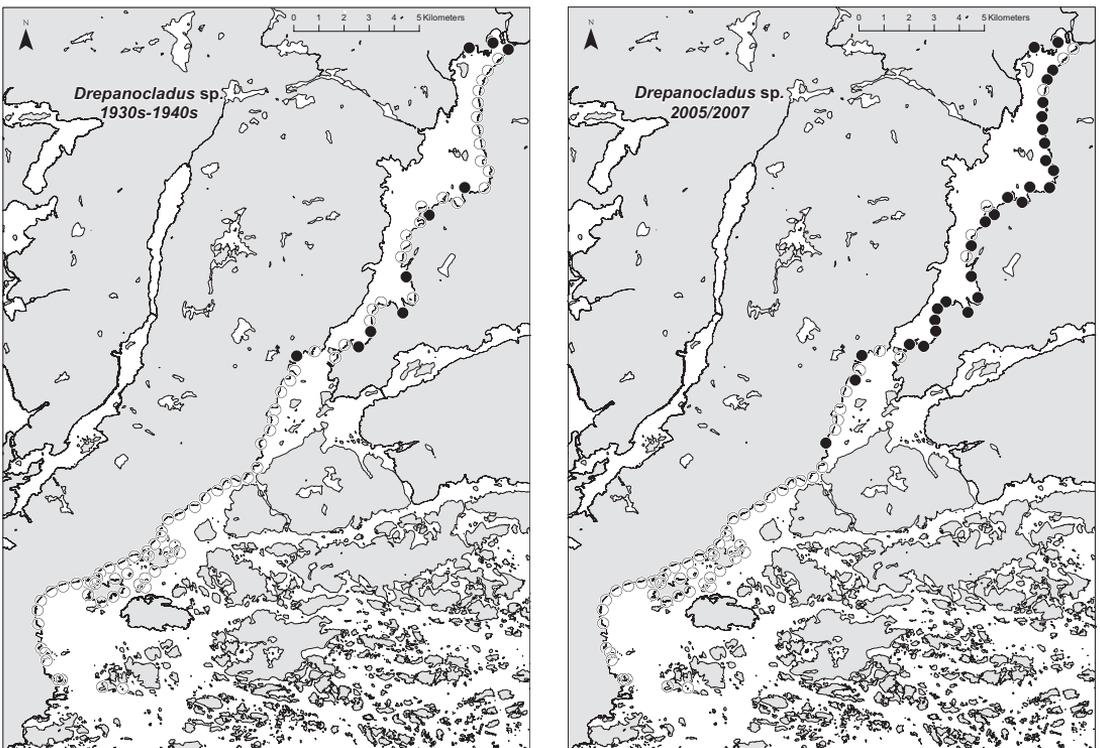


Fig. 4. Distribution of *Drepanocladus* sp. ● presence, ○ absence.

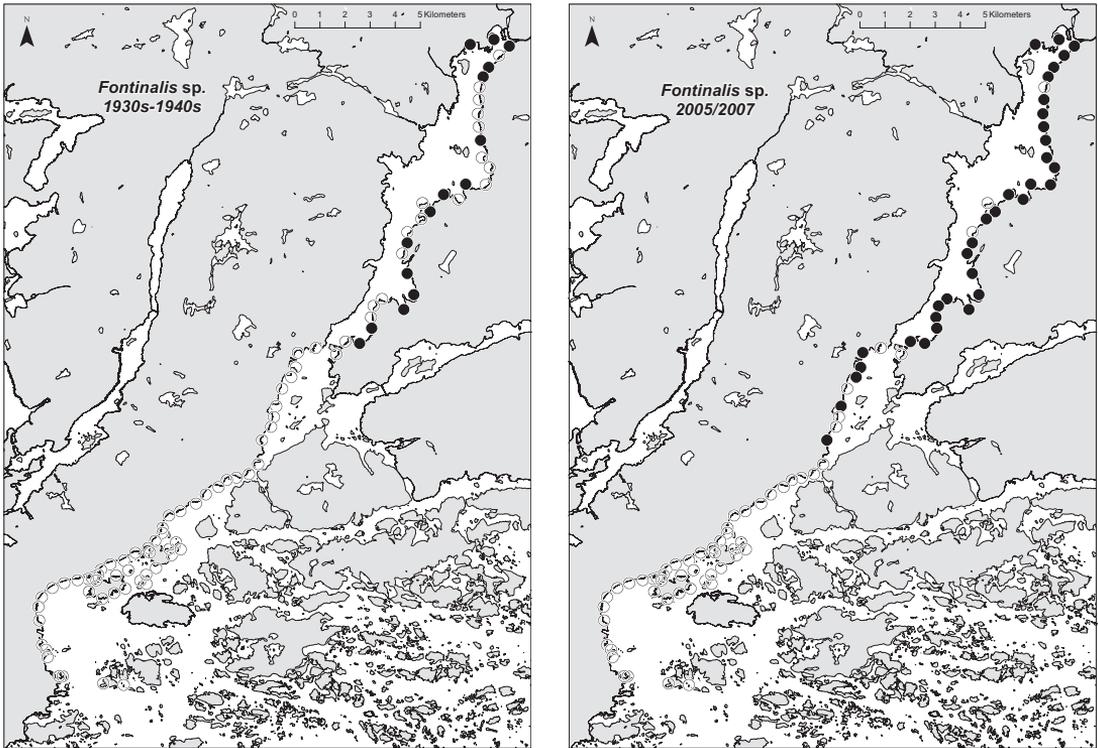


Fig. 5. Distribution of *Fontinalis* sp. ● presence, ○ absence.

bryophytes increased from 15 to 29 occurrences in PZ. On the MZ transects, the species of this group had not been present in the 1930s–1940s. In 2005/2007, five occurrences were found in MZ. The most likely species to occur in the low-salinity parts of the area is *F. antipyretica*.

Lemna trisulca (Fig. 6)

As a pleustophyte, in the 1930s–1940s surveys it had been concentrated, although scarcely, at sheltered and nutrient-rich sites in low-salinity PZ and MZ. Its frequency increased from 5 to 19 occurrences in PZ and from 1 to 5 occurrences in MZ.

Myriophyllum spicatum s. lato (Fig. 7)

This species was ubiquitous in the area with regard to salinity, bottom type and exposure, although it prospered at more sheltered sites with gyttja bottom. Its occurrence frequency increased in both the inner and outer parts of the area.

Myriophyllum verticillatum (Fig. 8)

The species was limited to the less saline inner parts of the area, although it spread outwards within MZ. In PZ, the species had been present on 8 transects in the 1930s–1940s, while in 2005/2007 it was found on 14 transects.

Nitellopsis obtusa (Fig. 9)

This is one of the species whose frequency increased the most (from 4 to 25 occurrences). It increased not only in PZ but also in MZ. The species had been noticed for the first time in the low-salinity parts of the study area in 1935 (Luther 1951b). It is very rare in the Baltic Sea, the Pojoviken–Ekenäs area being one of its three occurrence sites (Urbaniak 2003).

Phragmites australis (in the historical data *P. communis*) (Fig. 10)

In both surveys, the common reed *Phragmites australis* was more widespread in the inner parts

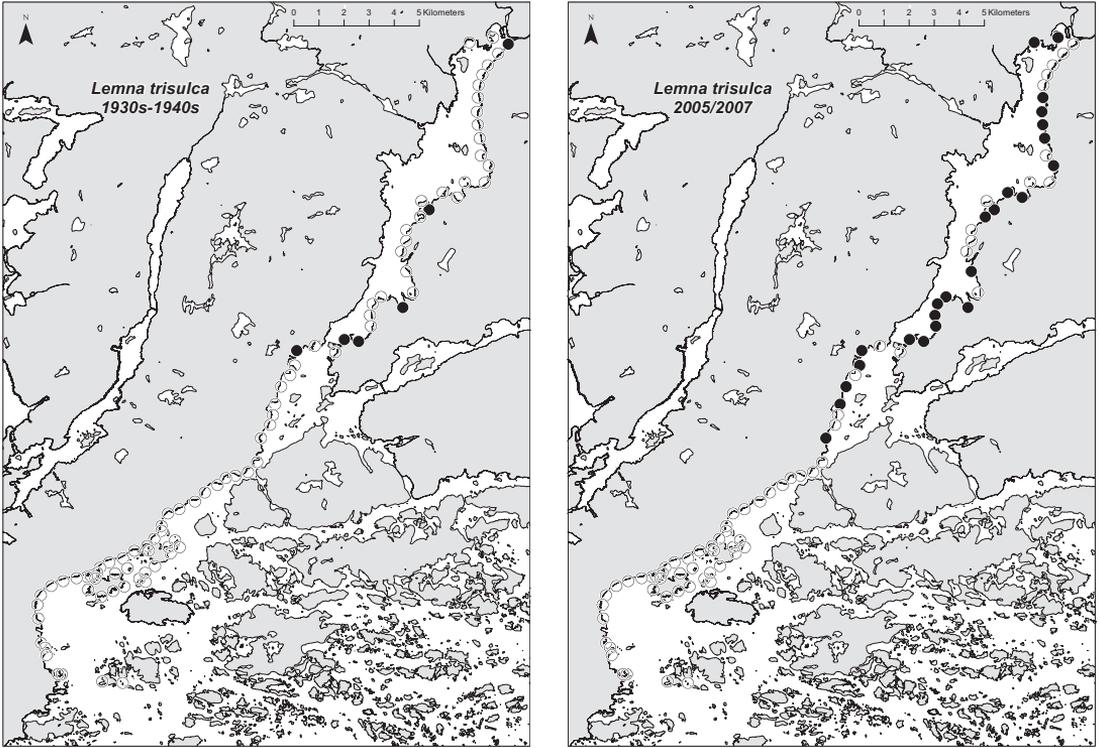


Fig. 6. Distribution of *Lemna trisulca*. ● presence, ○ absence.

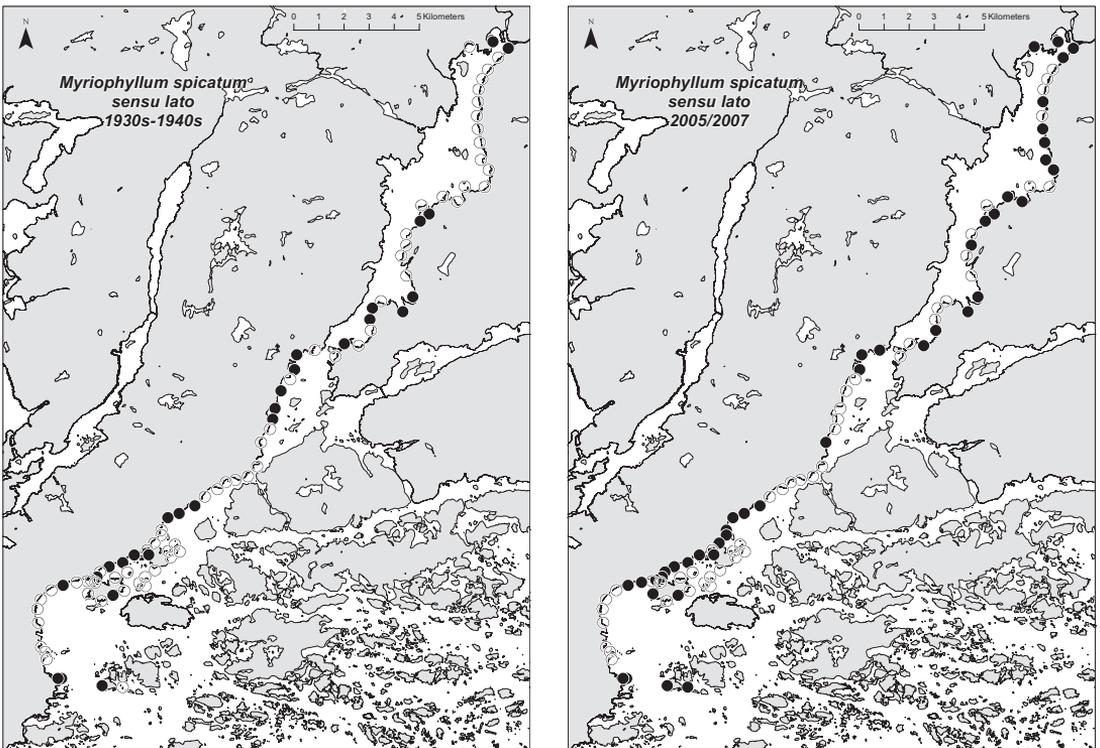


Fig. 7. Distribution of *Myriophyllum spicatum sensu lato*. ● presence, ○ absence.

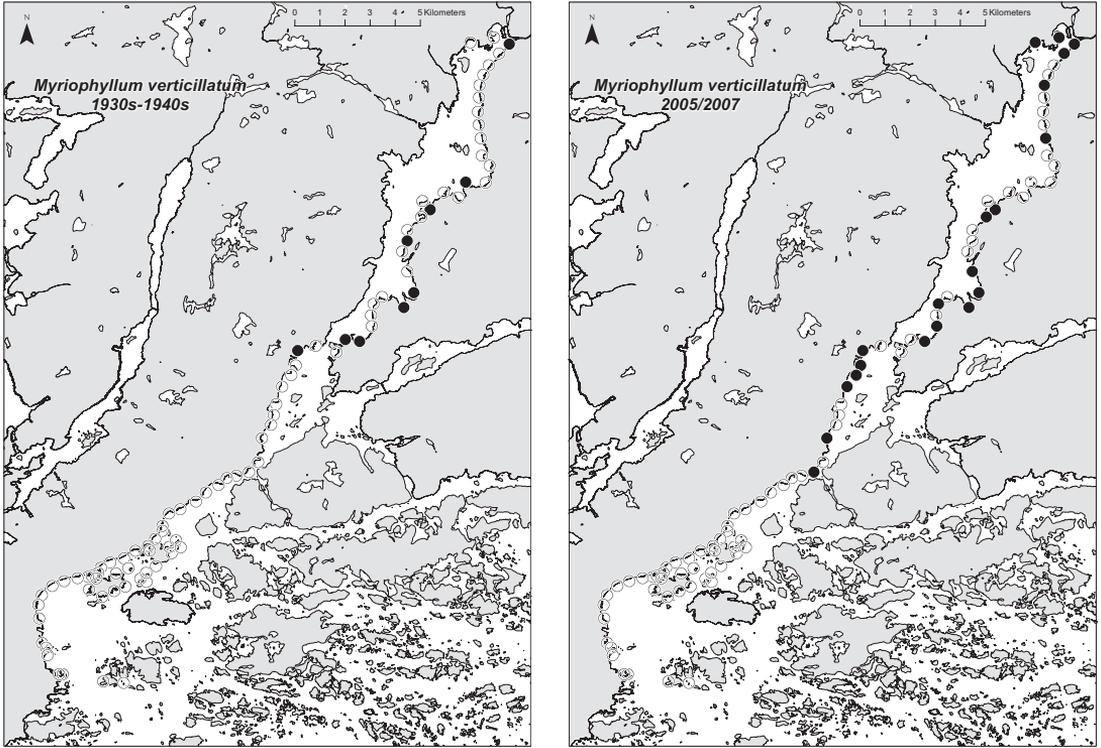


Fig. 8. Distribution of *Myriophyllum verticillatum*. ● presence, ○ absence.

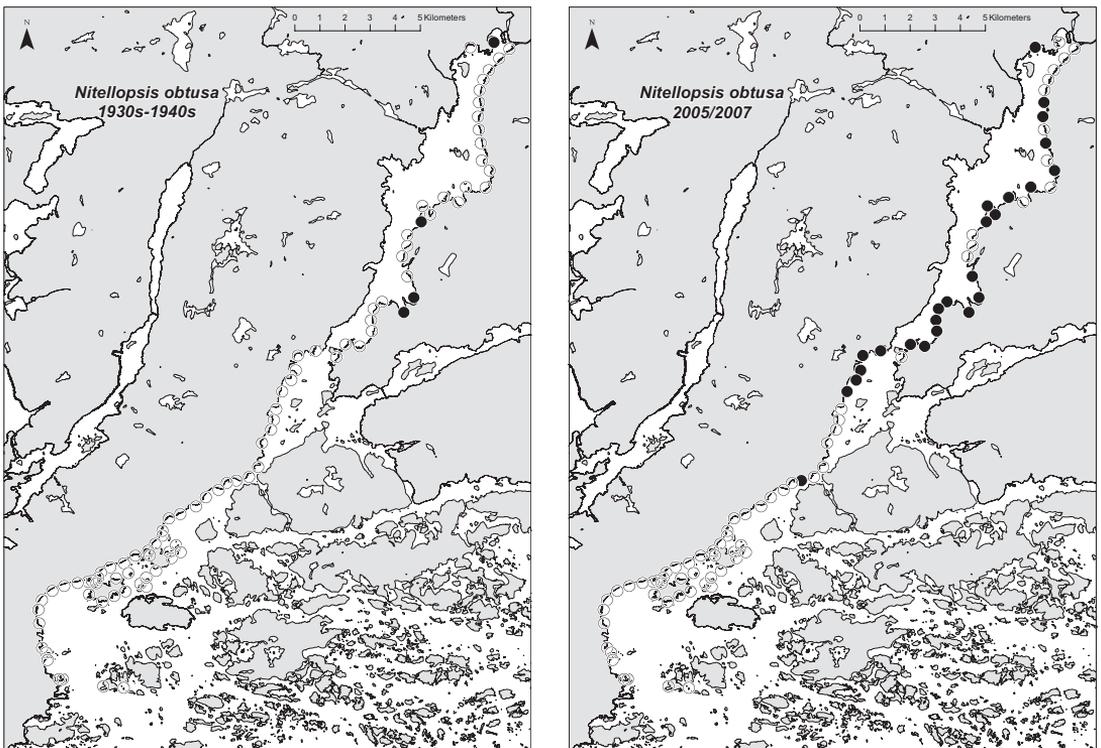


Fig. 9. Distribution of *Nitellopsis obtusa*. ● presence, ○ absence.

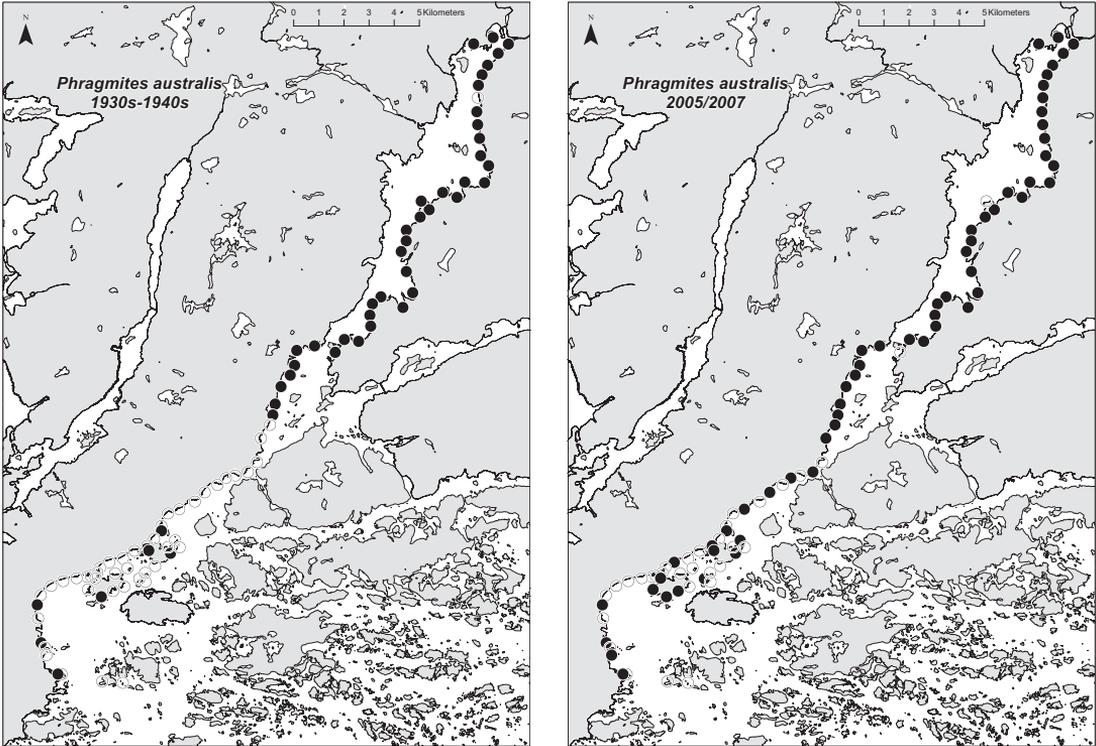


Fig. 10. Distribution of *Phragmites australis*. ● presence, ○ absence.

of the area than in the archipelago. A clear increase in the number of actual locations where *P. australis* colonized completely new shore stretches was found only in the archipelago area, in IZ–OMZ. The most dramatic change related to *P. australis* was, however, the thickening and widening of reed stands both vertically and horizontally throughout the study area. This was evident when comparing the transect descriptions in Luther’s 1930s–1940s field notes with our own field observations. This development was clearest in PZ and MZ, where environmental conditions, most importantly shelter and soft sedimentary bottom substrates, favour the reeds to form, at their largest, stands hundreds of meters wide, covering the majority of the shores. Naturally reed-free shoreline can nowadays be seen only very rarely in PZ and MZ. Only the most exposed shore stretches with coarse substrates were reed-free. The intensity of the reed growth weakened towards the archipelago, but was still vigorous in the inner archipelago and at the sheltered sites of OZ and OMZ. In IZ–OMZ, the reeds did not enter vertically as deep as they

did in PZ and MZ, and the size of individual straws was seldom even close to their size in the inner parts. Nonetheless, they had a similar effect on the aquatic plant community.

Potamogeton obtusifolius (Fig. 11)

This species had been quite rare in the area in the 1930s–1940s, being concentrated in the river mouths in the northernmost part of PZ. In 2005/2007, it was found at 13 sites in PZ, and 1 site in MZ. It prefers sheltered sites with gyttja bottoms (Luther 1951b).

Utricularia sp. (Fig. 12)

The pleustophytic species of this group had been found on altogether 8 sheltered transects throughout PZ in the 1930s–1940s. In the 2005/2007 surveys, 18 occurrences were found in PZ. In MZ, the species group remained as sparse as it had been in the 1930s–1940s. The most likely species to be found in the low-salinity parts of the area are *Utricularia vulgaris* and *U. intermedia*.

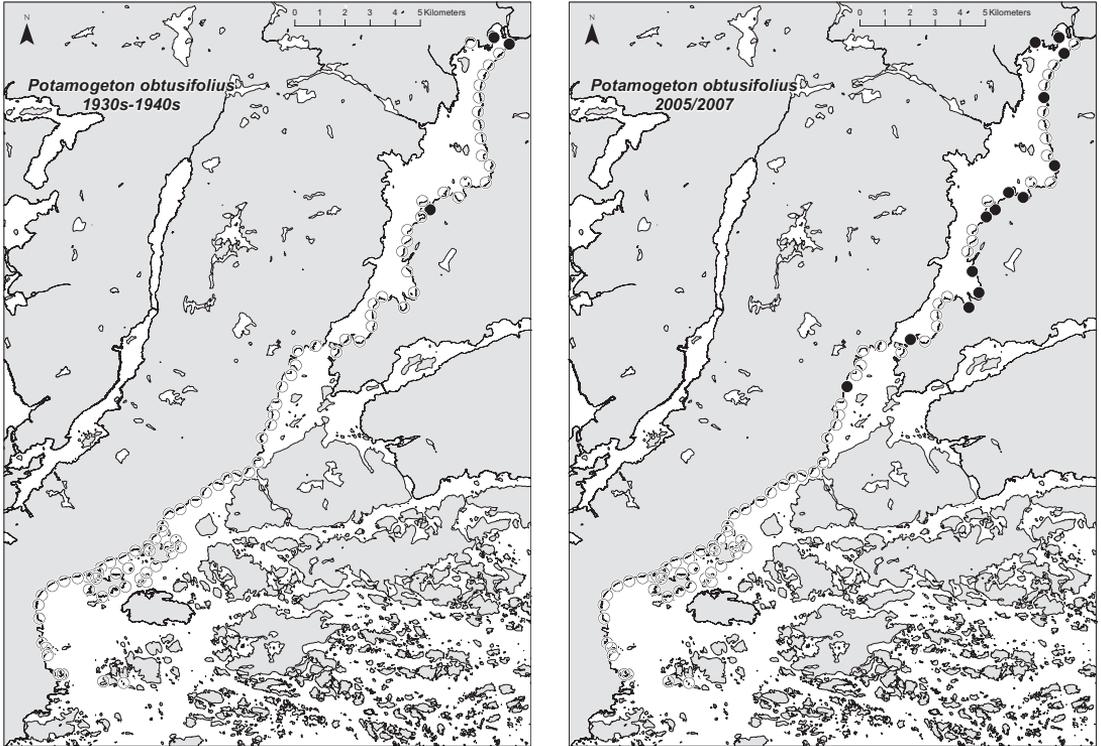


Fig. 11. Distribution of *Potamogeton obtusifolius*. ● presence, ○ absence.

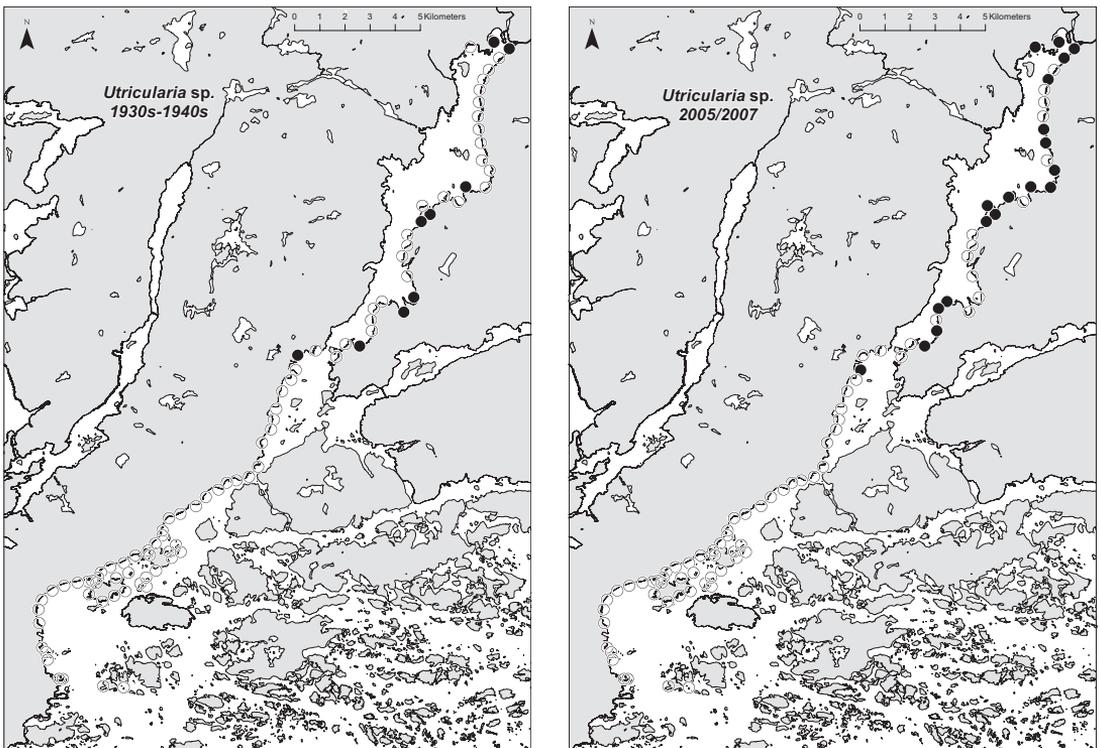


Fig. 12. Distribution of *Utricularia* sp. ● presence, ○ absence.

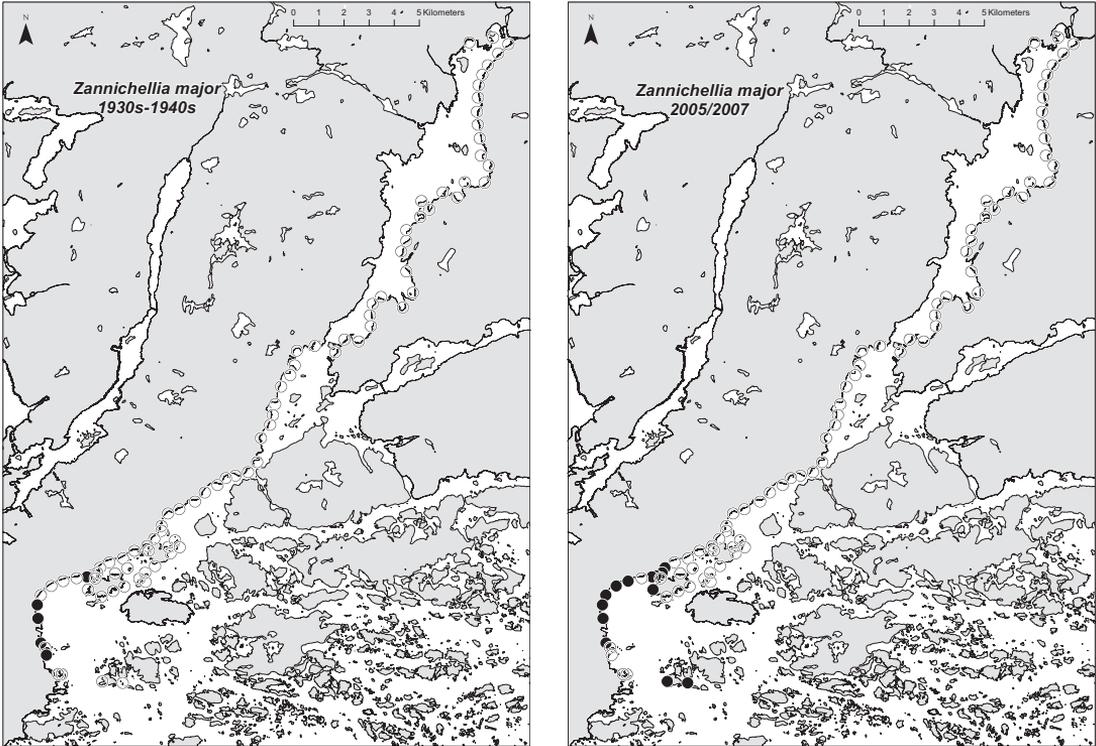


Fig. 13. Distribution of *Zannichellia major*. ● presence, ○ absence.

Zannichellia major (Fig. 13)

This species grew mainly on sand or sand-gyttja in higher-salinity OZ and OMZ and tolerated heavy exposure. The species showed a slight inward spread in OZ.

Potamogeton praelongus (Fig. 14)

The species was found growing mainly deeper, outside reeds in low-salinity PZ. It prefers gyttja bottoms (Luther 1951b). Its occurrences increased in PZ, from 9 to 12 locations. It also spread to MZ where it was found in the 2005/2007 surveys.

Ruppia maritima coll. (in the historical data *R. brachypus* and *R. rostellata*) (Fig. 15)

The two *R. maritima* variations occurring in the study area were limited to the archipelago zones. Both variations grew on sand or gyttja and had a wide exposure range. In both the historical and contemporary surveys, they were especially common in OMZ. In the 1930s–1940s,

Ruppia variations had not been found on OZ transects. In 2005/2007, they were present on four transects in OZ.

Species whose occurrence frequencies decreased

Alisma plantago-aquatica (Fig. 16)

Luther (1951b) had found the species on nutrient-rich gyttja or clay bottoms in low-salinity PZ and MZ. It requires shelter and grows only in shallow waters near the shoreline. It decreased from 17 to only 1 occurrence in PZ, and was not found in MZ in the 2005/2007 surveys.

Chara globularis (in the historical data *C. fragilis*) (Fig. 17)

The species can grow on a variety of bottom substrates. It has a wide tolerance for exposure, but prefers sheltered sites where it can grow in dense stands (Luther 1951b). The distribution

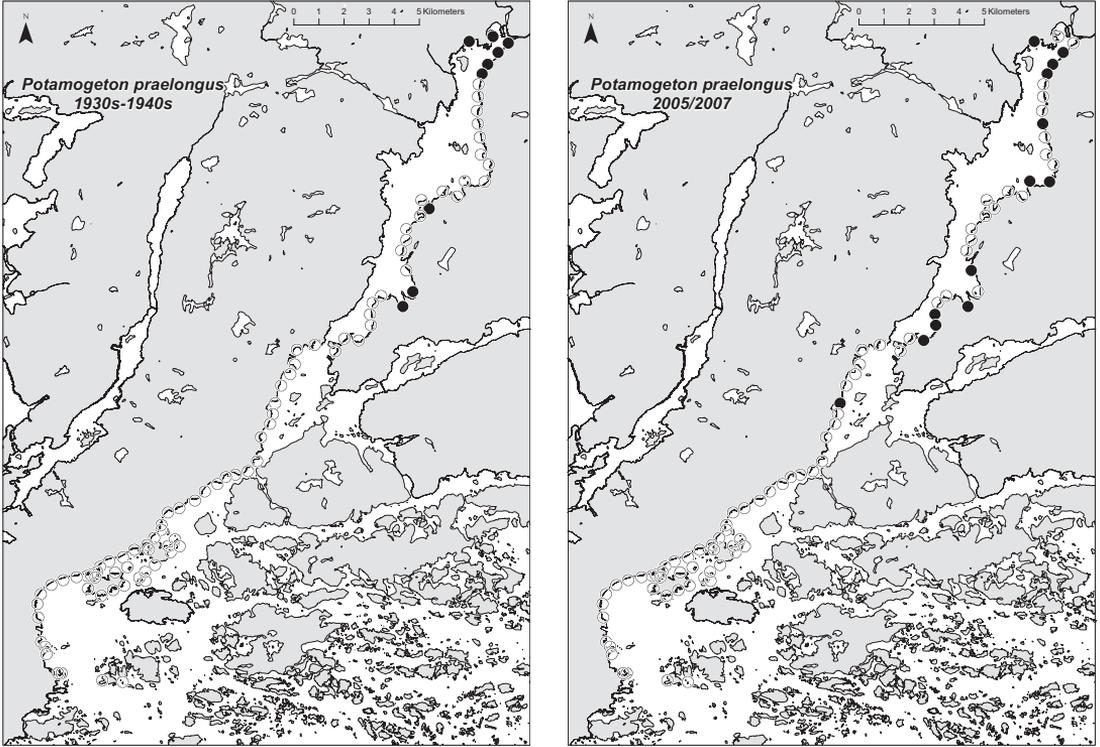


Fig. 14. Distribution of *Potamogeton praelongus*. ● presence, ○ absence.

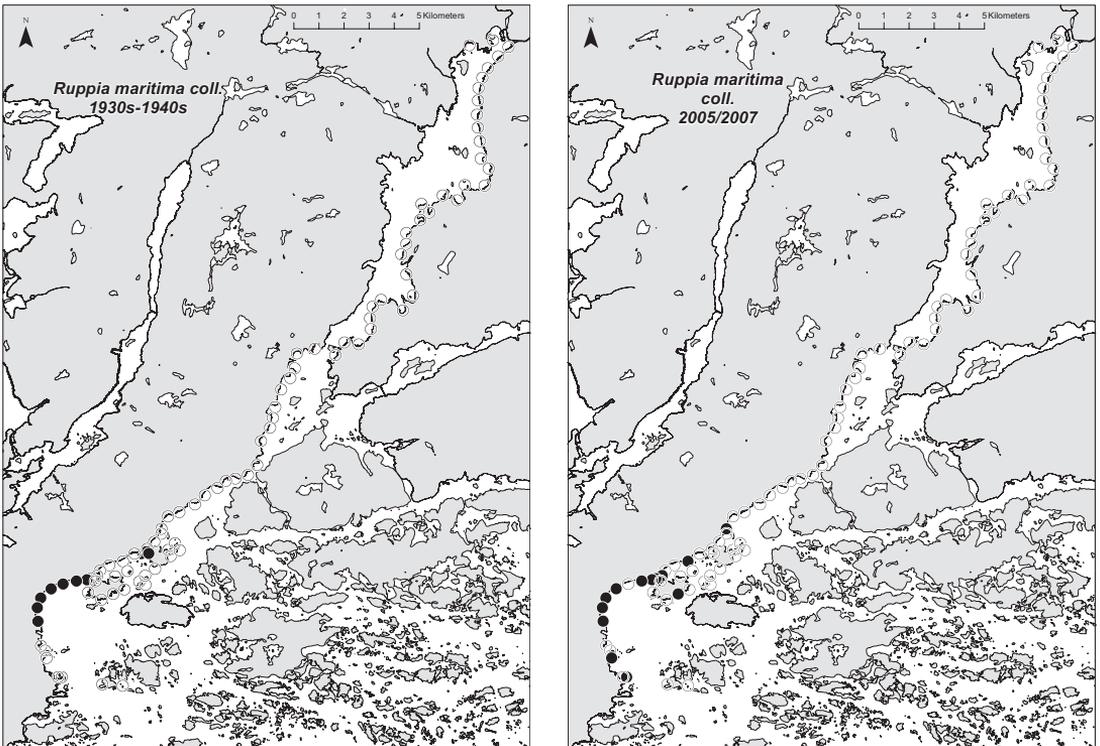


Fig. 15. Distribution of *Ruppia maritima* coll. ● presence, ○ absence.

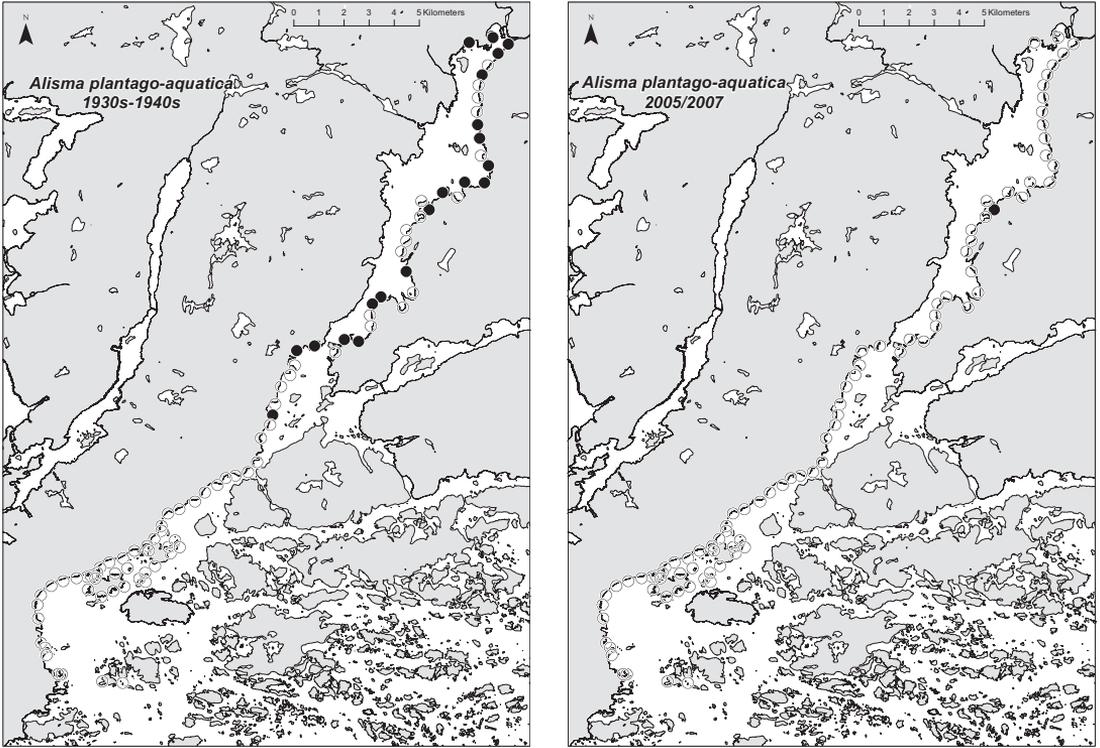


Fig. 16. Distribution of *Alisma plantago-aquatica*. ● presence, ○ absence.

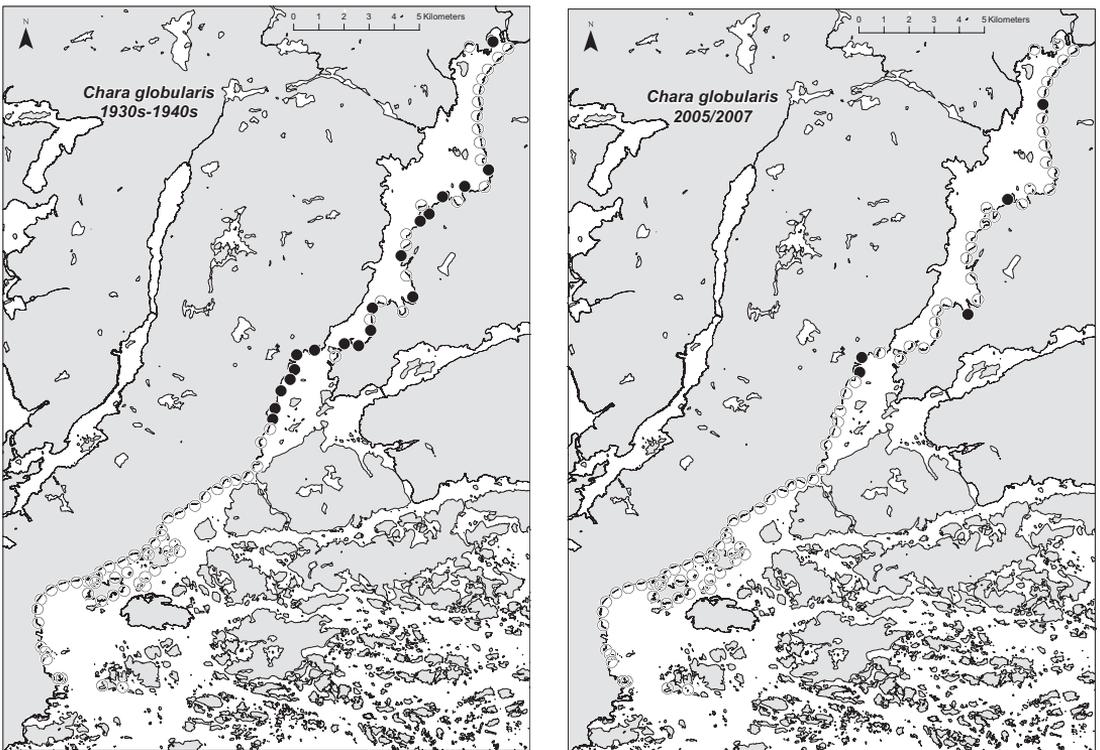


Fig. 17. Distribution of *Chara globularis*. ● presence, ○ absence.

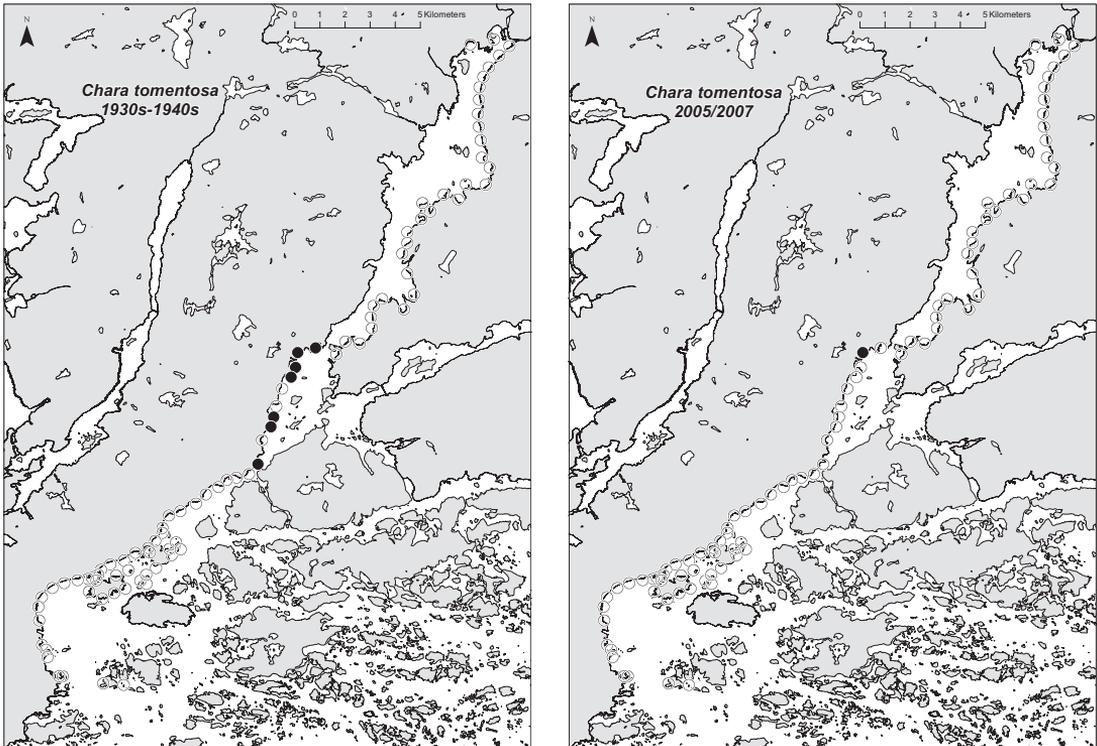


Fig. 18. Distribution of *Chara tomentosa*. ● presence, ○ absence.

of the species became considerably sparser, as in 2005/2007 it had 3 occurrences in PZ and 2 in MZ, as compared with 12 and 7 occurrences, respectively, in the 1930s–1940s.

Chara tomentosa (Fig. 18)

Seven occurrences of this alcaliphilous species had been found in MZ in the 1930s–1940s but only 1 in 2005/2007. In the 1930s–1940s, the species had occurred also in the archipelago zones, but not on the transects. It grows mainly at sheltered sites with soft organic substrate, and has an inner distribution border in MZ where the brackish water is mixed with acidic freshwater (Luther 1951b).

Eleocharis acicularis (in the historical data *Scirpus acicularis*) (Fig. 19)

This ubiquitous species was found throughout the study area. It had belonged to the most common species in the 1930s–1940s surveys. In 2005/2007, its distribution became fragmented.

It is a very small species, often forming dense carpets on shallow minerogenic bottoms.

Eleocharis parvula (in the historical data *Scirpus parvulus*) (Fig. 20)

It had been found at three sites in IZ in the 1930s–1940s, but not anymore in 2005/2007. It also decreased in OZ and OMZ. The species occurs on clay, sand or gyttja bottoms near the shoreline in the higher-salinity parts of the area, and is an inferior competitor to e.g. *E. acicularis* and *P. australis* (Luther 1951b).

Equisetum fluviatile (Fig. 21)

This emergent species occurs on the shoreline, preferably on soft clay and gyttja substrates (Luther 1951b). It was found in PZ and MZ in both surveys, but decreased from 13 to 2 occurrences.

Isoëtes lacustris (Fig. 22)

This species prefers oligotrophic conditions

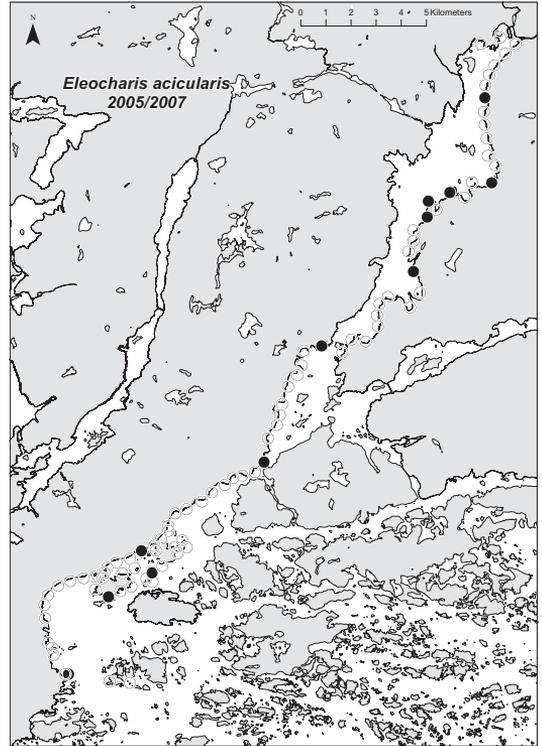
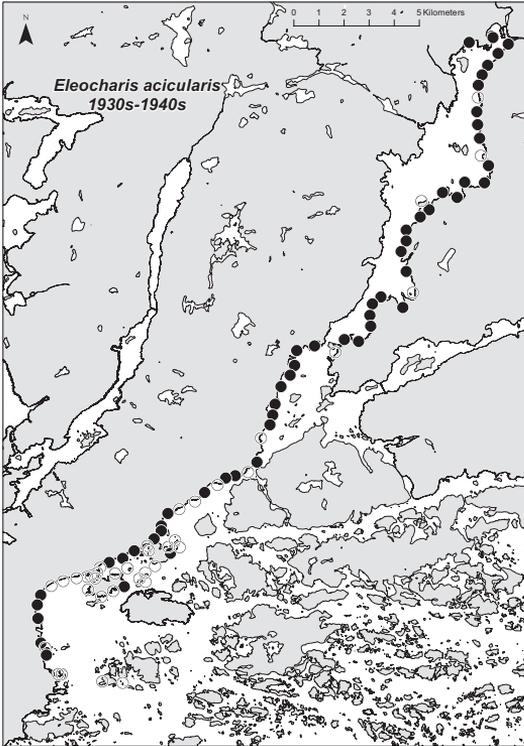


Fig. 19. Distribution of *Eleocharis acicularis*. ● presence, ○ absence.

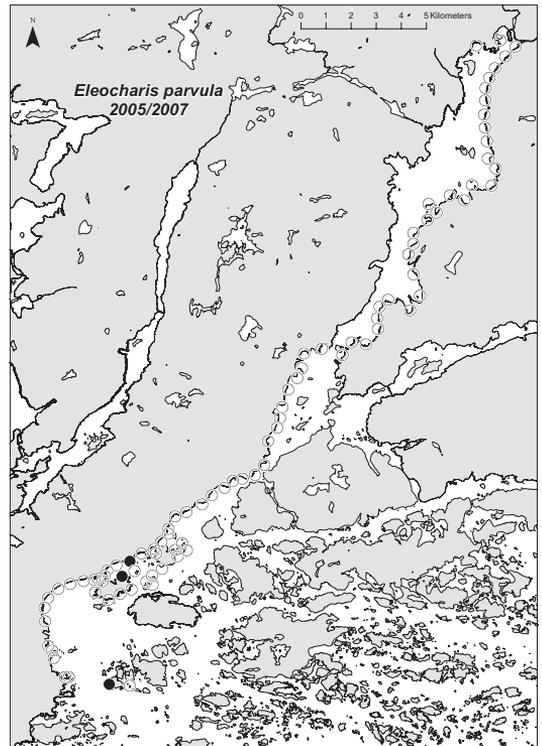
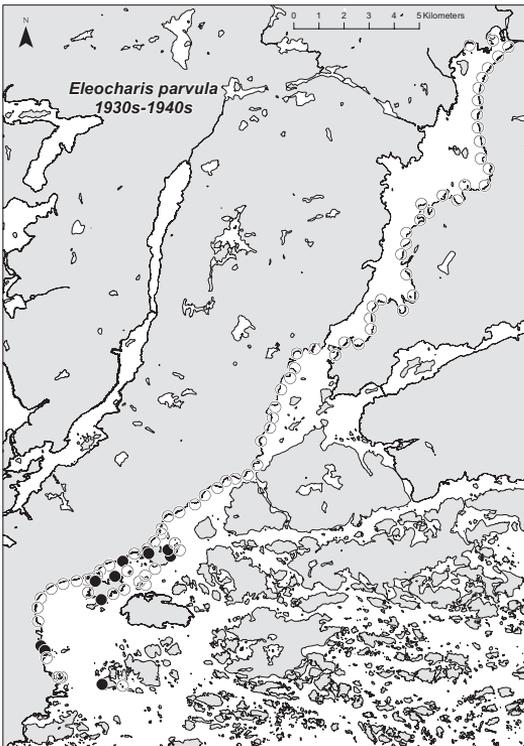


Fig. 20. Distribution of *Eleocharis parvula*. ● presence, ○ absence.

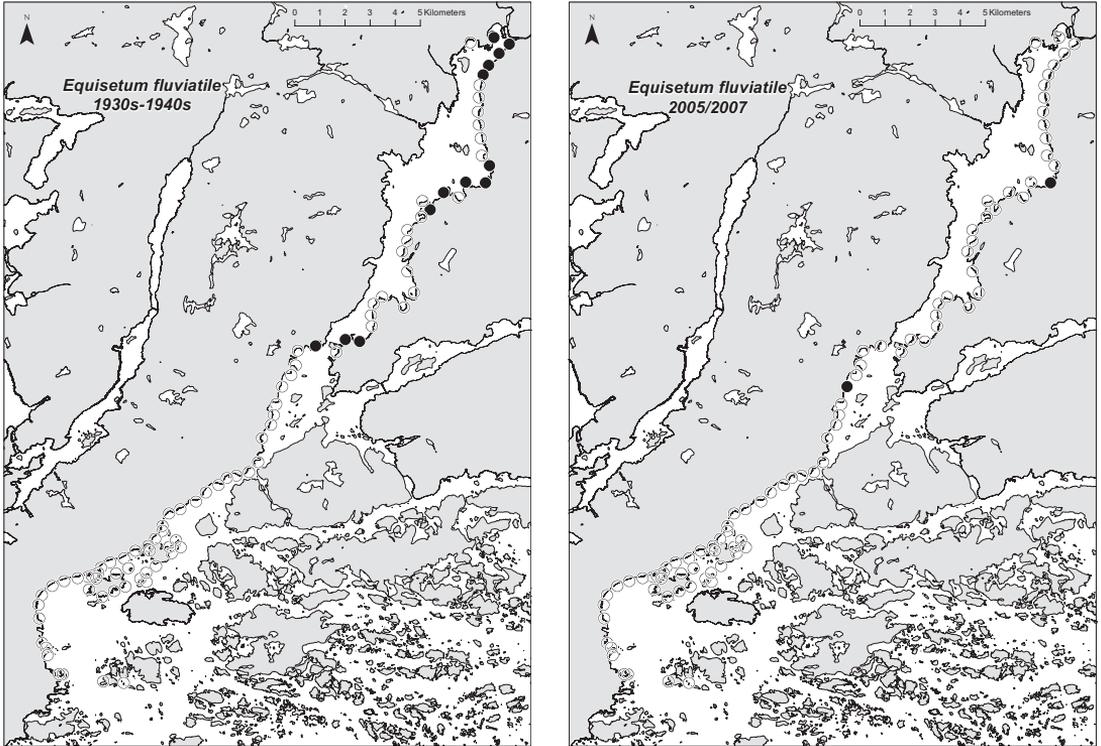


Fig. 21. Distribution of *Equisetum fluviatile*. ● presence, ○ absence.

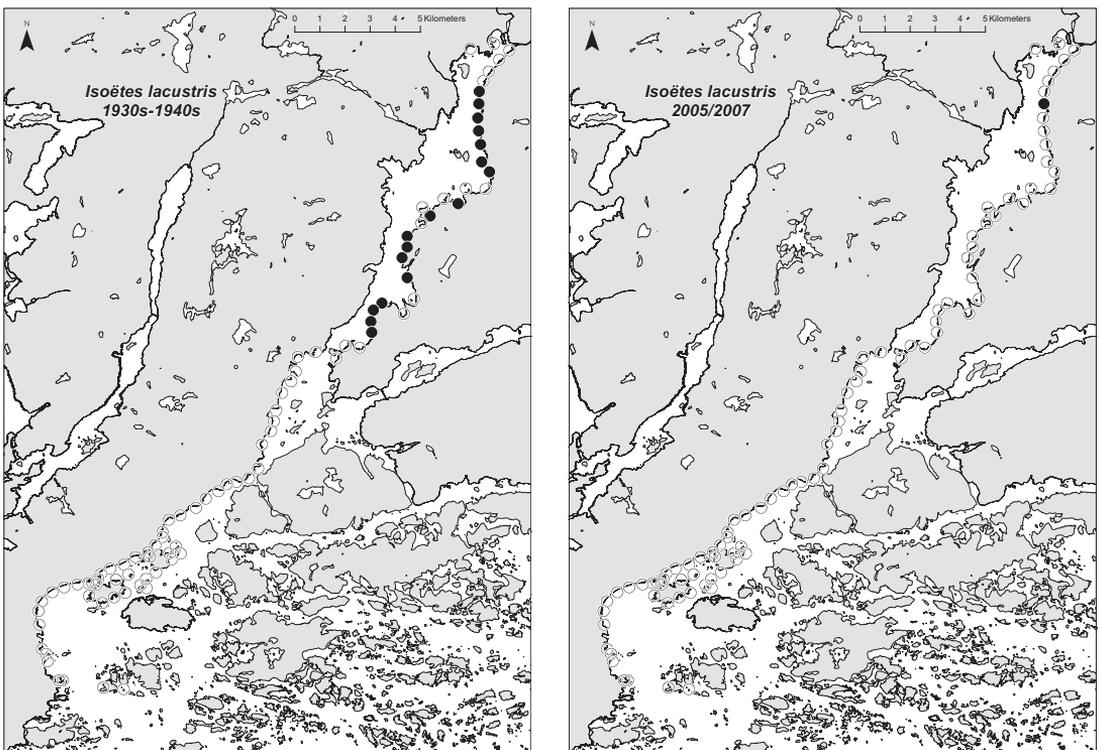


Fig. 22. Distribution of *Isoetes lacustris*. ● presence, ○ absence.

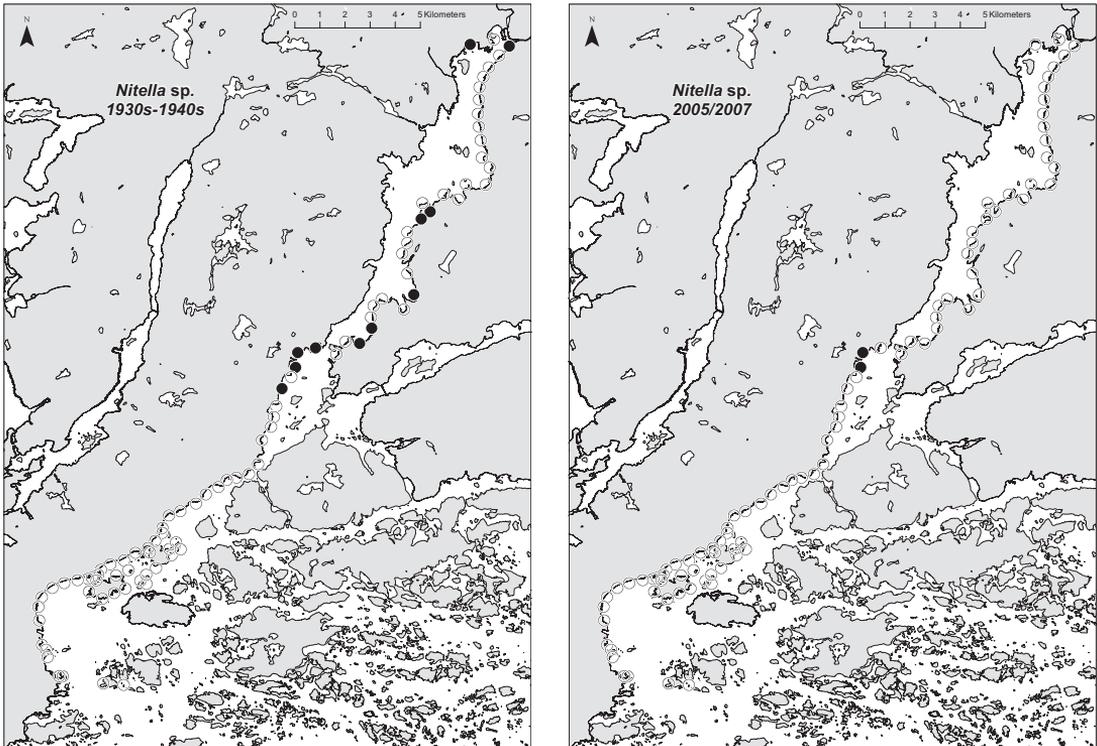


Fig. 23. Distribution of *Nitella* sp. ● presence, ○ absence.

(Luther 1951b). It was found only in low-salinity PZ. It had had 17 occurrences in the 1930s–1940s, but in 2005/2007 it was found only in 1 location with a sandy and clayish substrate.

Nitella sp. (Fig. 23)

The species of this group (mainly *N. flexilis*) had been sparsely distributed along low-salinity PZ and MZ in the 1930s–1940s, and were found only at 2 locations in MZ in the 2005/2007 surveys. The species prefer sheltered gyttja or clay bottoms, but are inferior competitors when the surrounding vegetation is particularly dense (Luther 1951b).

Nymphaea alba s. lato (Fig. 24)

This floating-leaved species is limited to low-salinity PZ and MZ (Luther 1951b), and occurs mainly on sheltered gyttja bottoms. It declined from 17 to 11 occurrences in PZ, and was no

longer present on the MZ transects in 2005/2007. The species was found either just outside the reed stands or in openings inside them.

Persicaria amphibia (in the historical data *Polygonum amphibium*) (Fig. 25)

This floating-leaved species occurred in low-salinity PZ where its frequency declined from 11 to 2 occurrences. It grew on clay or gyttja bottoms and also inside sparse reed stands.

Ranunculus peltatus ssp. *baudotii* (in the historical data *R. obtusiflorus*) (Fig. 26)

This species was limited to the higher-salinity outer zones (IZ–OMZ), where it grew mainly on sand. Its decrease was especially evident in IZ, where it had had seven occurrences in the 1930s–1940s, but was not found in 2005/2007, and in OMZ, where it decreased from 8 to 2 occurrences.

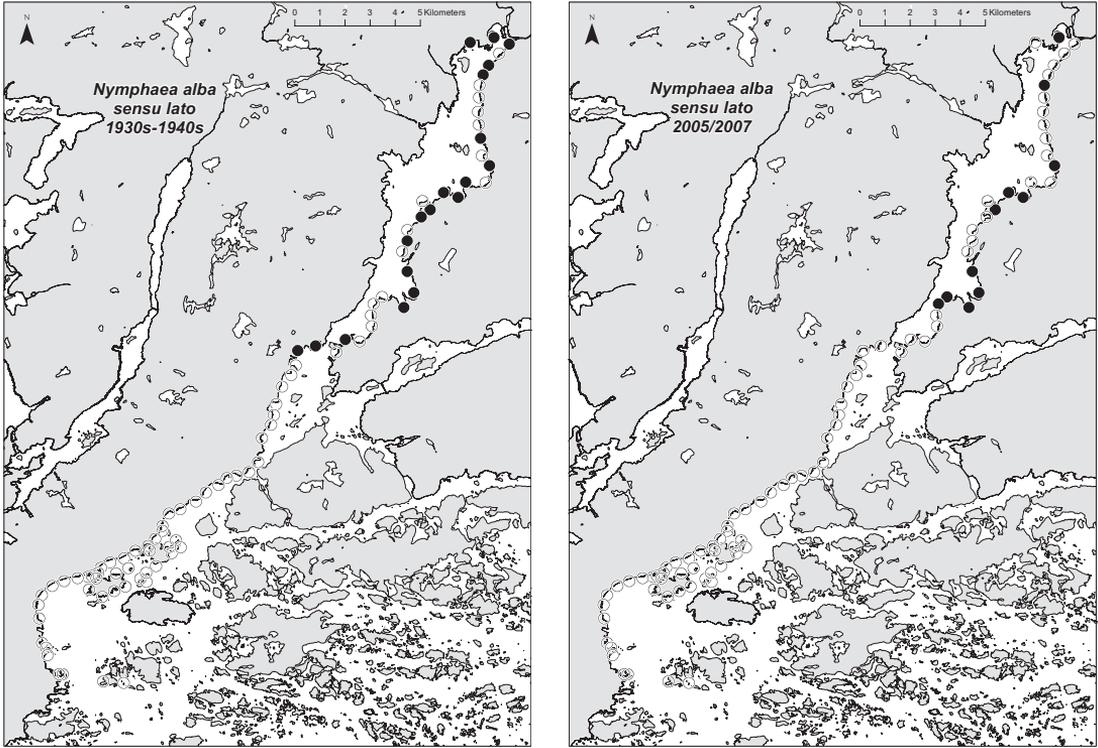


Fig. 24. Distribution of *Nymphaea alba sensu lato*. ● presence, ○ absence.

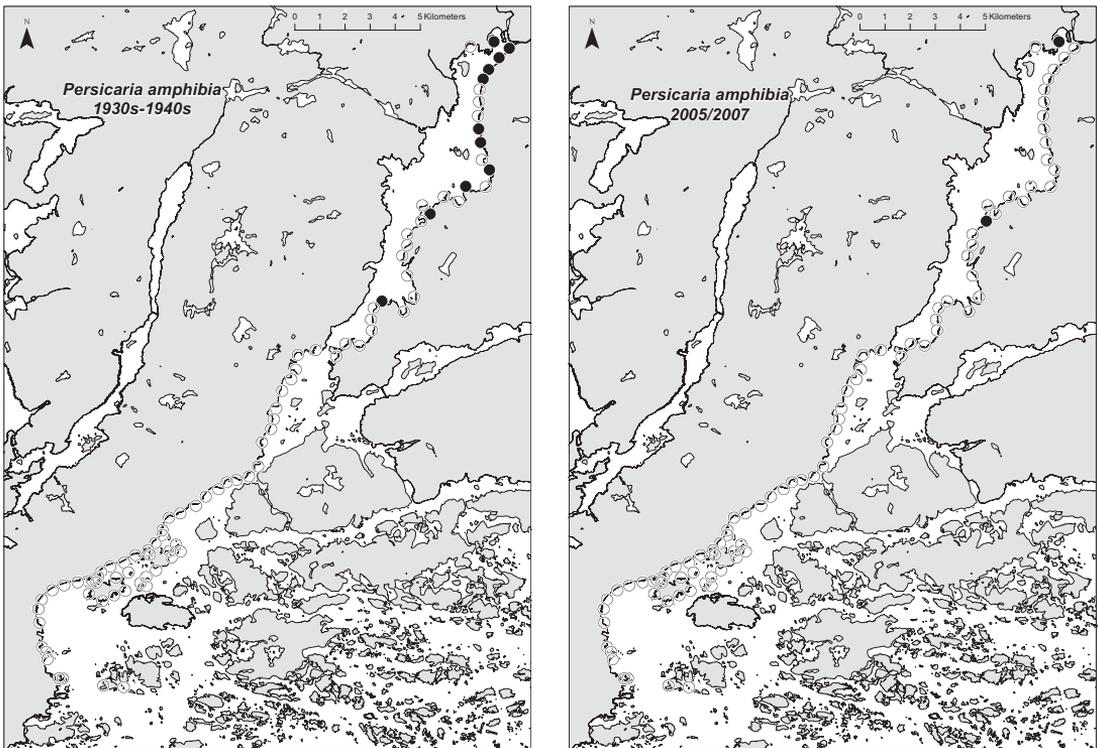


Fig. 25. Distribution of *Persicaria amphibia*. ● presence, ○ absence.

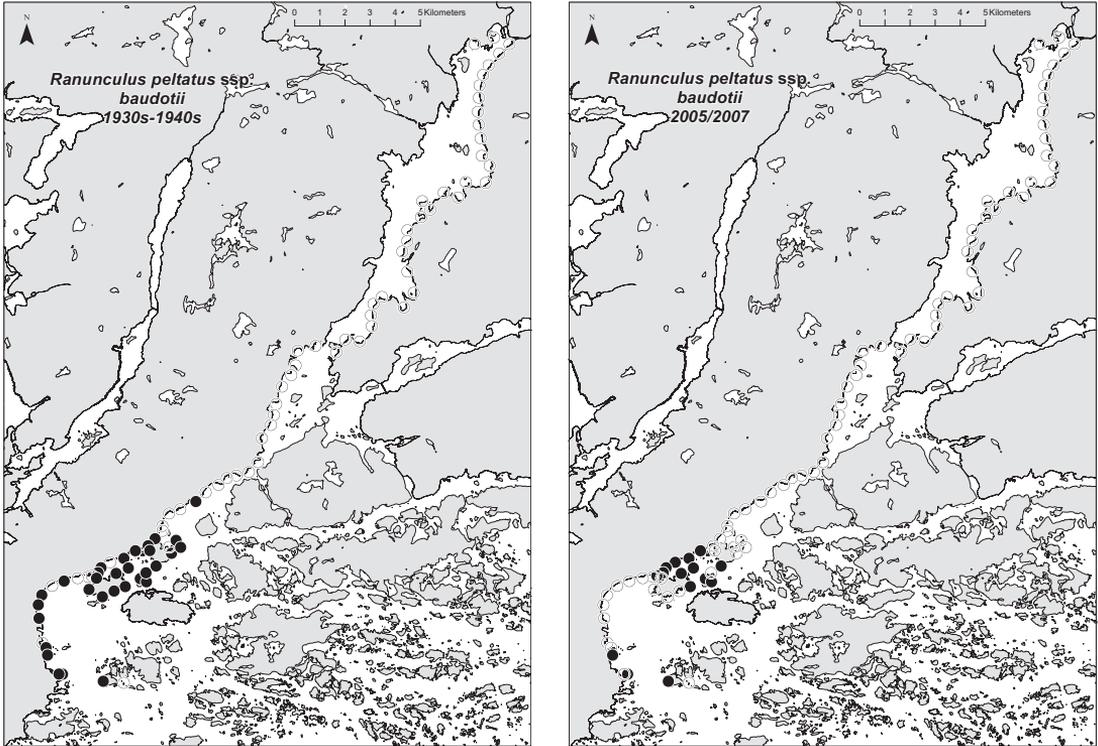


Fig. 26. Distribution of *Ranunculus peltatus* ssp. *baudotii*. ● presence, ○ absence.

Ranunculus reptans (Fig. 27)

This small-sized species forms carpet-like stands in shallow waters. The species is weak in competition with taller vegetation and prefers minerogenic bottom substrates (Luther 1951b, Kurimo 1970). It decreased in PZ–IZ from 23 to only 1 occurrence, but seemed to have held its place better in OZ.

Sagittaria sagittifolia (Fig. 28)

This species is salinity-limited and was found only in PZ. It had had 13 occurrences in the 1930s–1940s, but only 1 in 2005/2007. It is found primarily on sheltered gyttja bottoms (Luther 1951b).

Schoenoplectus sp. (in the historical data *Scirpus* sp.) (Fig. 29)

Two similar *Schoenoplectus* species (*S. lacustris* and *S. tabernaemontani*) occurred side by side in PZ, but in the archipelago only the more salinity-

tolerant *S. tabernaemontani* was found. *Schoenoplectus lacustris* favours more minerogenic bottoms than *S. tabernaemontani* (Luther 1951b). Both species grow mainly at < 1 m depths and are often superseded by *P. australis* in competition for growing space (Luther 1951b).

Stuckenia filiformis (syn. *Potamogeton filiformis*) (Fig. 30)

In both surveys, this alcaliphilous species occurred mainly in shallow waters on minerogenic and exposed shores of IZ–OMZ. In the 1930s–1940s, it had also scarcely occurred between the MZ transects, but not farther inwards in the area (see *Chara tomentosa*). The distribution of the species became fragmented, especially in IZ.

Typha angustifolia (Fig. 31)

This emergent species thrived on nutrient-rich gyttja bottoms in PZ and MZ. In the 1930s–1940s, it had also been present in OMZ in the vicinity of Koverhar (see Fig. 1), where local

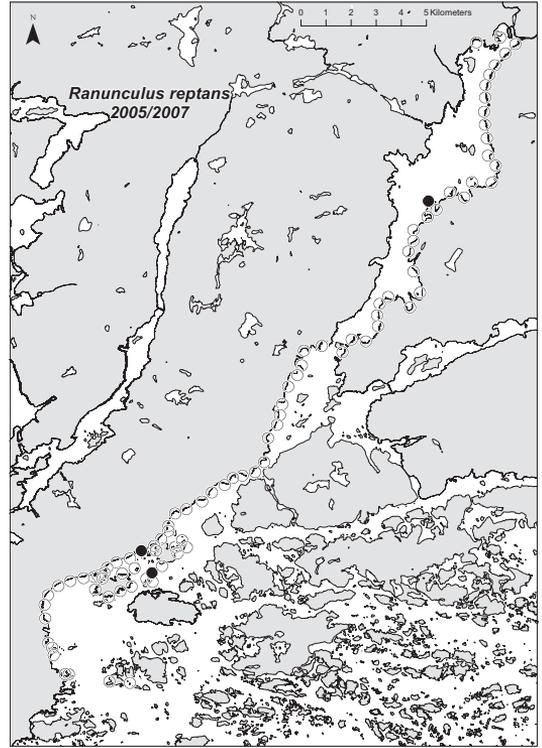
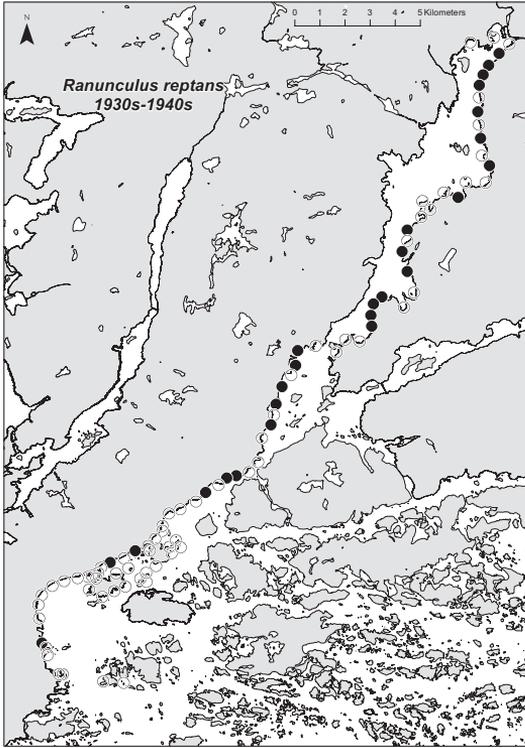


Fig. 27. Distribution of *Ranunculus reptans*. ● presence, ○ absence.

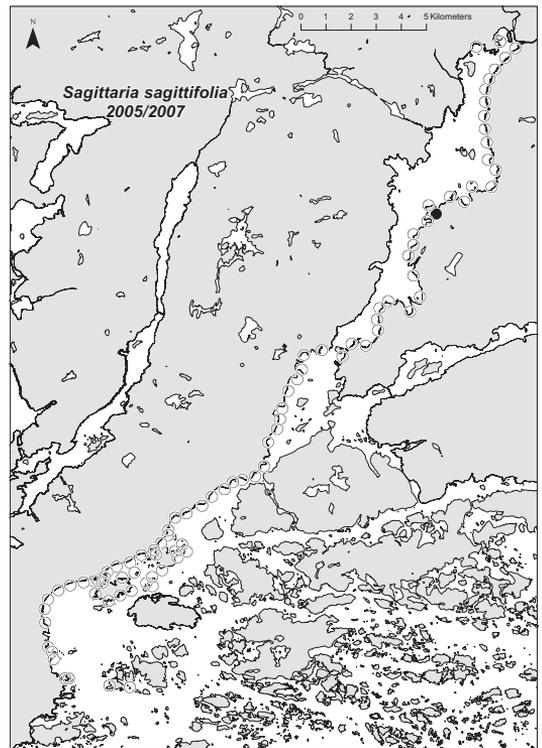
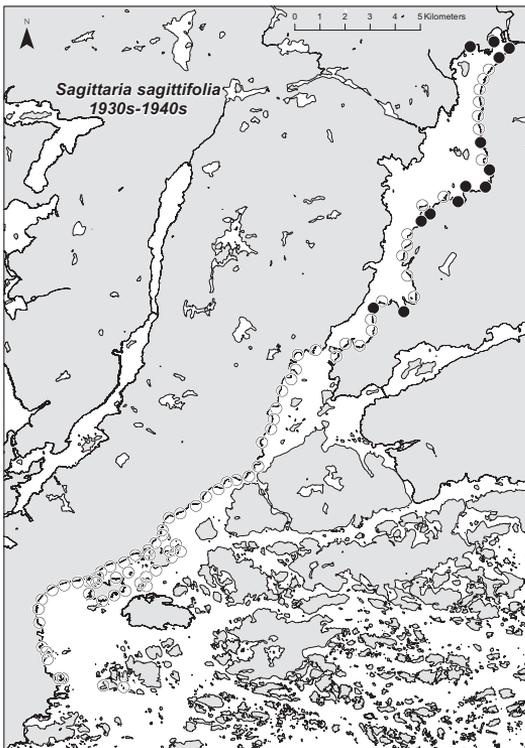


Fig. 28. Distribution of *Sagittaria sagittifolia*. ● presence, ○ absence.

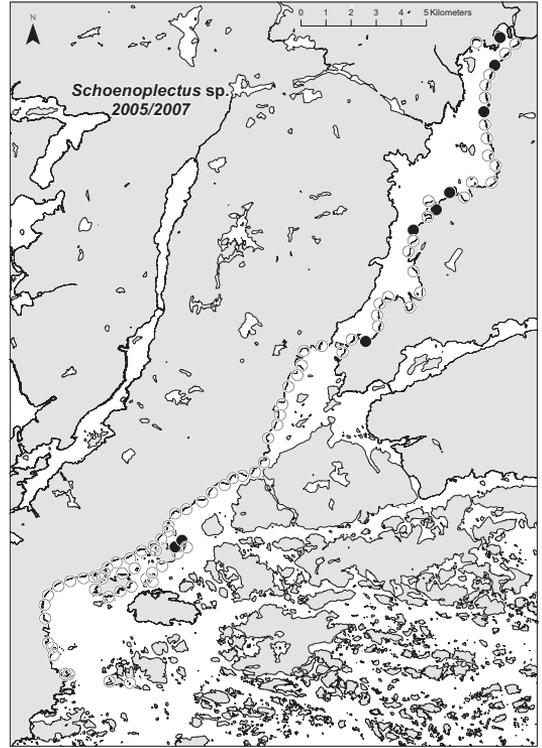
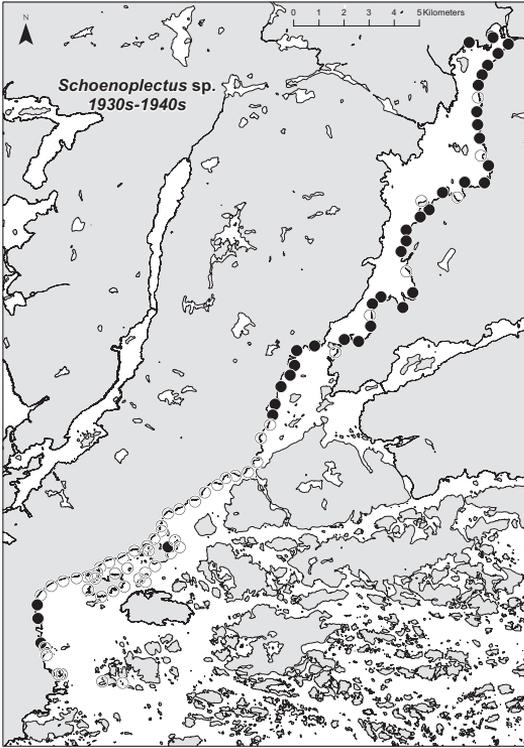


Fig. 29. Distribution of *Schoenoplectus* sp. ● presence, ○ absence.

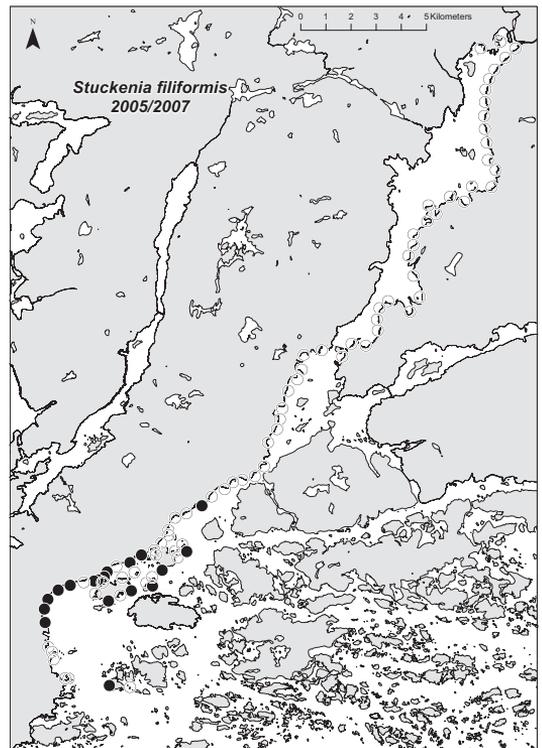
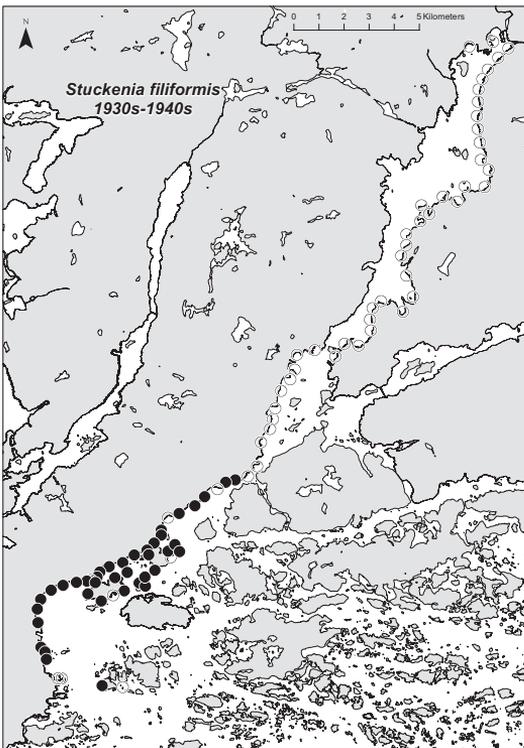


Fig. 30. Distribution of *Stuckenia filiformis*. ● presence, ○ absence.

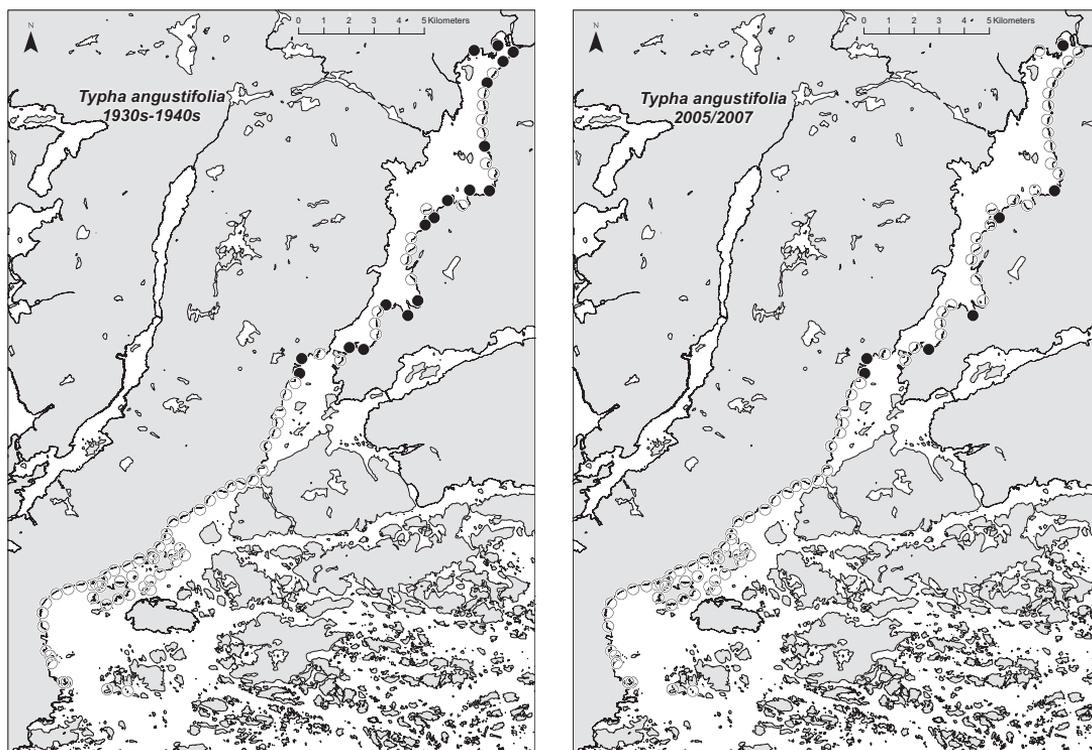


Fig. 31. Distribution of *Typha angustifolia*. ● presence, ○ absence.

freshwater inputs are found (Luther 1951b). However, these sparse occurrences had not been situated on the transects. In PZ, the frequency of the species decreased from 16 to 5 occurrences, and its distribution became more scattered. As compared with *P. australis*, it is an inferior competitor (Luther 1951b).

Typha latifolia (Fig. 32)

This species occurred less frequently in the area than *T. angustifolia*. In the 1930s–1940s, it had been present on 5 transects in PZ and OMZ (local freshwater inputs found), but in the 2005/2007 surveys it was found only on one transect in PZ. The species prefers gyttja bottoms. As compared with *P. australis*, it is an inferior competitor for space (Luther 1951b).

Plantago uniflora (syn. *Littorella uniflora*) (Fig. 33)

This isoetid species prefers minerogenic substrates on exposed sites (Luther 1951b). In

the 1930s–1940s, it had been found on eight transects in low-salinity PZ; in 2005/2007 it was found only on three.

Species whose occurrence frequencies remained unchanged

Butomus umbellatus (Fig. 34)

The species prospers on eutrophic gyttja bottoms in the low-salinity parts of the area, but is weak in competition for space (Luther 1951b). In the 1930s–1940s, it had mostly been found in the northern parts of PZ and had occurred also very rarely in MZ, but not on the transects. In 2005/2007, the species was found on one transect in MZ. In both surveys, six occurrences were found in PZ.

Callitriche hermaphroditica (in the historical data *C. autumnalis*) (Fig. 35)

In the 1930s–1940s, the species had been found

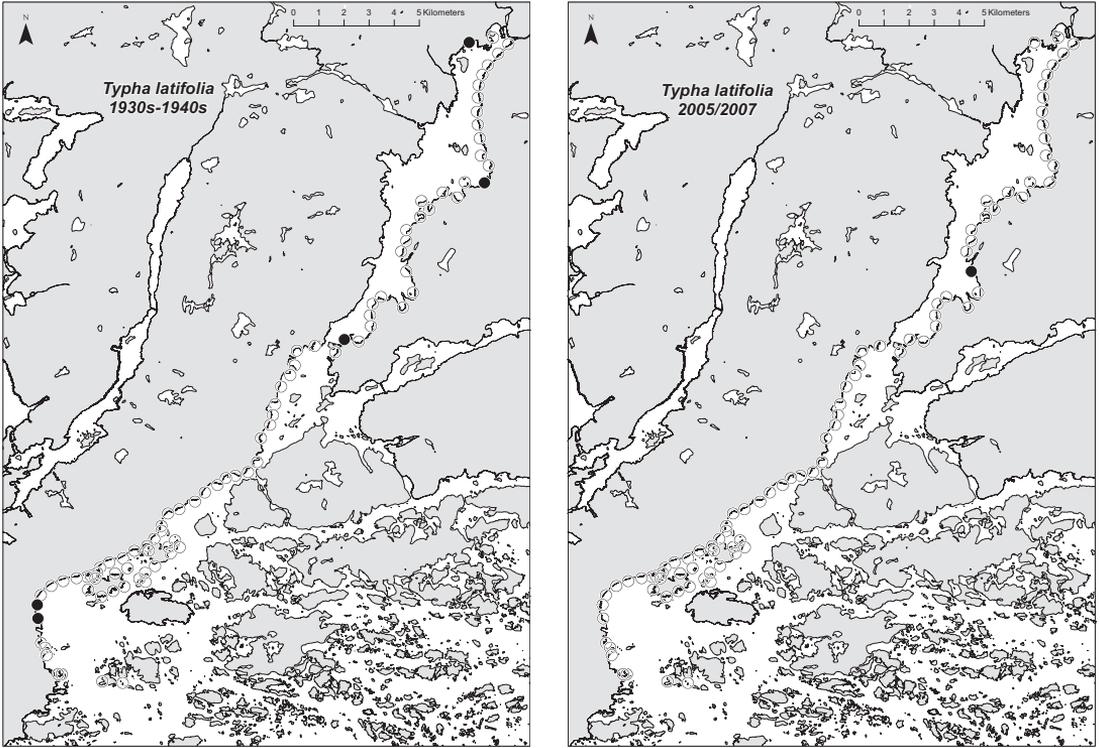


Fig. 32. Distribution of *Typha latifolia*. ● presence, ○ absence.

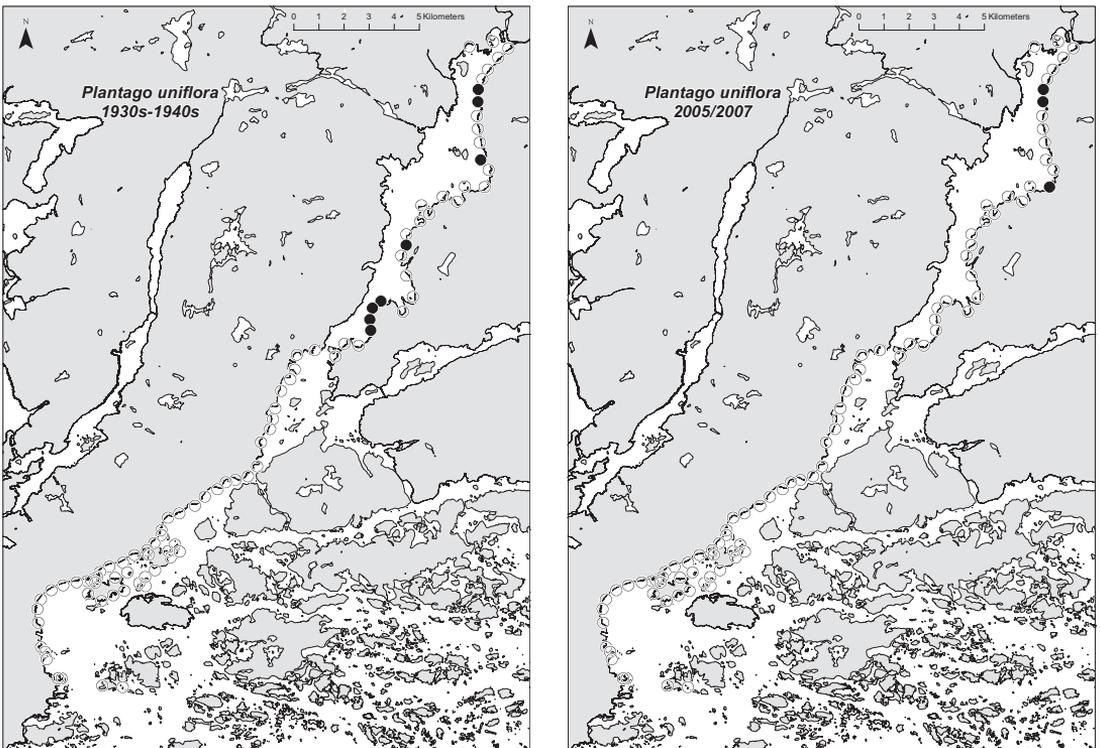


Fig. 33. Distribution of *Plantago uniflora*. ● presence, ○ absence.

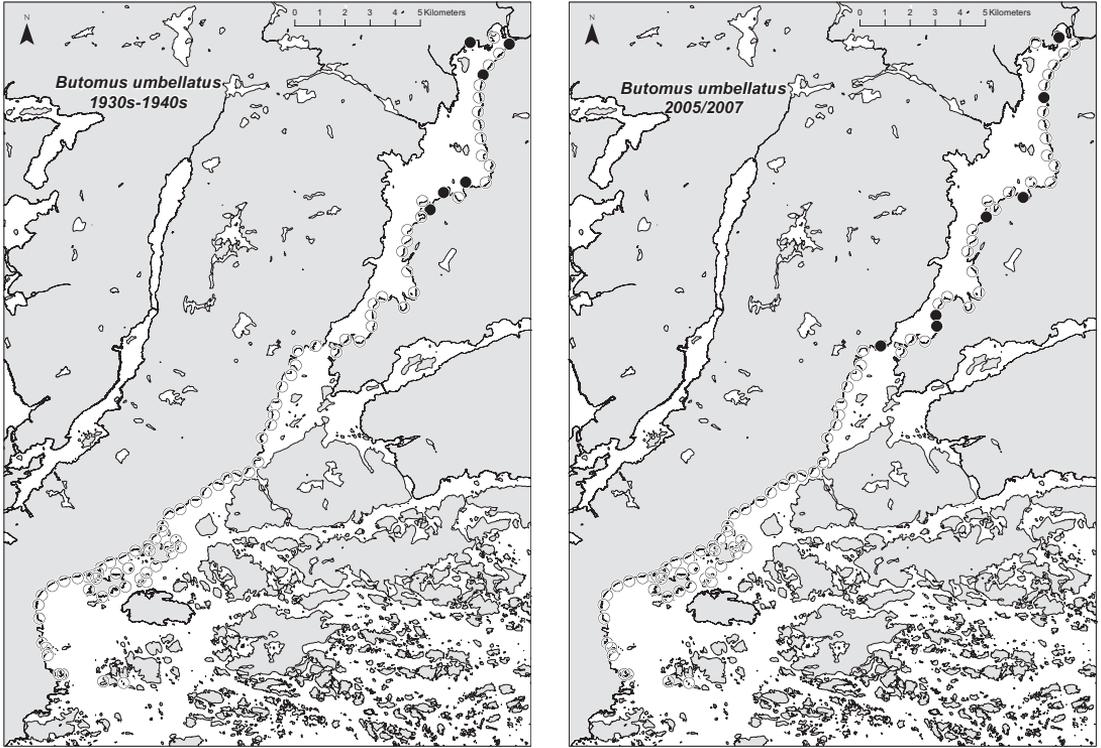


Fig. 34. Distribution of *Butomus umbellatus*. ● presence, ○ absence.

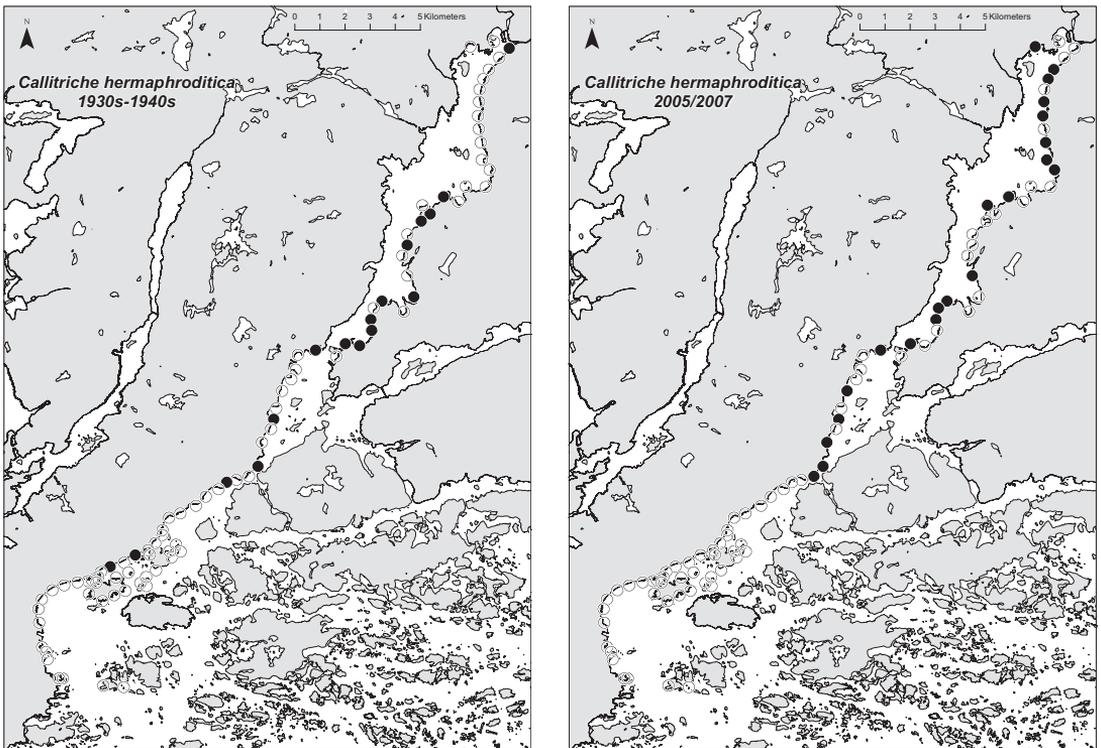


Fig. 35. Distribution of *Callitriche hermaphrodita*. ● presence, ○ absence.

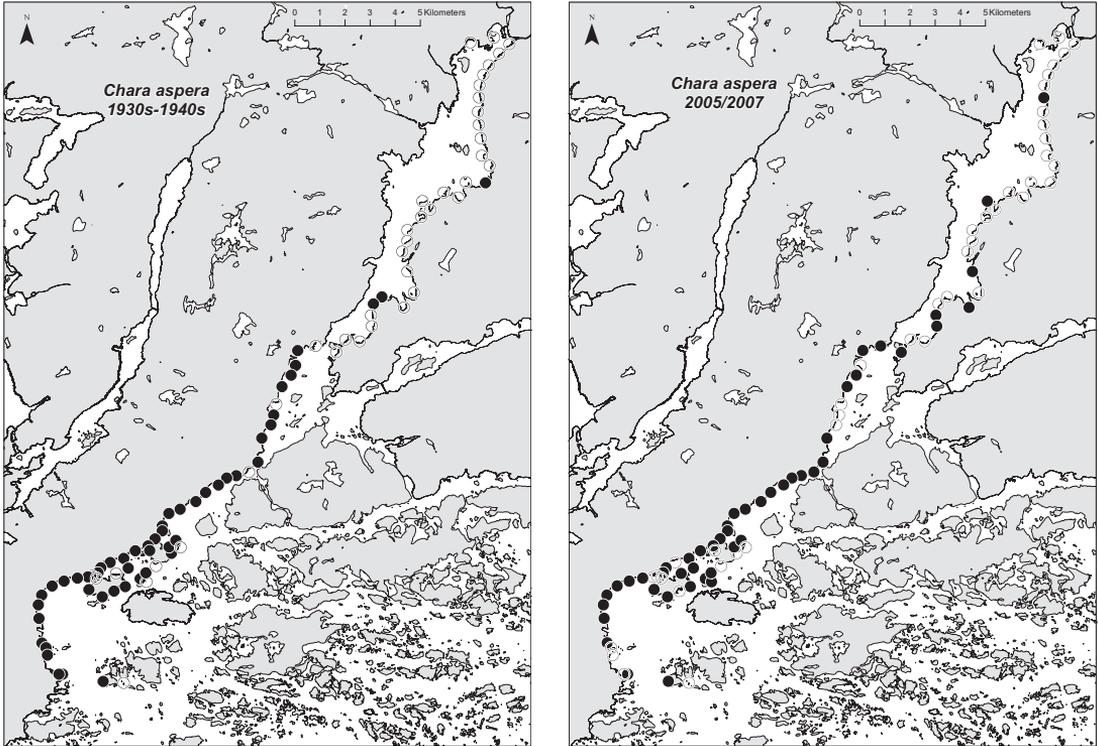


Fig. 36. Distribution of *Chara aspera*. ● presence, ○ absence.

throughout the study area. In 2005/2007, it was not present in the outer zones but had spread to the Sjösång area in PZ (see Fig. 1). The species prefers gyttja bottoms (Luther 1951b).

Chara aspera (Fig. 36)

This most common charophyte in the area tolerates a wide range of exposure and habitat types. It was especially frequent in the outer zones, and occurred more sporadically in MZ and PZ.

Elodea canadensis (Fig. 37)

It is a non-indigenous species introduced to Finland in 1884 (Hintikka 1917). It was found in PZ for the first time in 1935 (Luther 1951b), and it prefers sheltered gyttja bottoms.

Hippuris vulgaris (Fig. 38)

In both surveys, this species was found on clay-

gyttja substrates at only one location in PZ.

Hydrocharis morsus-ranae (Fig. 39)

This floating species was found only in sheltered and eutrophic locations in the northernmost end of low-salinity PZ.

Lemna minor (Fig. 40)

This floating species occurred mainly on nutrient-rich sites in low-salinity PZ. The species spread to MZ, but did not increase in frequency.

Najas marina (Fig. 41)

This annual species occurred mainly in MZ and the southern part of PZ. According to Luther (1951b), this alcaliphilous species has an inner distribution border in the area because of the influence of more acidic freshwater (as for *Chara tomentosa*), and it prefers sheltered locations with gyttja bottoms.

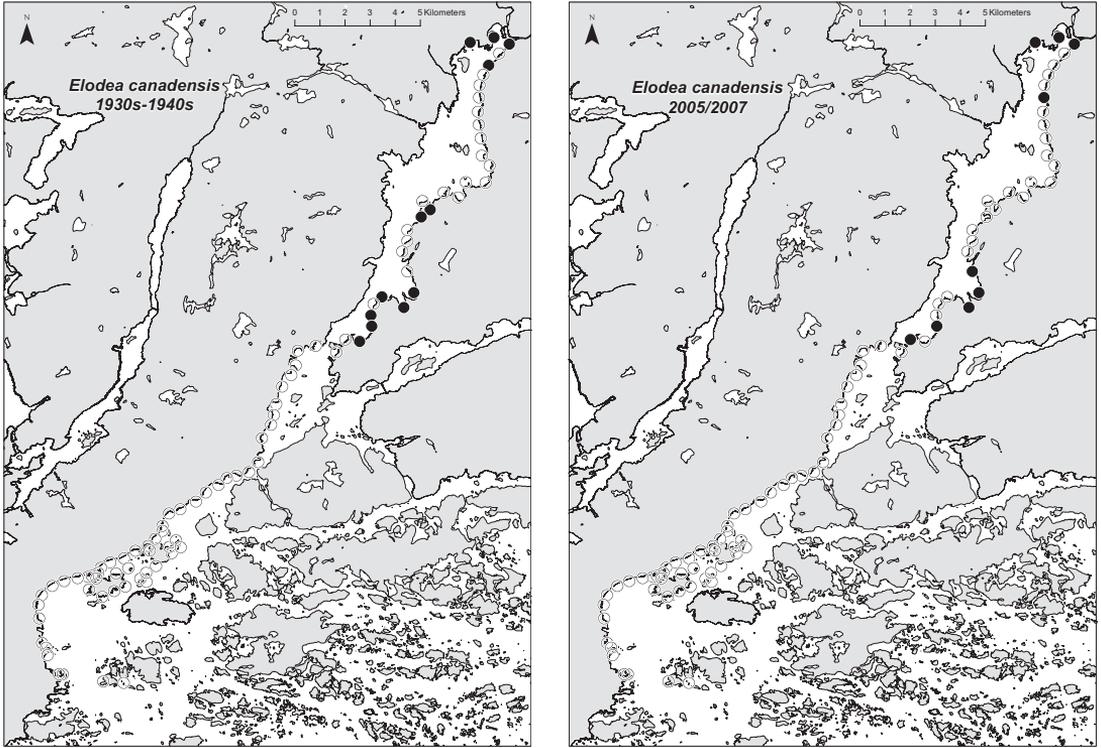


Fig. 37. Distribution of *Elodea canadensis*. ● presence, ○ absence.

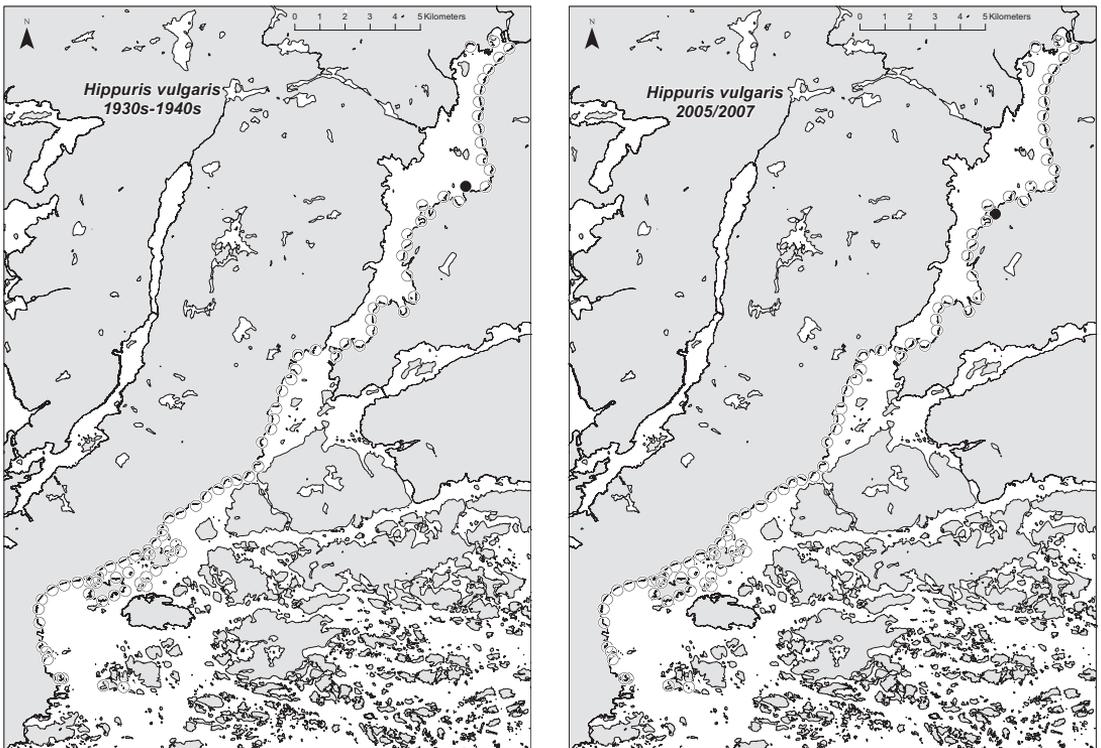


Fig. 38. Distribution of *Hippuris vulgaris*. ● presence, ○ absence.

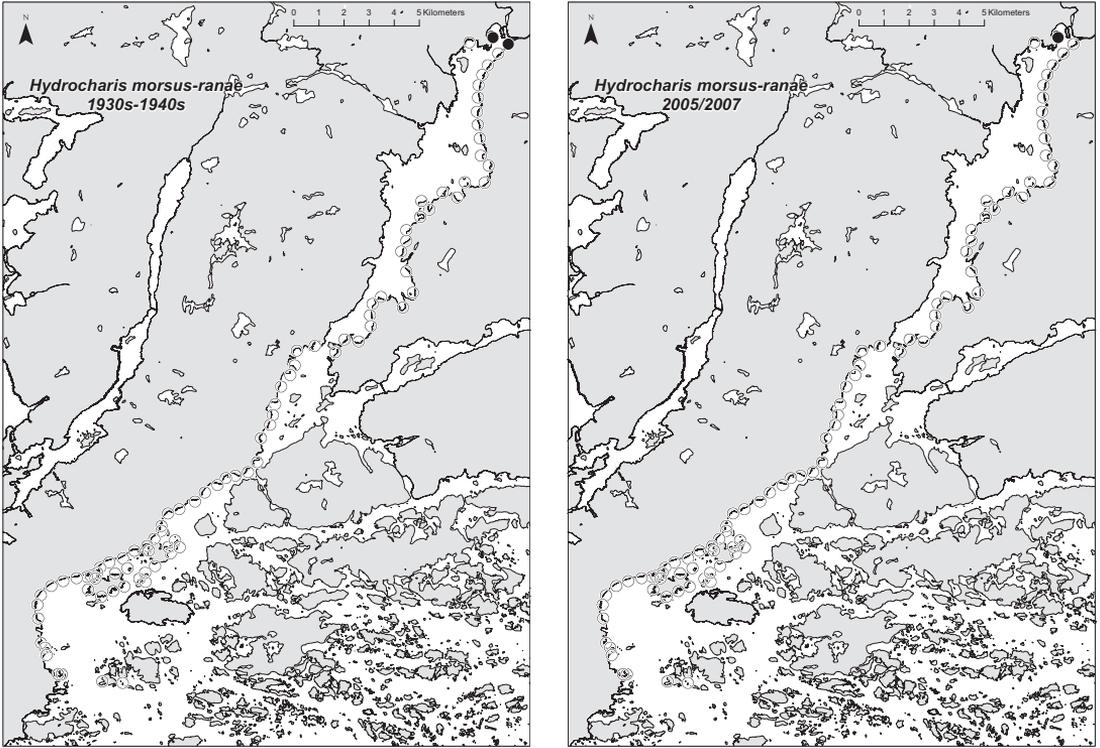


Fig. 39. Distribution of *Hydrocharis morsus-ranae*. ● presence, ○ absence.

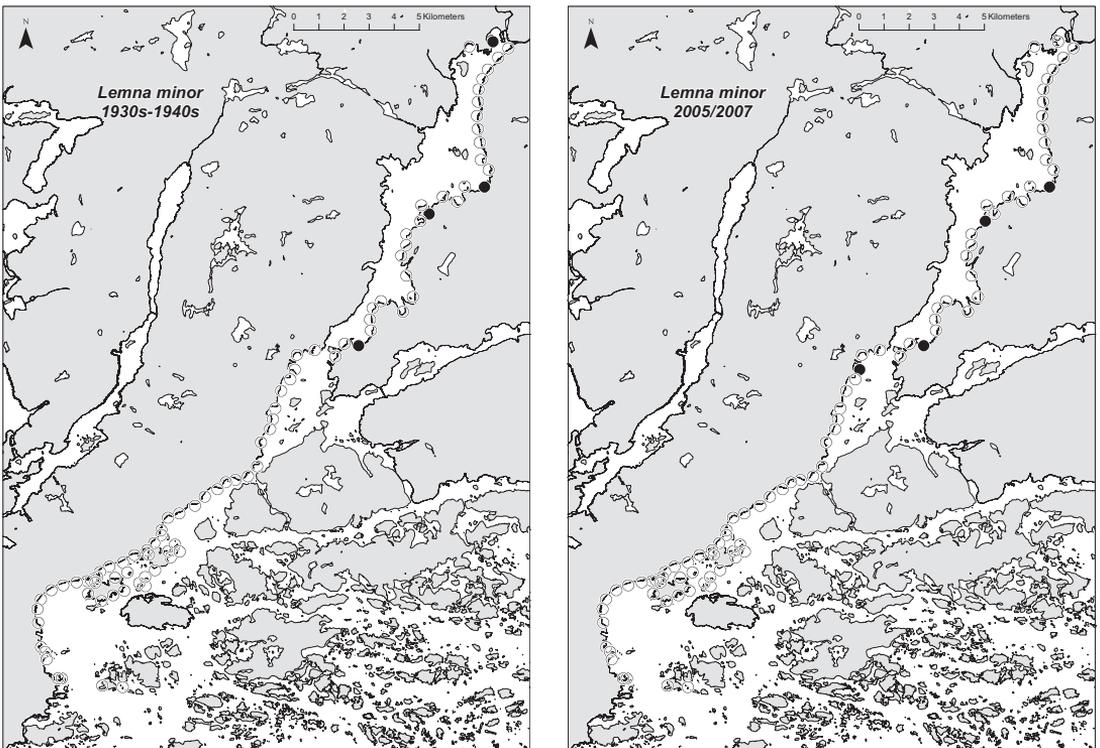


Fig. 40. Distribution of *Lemna minor*. ● presence, ○ absence.

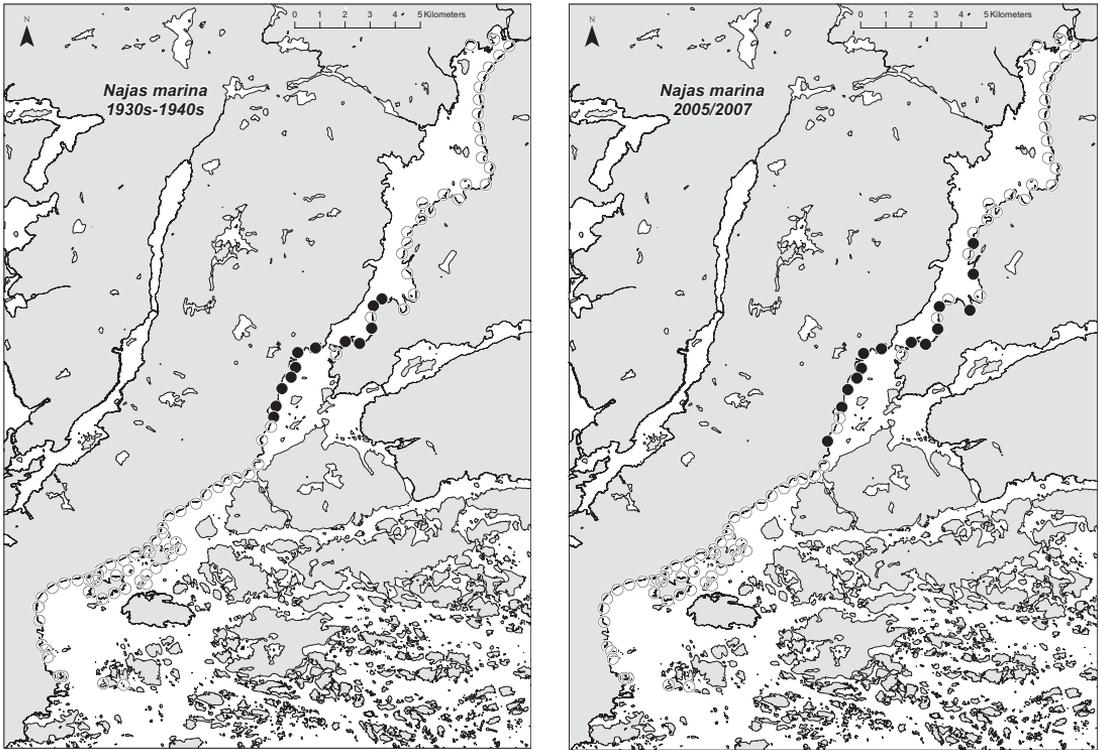


Fig. 41. Distribution of *Najas marina*. ● presence, ○ absence.

Nuphar lutea (Fig. 42)

This floating-leaved species occurred in low-salinity PZ. In the 1930s–1940s, it also had one occurrence in MZ. It grew on a variety of bottom substrates outside reeds.

Potamogeton natans (Fig. 43)

This floating-leaved species was found especially in the northern parts of PZ. It occurs on clay or gyttja (Luther 1951b). In the 1930s–1940s surveys, it had had four occurrences and in the 2005/2007 two.

Potamogeton perfoliatus (Fig. 44) and
Stuckenia pectinata (syn. *Potamogeton pectinatus*) (Fig. 45)

These ubiquitous species were the most common in all the zones of the study area in both the historical and contemporary surveys.

Potamogeton pusillus (in the historical data *P. panormitanus*) (Fig. 46)

The overall frequency of the species did not change in the study area. However, in the 1930s–1940s the species had been more frequent in PZ and MZ than in 2005/2007. In the archipelago area, the species had occurred very sparsely and not on the transects. In 2005/2007, the situation was opposite, as the species increased in IZ and OZ, but decreased in PZ and MZ. This small species was most common on gyttja and sand-gyttja bottoms.

Ranunculus circinatus (Fig. 47)

Occasionally, this pleustophytic species roots lightly on gyttja bottoms (Luther 1951b). Its distribution in the 1930s–1940s had resembled that of *Ceratophyllum demersum*, as it had been concentrated in the northernmost and southernmost parts of PZ and had also sparsely occurred in MZ. Occurrences in the archipelago had been very sparse and not located on the transects. In

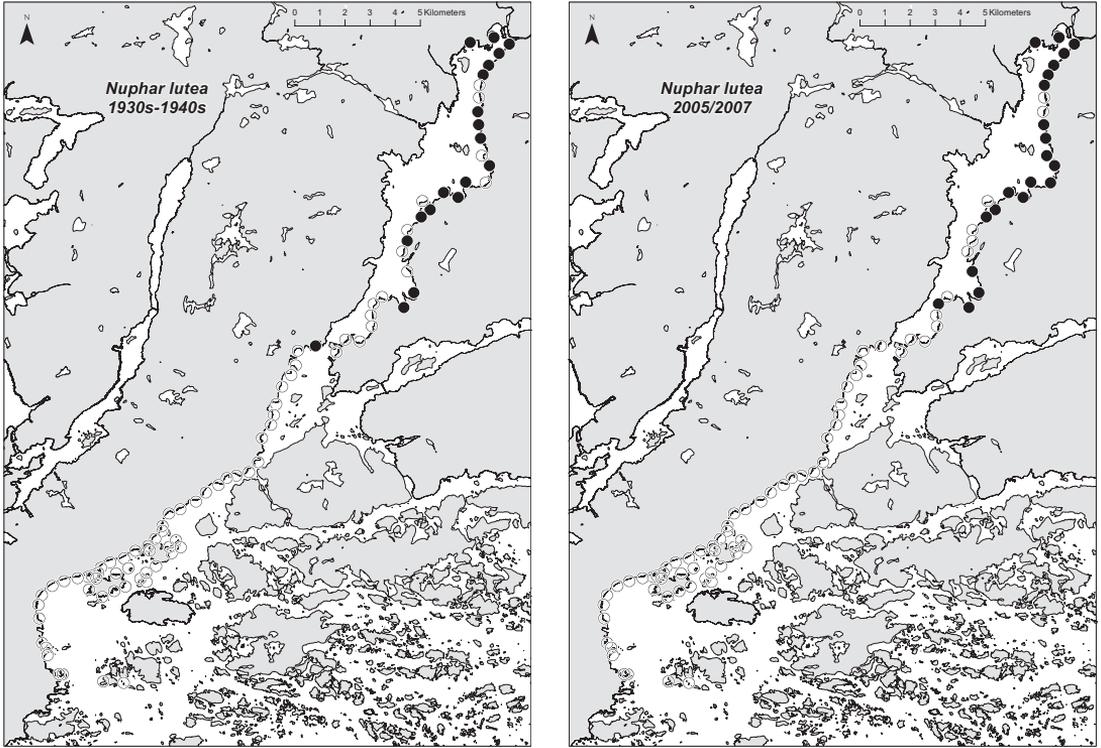


Fig. 42. Distribution of *Nuphar lutea*. ● presence, ○ absence.

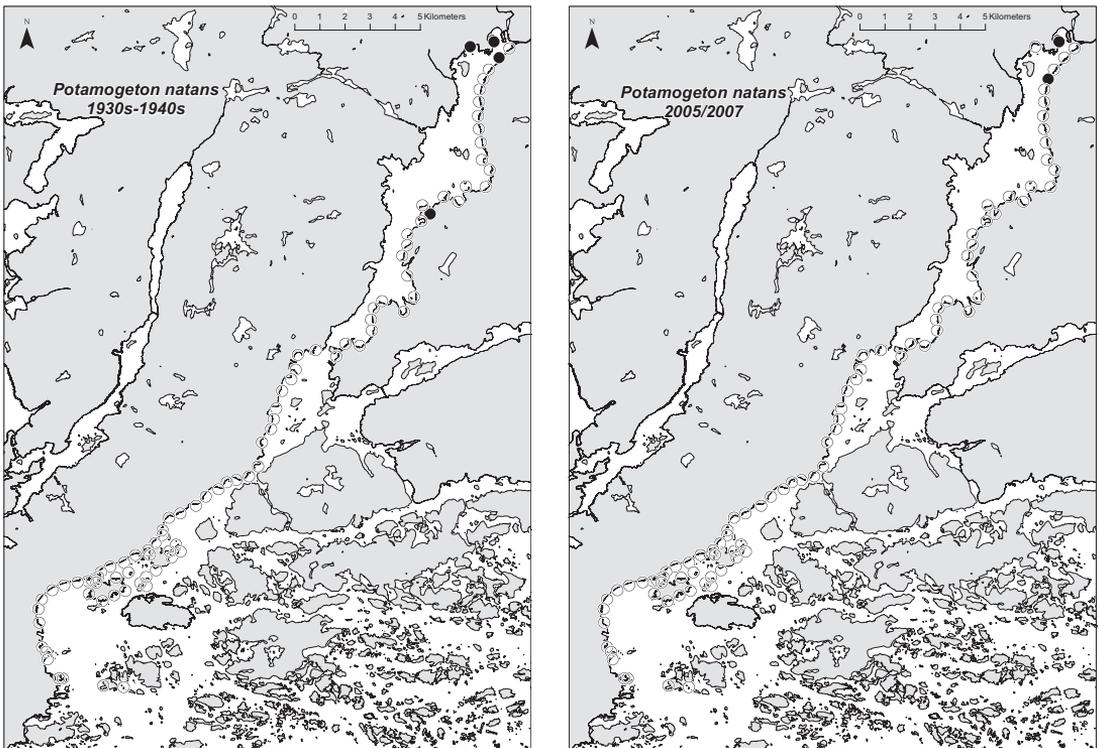


Fig. 43. Distribution of *Potamogeton natans*. ● presence, ○ absence.

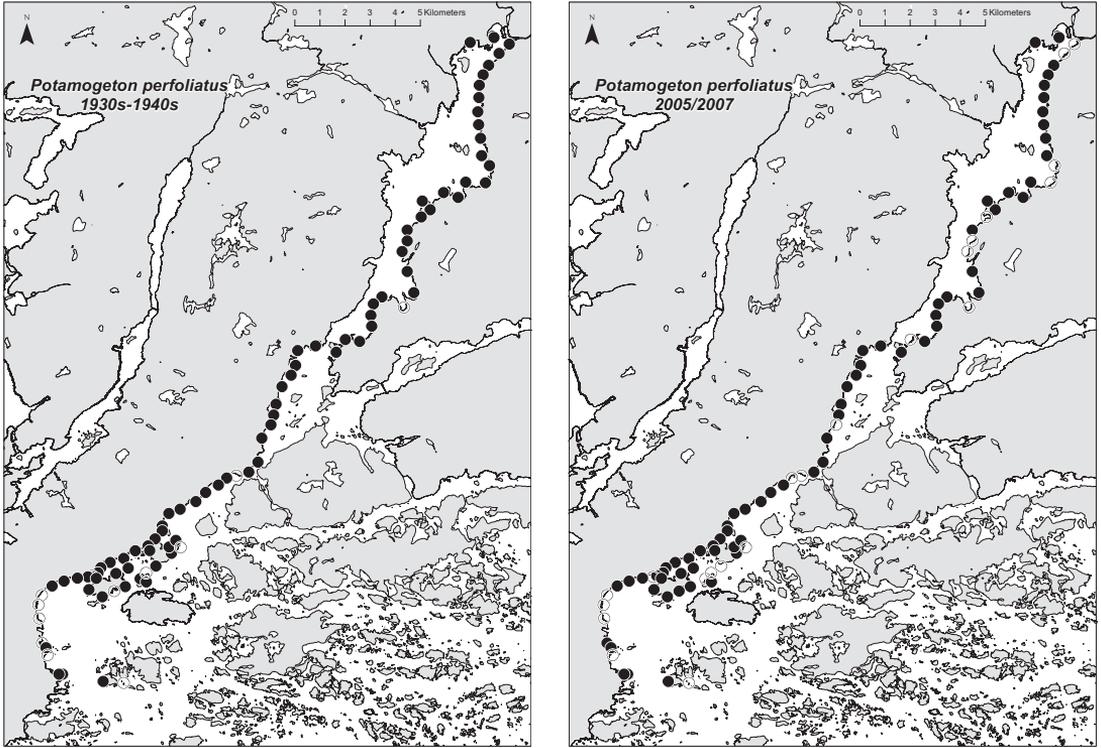


Fig. 44. Distribution of *Potamogeton perfoliatus*. ● presence, ○ absence.

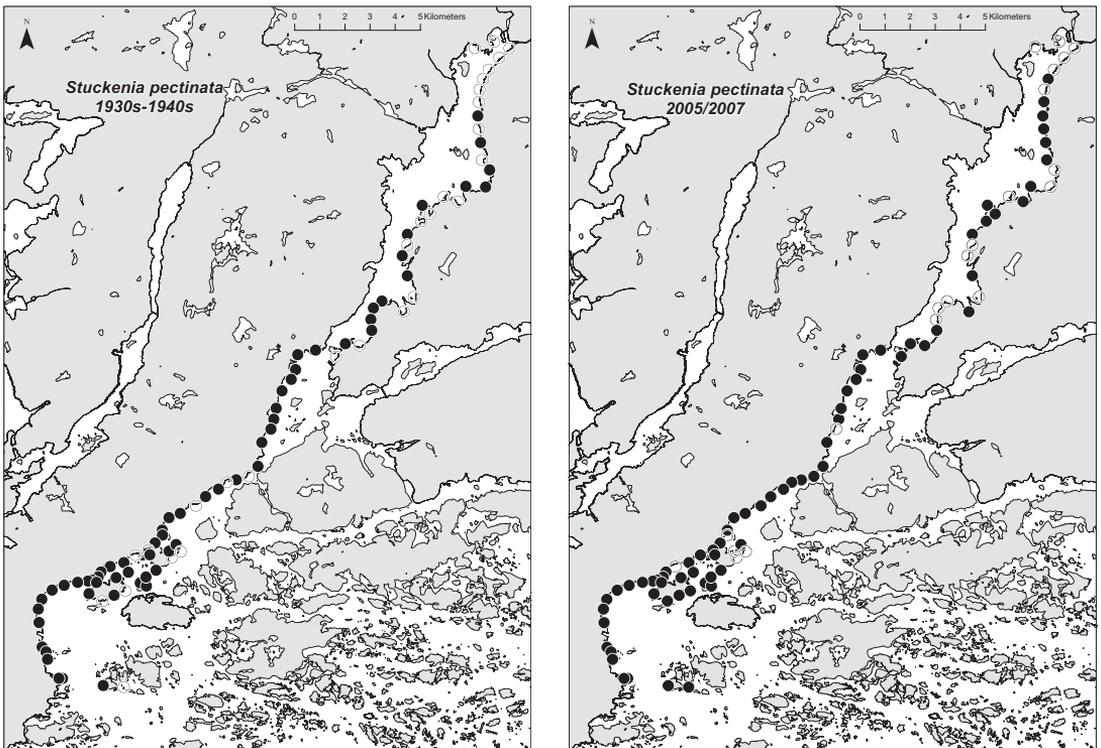


Fig. 45. Distribution of *Stuckenia pectinata*. ● presence, ○ absence.

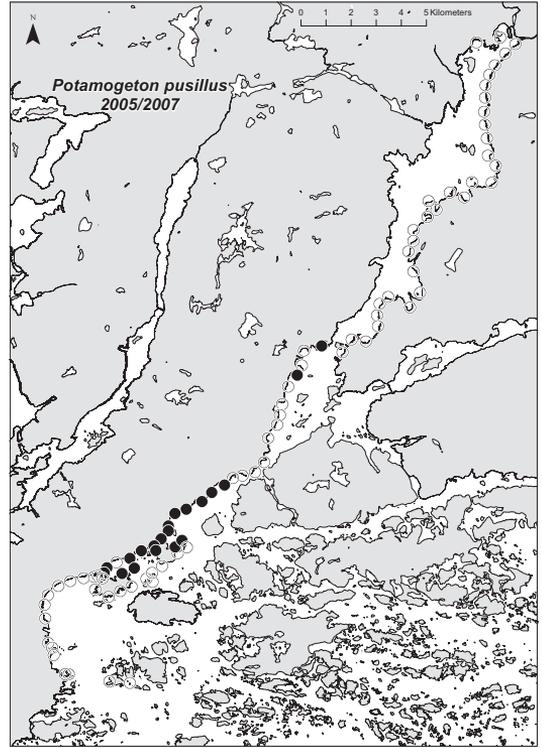
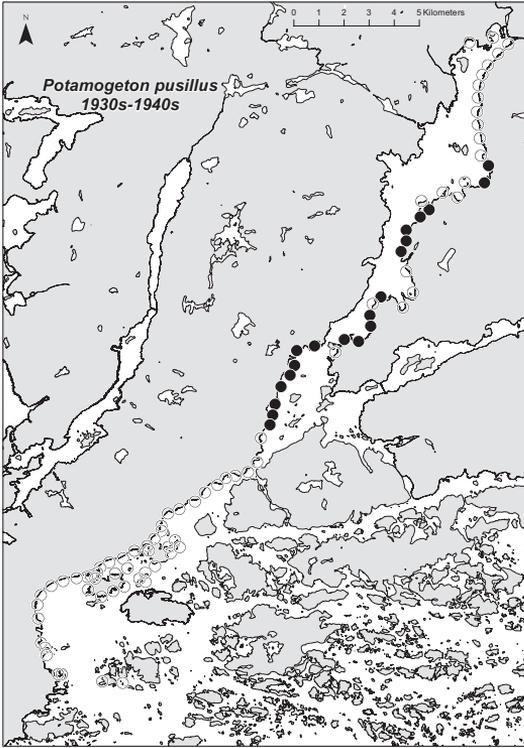


Fig. 46. Distribution of *Potamogeton pusillus*. ● presence, ○ absence.

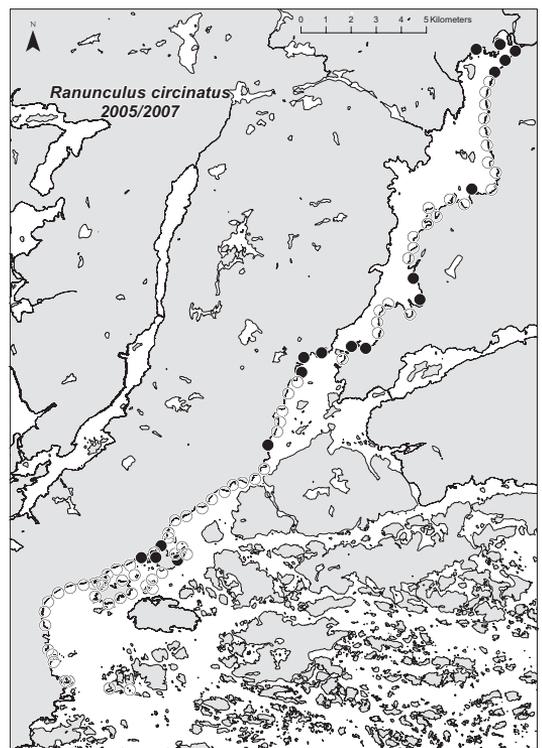
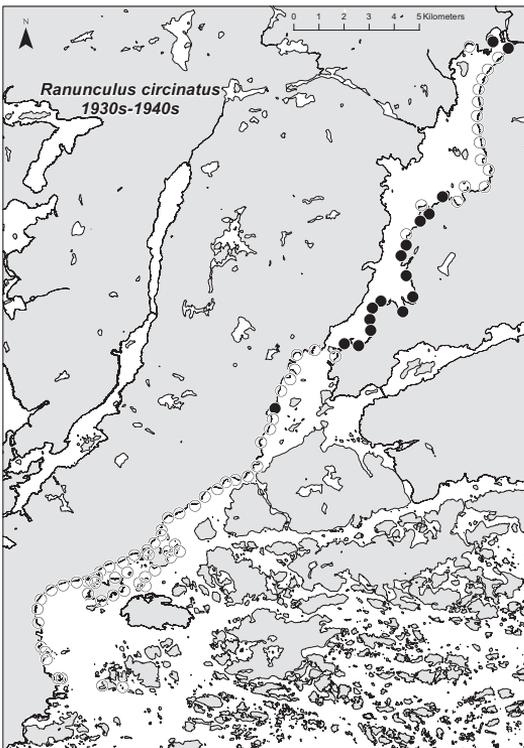


Fig. 47. Distribution of *Ranunculus circinatus*. ● presence, ○ absence.

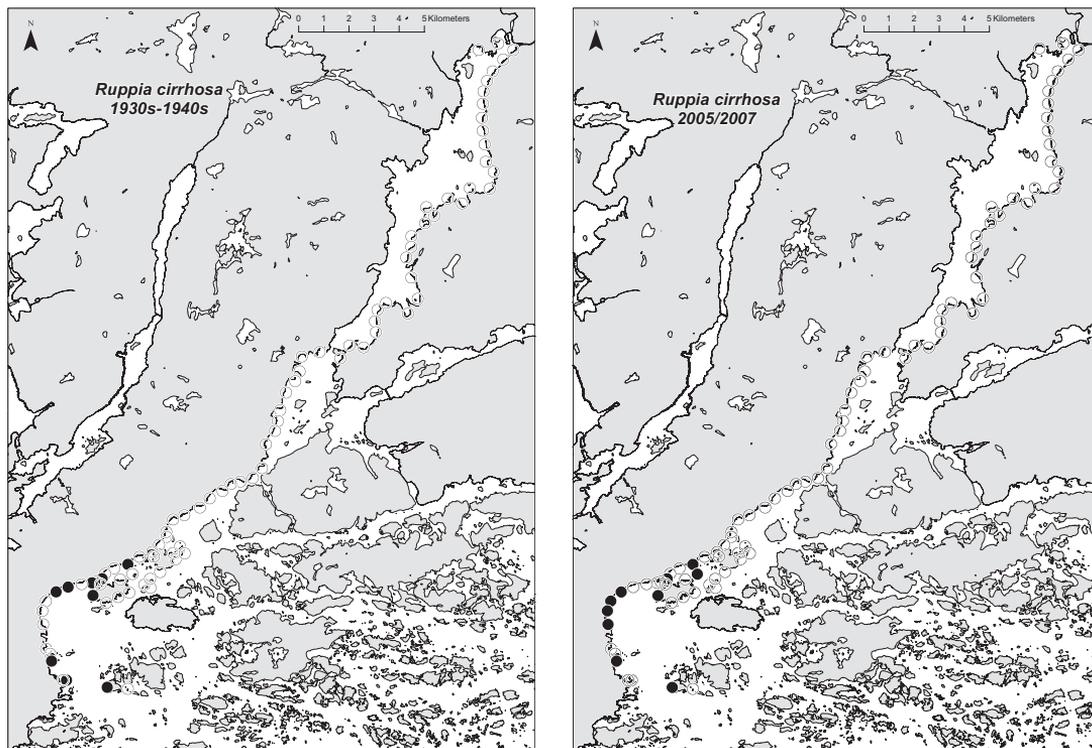


Fig. 48. Distribution of *Ruppia cirrhosa*. ● presence, ○ absence.

2005/2007, the overall frequency of the species remained unchanged, but a local frequency increase could be observed in the sheltered parts of IZ and OZ.

Ruppia cirrhosa (in the historical data *R. spiralis*) (Fig. 48)

It is a species of sandy and exposed shores of higher-salinity OZ and OMZ.

***Sparganium* sp.** (Fig. 49)

The species of this group were found in PZ mainly on gyttja-clay bottoms. In the 1930s–1940s, the group had had one occurrence also in MZ. The most likely species to occur in the area is *Sparganium emersum* (syn. *S. simplex*).

***Zannichellia palustris* coll.** (in the historical data *Z. repens* and *Z. pedunculata*) (Fig. 50)

The distribution of the species in the archipelago

became more coherent. The ubiquitous variation *Z. palustris* var. *palustris* occurred throughout the study area, but was most common in the outer parts of the area, in MZ–OMZ. *Zannichellia palustris* var. *pedicellata* had been limited to higher-salinity IZ–OMZ. In the 1930s–1940s, it had occurred very sparsely in OZ and IZ, and was not found on the transects. In 2005/2007, this variation occurred quite frequently on more or less sheltered gyttja bottoms of the archipelago.

Species not categorized

Chara canescens (Fig. 51) and ***Tolypella nidifica*** (Fig. 52)

Both species are annual charophytes with considerable frequency fluctuations between years (Luther 1951b, Riggert Munsterhjelm pers. comm.). *Chara canescens* was restricted to the archipelago, whereas *T. nidifica* could occur also in MZ.

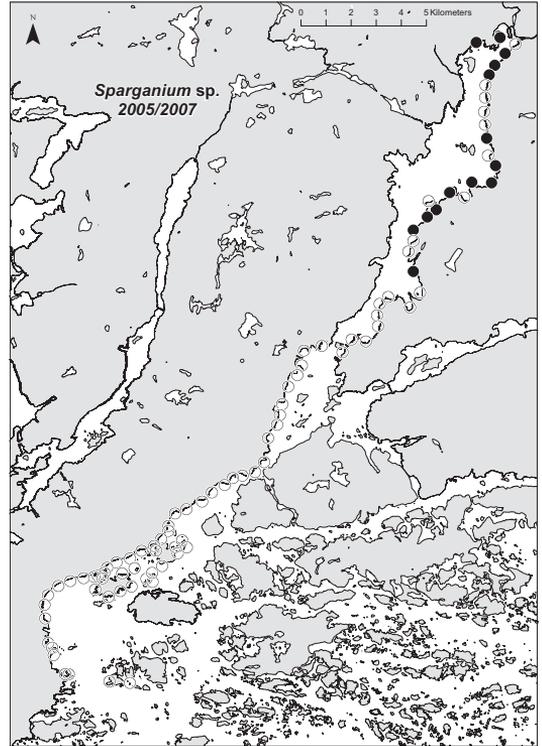
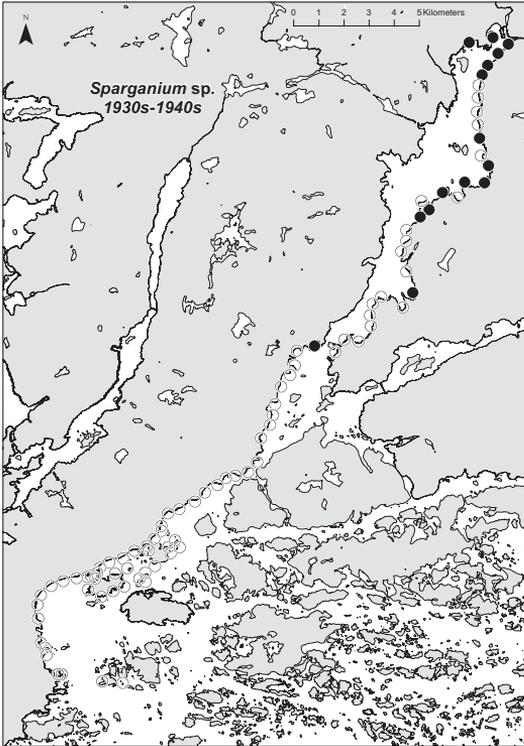


Fig. 49. Distribution of *Sparganium* sp. ● presence, ○ absence.

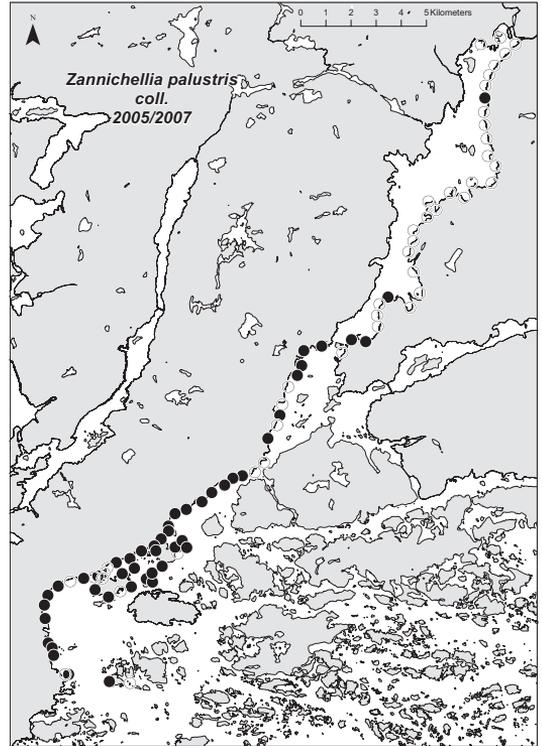
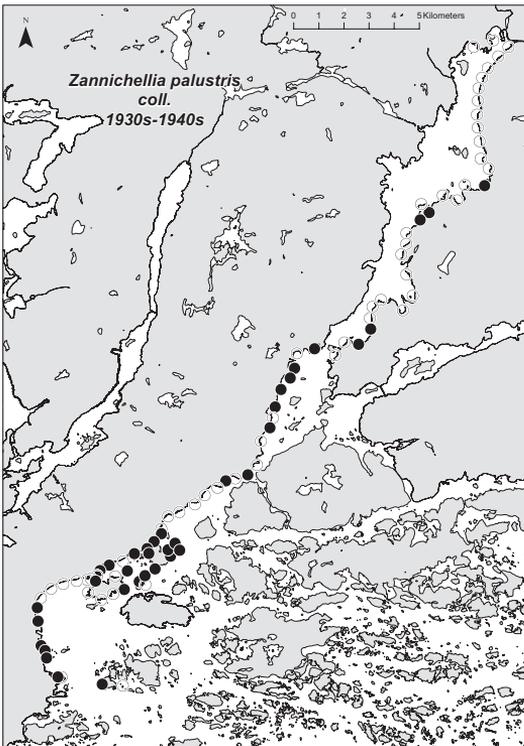


Fig. 50. Distribution of *Zannichellia palustris* coll. ● presence, ○ absence.

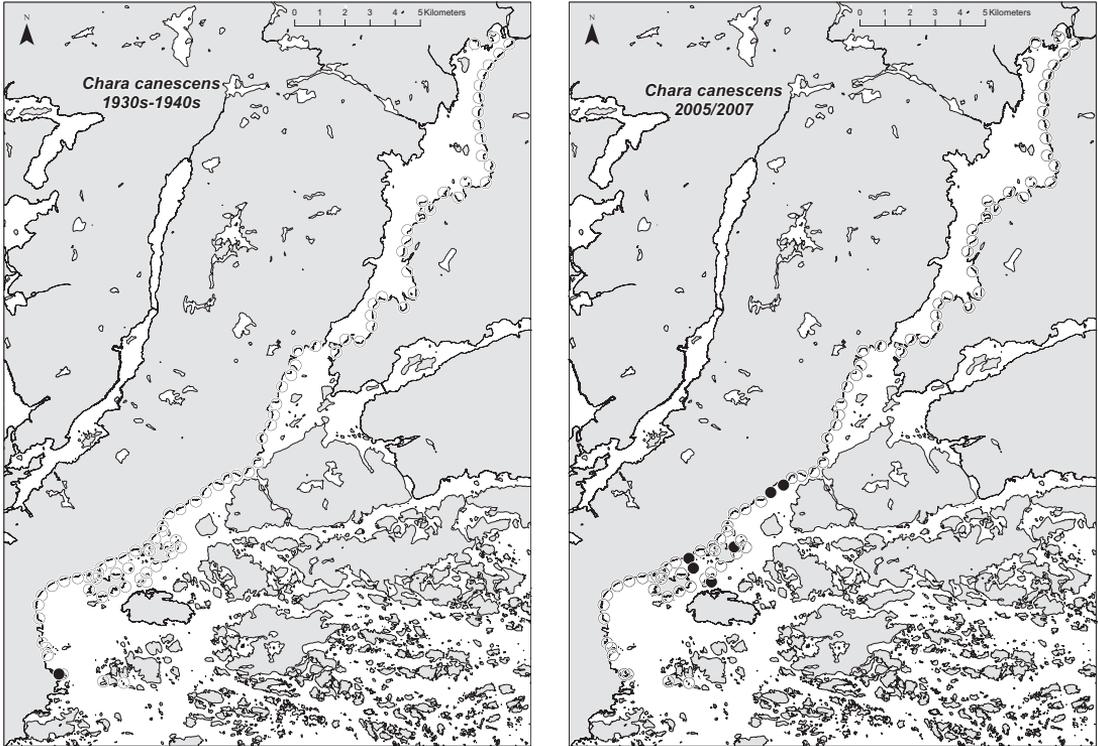


Fig. 51. Distribution of *Chara canescens*. ● presence, ○ absence.

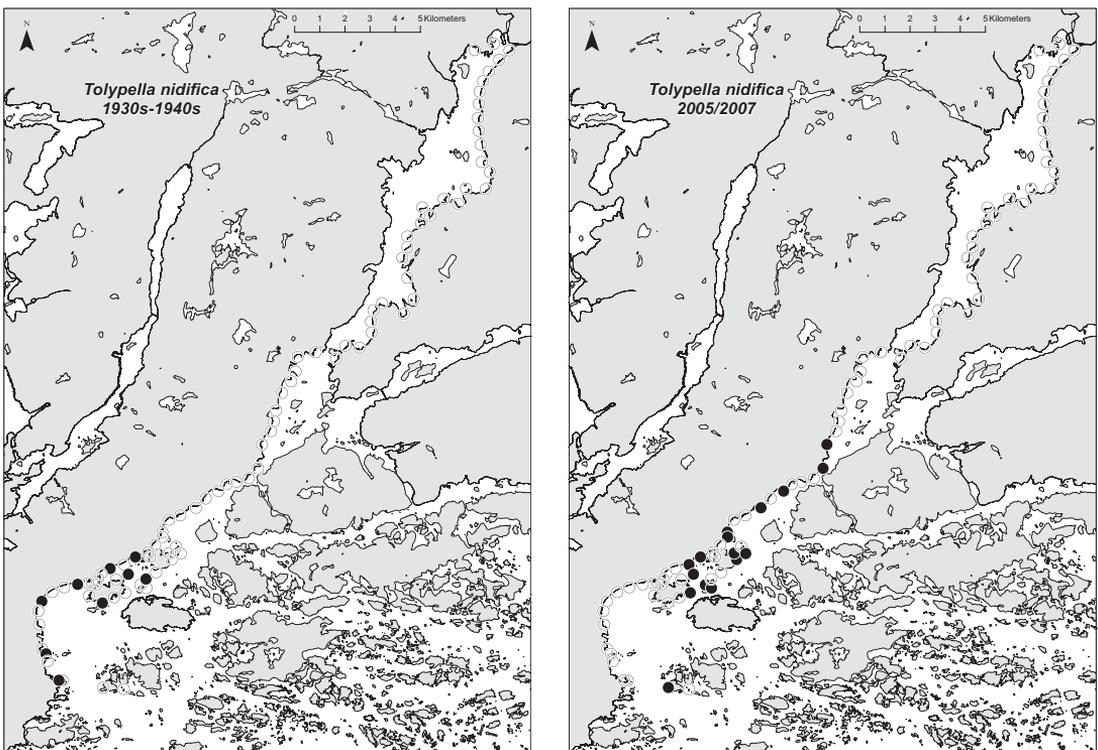


Fig. 52. Distribution of *Tolypella nidifica*. ● presence, ○ absence.

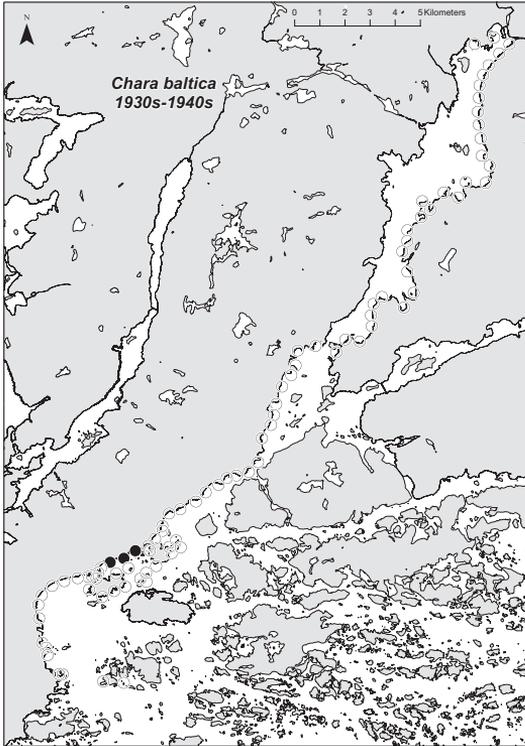


Fig. 53. Distribution of *Chara baltica*. ● presence, ○ absence.

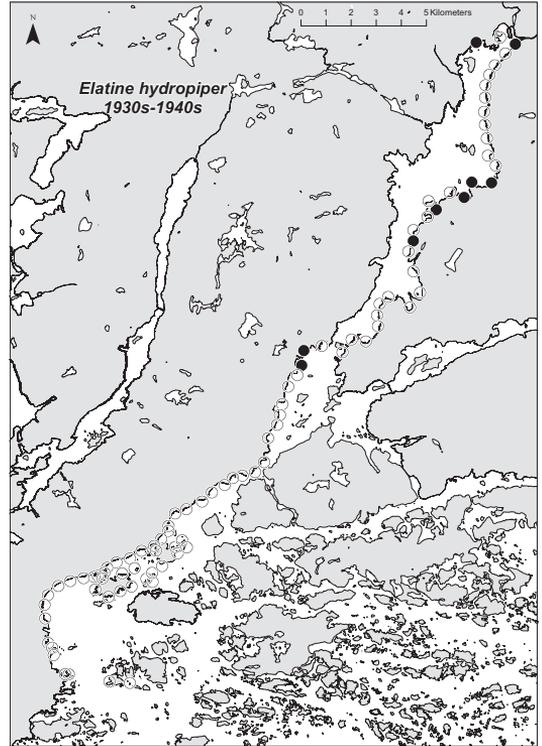


Fig. 54. Distribution of *Elatine hydropiper*. ● presence, ○ absence.

Species found only in the 1930s–1940s surveys

Chara baltica (Fig. 53)

This charophyte species was limited to exposed, minerogenic bottoms in higher-salinity OZ.

Elatine hydropiper (Fig. 54)

Elatine hydropiper was found at sheltered sites in low-salinity PZ and MZ. According to Luther (1951b), this small annual species is a weak competitor, and prefers minerogenic substrates mixed with gyttja.

Elatine triandra (Fig. 55)

This weak competitor was restricted to low-salinity PZ and MZ. It tolerates more exposure than *E. hydropiper* and prefers clay-gyttja substrates (Luther 1951b). Both *Elatine* species were most commonly found growing near the

shoreline, but they did also occur down to 1.8 m depth (Luther 1951b).

Isoëtes echinospora (Fig. 56)

The species occurred on minerogenic bottoms in low-salinity PZ. Also, the intensity of exposure and competition influenced the selection of growing sites (Luther 1951b).

Myriophyllum alterniflorum (Fig. 57)

This oligotraphent *Myriophyllum*-species was found at exposed and minerogenic sites in low-salinity PZ, and is a weak competitor (Luther 1951b).

Potamogeton alpinus (Fig. 58)

The species was sparsely distributed in PZ and MZ, mainly at sites where small streams emanate.

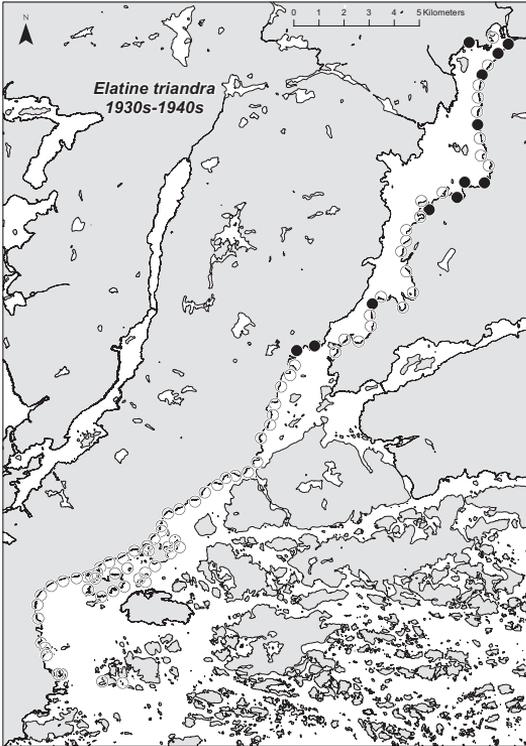


Fig. 55. Distribution of *Elatine triandra*. ● presence, ○ absence.

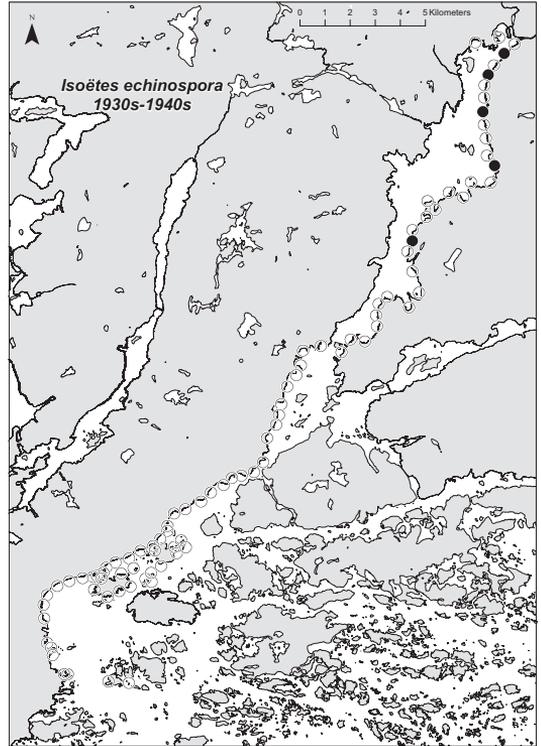


Fig. 56. Distribution of *Isoetes echinospora*. ● presence, ○ absence.

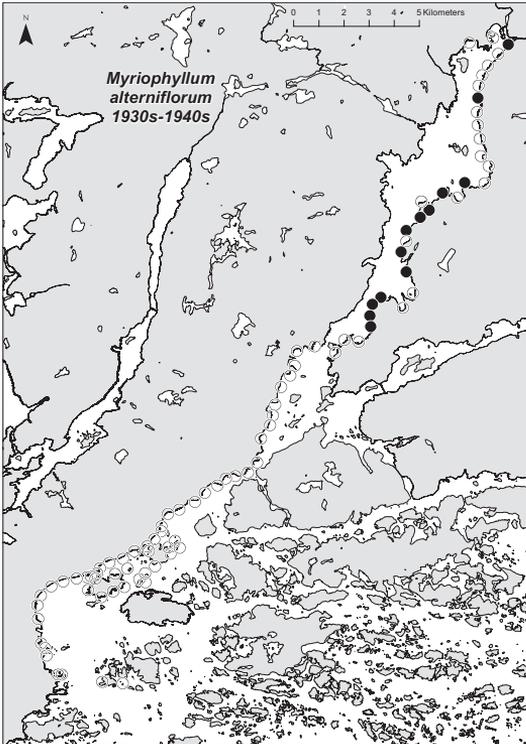


Fig. 57. Distribution of *Myriophyllum alterniflorum*. ● presence, ○ absence.

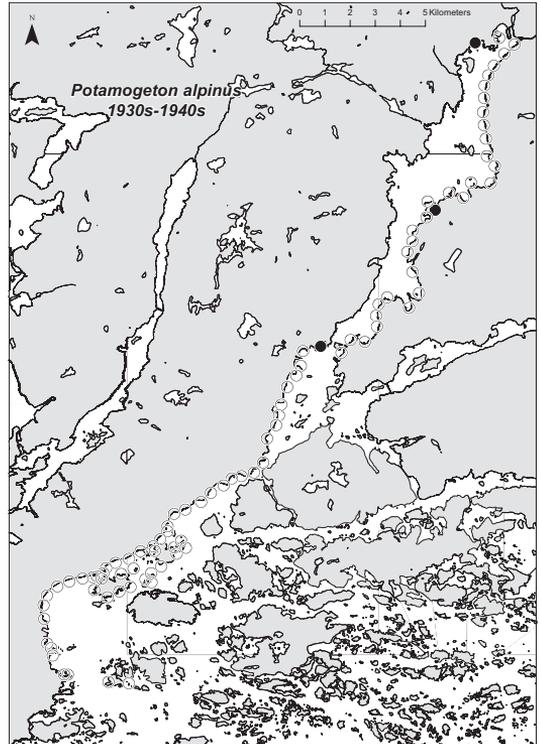


Fig. 58. Distribution of *Potamogeton alpinus*. ● presence, ○ absence.

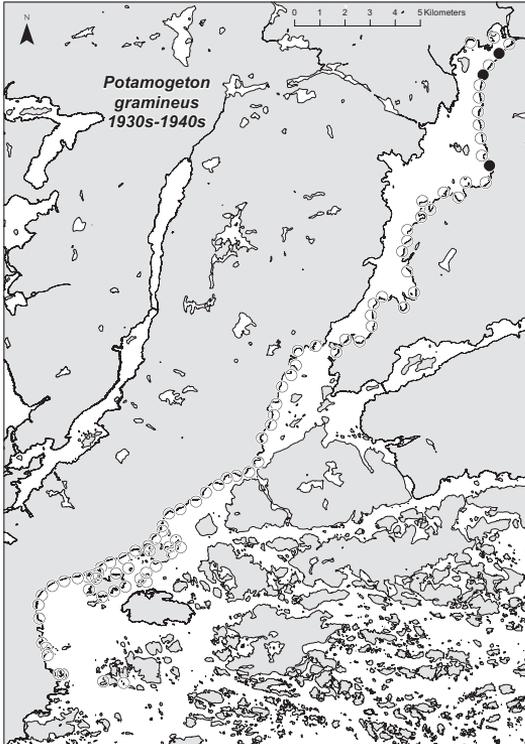


Fig. 59. Distribution of *Potamogeton gramineus*. ● presence, ○ absence.

Potamogeton gramineus (Fig. 59)

This species occurred on minerogenic substrates on the more oligotrophic shores of low-salinity PZ.

Potamogeton gramineus × *perfoliatus* (syn. *P. × nitens*) (Fig. 60)

It was found in PZ, often growing on the shore side of reeds in quite exposed locations. The species prefers minerogenic substrates (Luther 1951b).

Ranunculus confervoides (Fig. 61)

The species grew sparsely on grazed shores of low-salinity PZ.

Schoenoplectus maritimus (in the historical data *Scirpus maritimus*) (Fig. 62)

This emergent species was rare and quite randomly distributed in the area. According to

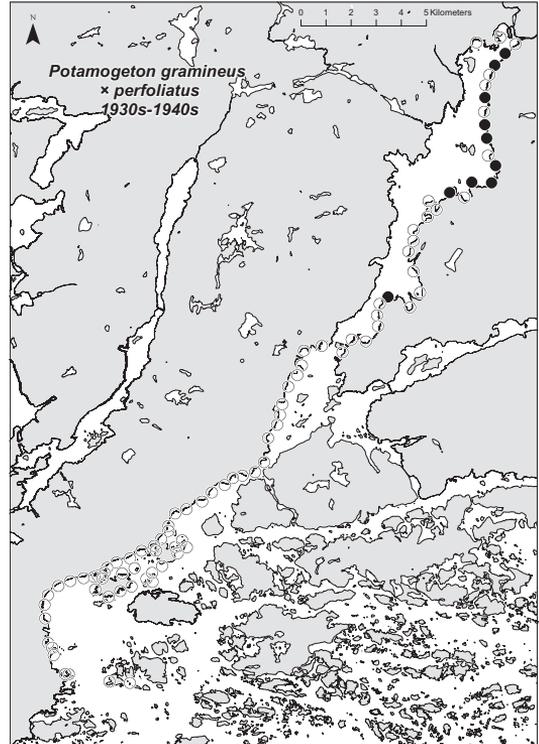


Fig. 60. Distribution of *Potamogeton gramineus* × *perfoliatus*. ● presence, ○ absence.

Luther (1951b), it prefers gyttja bottoms and is a weak competitor. In the 1930s–1940s, the species was found on one transect in PZ.

Species found only in the 2005/2007 surveys

Fissidens fontanus (in the historical data *F. julianus*; syn. *Octodiceras fontanum*) (Fig. 63)

Luther (1951b) had found this bryophyte as a new species for the area during the 1930s–1940s surveys. The species had been limited to the northernmost part of PZ and had been very rare. Therefore, it did not occur on the transects. In the 2005/2007 surveys, the species was found on eight transects scattered across low-salinity PZ. It occurred mainly on clay-gyttja bottoms.

Spirodela polyrhiza (Fig. 64)

In 2005/2007, this rare floating species was present in two sheltered and eutrophic locations

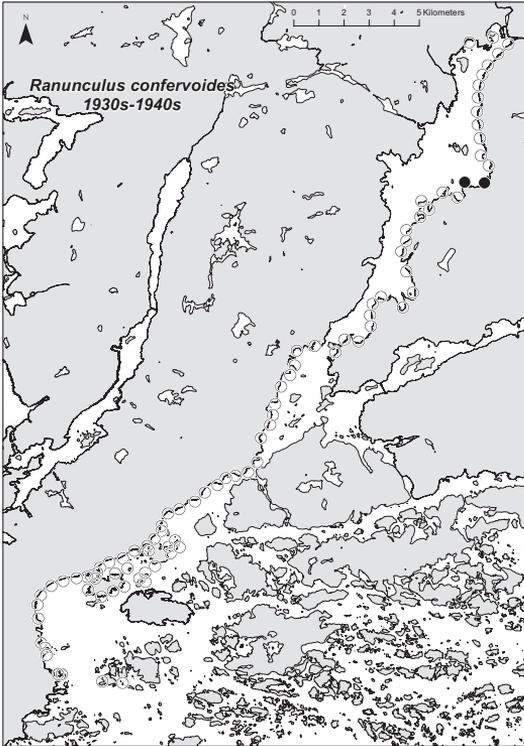


Fig. 61. Distribution of *Ranunculus confervoides*. ● presence, ○ absence.

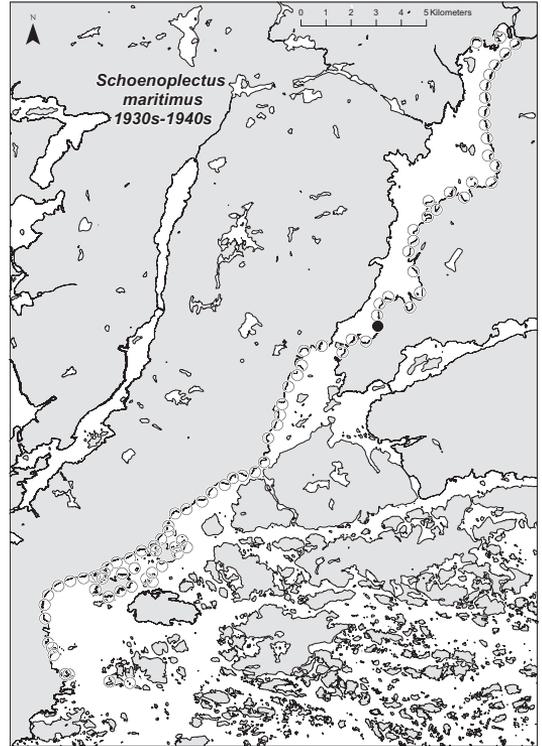


Fig. 62. Distribution of *Schoenoplectus maritimus*. ● presence, ○ absence.

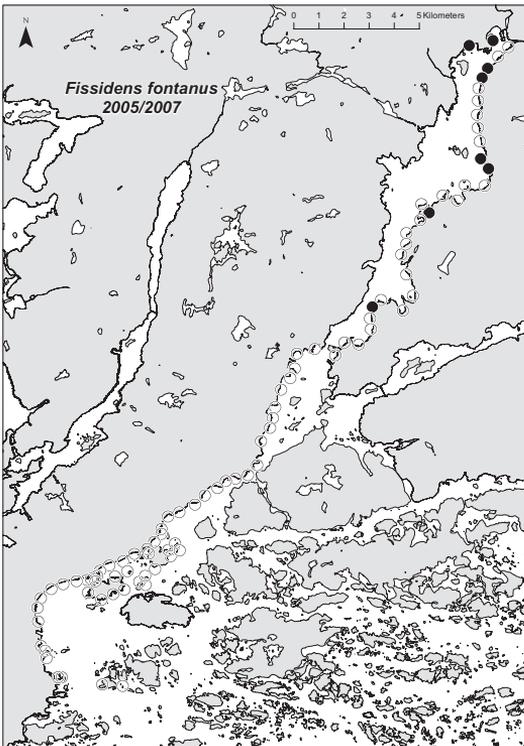


Fig. 63. Distribution of *Fissidens fontanus*. ● presence, ○ absence.

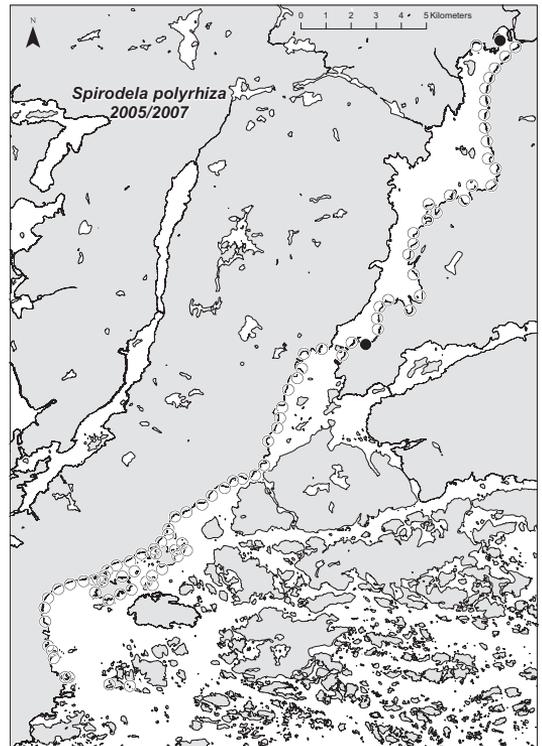


Fig. 64. Distribution of *Spirodela polyrhiza*. ● presence, ○ absence.

in low-salinity PZ. It had been found for the first time in the northernmost part of PZ in 1979 (Luther & Munsterhjelm 1983).

Characteristics of the species in the categories

The majority of the species whose occurrence frequencies increased between the two surveys represent submerged or pleustophytic perennial plants that tolerate a wide amplitude of depths (Tables 1 and 2). The species whose occurrence frequencies decreased are mainly perennial bottom-leaved isoetids and emergent species found in shallow waters (< 1.5 m). Species with an unchanged frequency are primarily submerged plants occurring also deeper than 1.5 m. The largest share of species present only in the 1930s–1940s surveys consists of submerged and bottom-leaved shallow-water plants. Species found only during the 2005/2007 surveys are equally divided between perennial floating plants and bryophytes. A minority of the vascular plant species found in the area are annuals. Many of the charophytes occurring in the area are considered to be annuals in shallow but perennials in deeper waters. Only those that are either annuals or perennials were used in the categorization. Occurrence frequencies of annual species either did not change between the surveys or they had been found only during the 1930s–1940s.

Changes in the ranking of the species

Two ubiquitous species *Potamogeton perfoliatus* and *Stuckenia pectinata* have remained as the most common species in the area (Table 3). Also *Phragmites australis* and *Chara aspera* are among the most frequent species of both surveys. Otherwise, some formerly common species e.g. *Eleocharis acicularis*, *Ranunculus reptans*, *Schoenoplectus* sp. and *Stuckenia filiformis* have clearly declined in frequency. At the same time, several species have increased distinctly in relation to other species, especially *Nitellopsis obtusa*, *Drepanocladus* sp., *Ceratophyllum demersum* and *Fontinalis* sp.

Table 1. Percentages of different life forms in the categories.

Category	Total number of species	Bottom-leaved	Submerged	Pleustophyte	Floating-leaved	Floating	Emergent	Charophyte	Bryophyte
Increased	13	0	46.2	23.1	0	0	7.7	7.7	15.4
Decreased	18	27.8	11.1	0	11.1	0	33.3	16.7	0
Unchanged	17	0	47.1	11.8	17.6	11.8	5.9	5.9	0
Exclusive to 1930s–1940s	10	30	50	0	0	0	10	10	0
Exclusive to 2005/2007	2	0	0	0	0	50	0	0	50

Table 2. Percentages of annual, perennial, shallow (< 1.5 m) and deep-occurring (> 1.5 m) species in the categories.

Category	Total number of species	Annual	Perennial	Shallow	Deep
Increased	13	0	100	38.5	61.5
Decreased	18	0	100	72.8	27.8
Unchanged	17	12.5	87.5	35.3	64.7
Exclusive to 1930s–1940s	10	33.3	66.7	80	20
Exclusive to 2005/2007	2	0	100	50	50

Table 3. The number of transects (out of 91) where the species were present in the historical (1930s–1940s) and contemporary surveys (2005/2007), and the relative change in their occurrence frequencies (ΔF_{rel}). Species names set in boldface = considerable decrease, species names underlined = considerable increase.

Species	1930s–1940s	2005/2007	ΔF_{rel} (%)
<i>Potamogeton perfoliatus</i>	79	69	–13
<i>Stuckenia pectinata</i>	62	70	13
<i>Eleocharis acicularis</i>	54	12	–78
<i>Chara aspera</i>	51	48	–8
<i>Phragmites australis</i>	46	59	19
<i>Stuckenia filiformis</i>	39	18	–54
<i>Schoenoplectus</i> sp.	37	9	–76
<i>Zannichellia palustris</i>	37	48	23
<i>Ranunculus peltatus</i> ssp. <i>baudotii</i>	31	15	–52
<i>Myriophyllum spicatum</i> s.l.	27	43	37
<i>Ranunculus reptans</i>	26	3	–88
<i>Alisma plantago-aquatica</i>	20	1	–95
<i>Potamogeton pusillus</i>	20	20	0
<i>Nymphaea alba</i> s.l.	19	11	–45
<i>Chara globularis</i>	19	5	–74
<i>Nuphar lutea</i>	19	21	10
<i>Typha angustifolia</i>	18	7	–61
<i>Callitriche hermaphroditica</i>	17	21	19
<i>Isoetes lacustris</i>	17	1	–94
<i>Ranunculus circinatus</i>	17	18	6
<u><i>Ceratophyllum demersum</i></u>	16	49	67
<i>Sparganium</i> sp.	15	14	–13
<u><i>Fontinalis</i> sp.</u>	15	34	56
<i>Equisetum fluviatile</i>	13	2	–85
<i>Myriophyllum alterniflorum</i>	13	0	–100
<i>Sagittaria sagittifolia</i>	13	1	–92
<i>Elatine triandra</i>	12	0	–100
<i>Elodea canadensis</i>	12	9	–25
<i>Najas marina</i>	12	14	14
<i>Nitella</i> sp.	11	2	–82
<i>Persicaria amphibia</i>	11	2	–82
<u><i>Drepanocladus</i> sp.</u>	10	29	66
<i>Eleocharis parvula</i>	10	3	–70
<i>Potamogeton gramineus</i> × <i>perfoliatus</i>	10	0	–100
<i>Elatine hydropiper</i>	9	0	–100
<u><i>Myriophyllum verticillatum</i></u>	9	20	55
<i>Potamogeton praelongus</i>	9	13	31
<i>Ruppia cirrhosa</i>	9	10	10
<i>Tolypella nidifica</i>	9	16	44
<i>Utricularia</i> sp.	9	19	58
<i>Plantago uniflora</i>	8	3	–63
<i>Ruppia maritima</i> coll.	8	13	38

continued

Table 3. Continued.

Species	1930s–1940s	2005/2007	ΔF_{rel} (%)
<i>Chara tomentosa</i>	7	1	–86
<i>Butomus umbellatus</i>	6	7	14
<i>Lemna trisulca</i>	6	24	71
<i>Isoëtes echinospora</i>	5	0	–100
<i>Typha latifolia</i>	5	1	–80
<i>Zannichellia major</i>	5	13	62
<i>Lemna minor</i>	4	4	0
<i>Nitellopsis obtusa</i>	4	25	84
<i>Potamogeton natans</i>	4	2	–50
<i>Chara baltica</i>	3	0	–100
<i>Potamogeton alpinus</i>	3	0	–100
<i>Potamogeton gramineus</i>	3	0	–100
<i>Potamogeton obtusifolius</i>	3	14	79
<i>Hydrocharis morsus-ranae</i>	2	1	–50
<i>Ranunculus confervoides</i>	2	0	–100
<i>Chara canescens</i>	1	6	83
<i>Hippuris vulgaris</i>	1	1	0
<i>Schoenoplectus maritimus</i>	1	0	–100
<i>Fissidens fontanus</i>	0	8	100
<i>Spirodela polyrhiza</i>	0	2	100

Changes in the geographical distribution

Geographical distribution changes were mainly decline and expansion of the species within the same archipelago zones where the species had been present also in the 1930s–1940s surveys. Exceptionally, three species whose frequencies increased (*Nitellopsis obtusa*, *Potamogeton obtusifolius* and *P. praelongus*) and one species whose frequency remained unchanged (*Lemna minor*) colonized new archipelago zones, although rather sparsely.

The species that increased in frequency and/or spread occurred predominantly in PZ or MZ. The main spreading direction of the species was outwards. This indicates that certain conditions (related with e.g. productivity) typical for the inner parts of the area extended outwards, enabling species to expand their distribution or become more frequent also in the outer zones. The spreading of species primarily took place within PZ and MZ. In addition, *Ceratophyllum demersum*, *Ranunculus circinatus* and *Potamogeton pusillus*, which had been most common in MZ, became more frequent in IZ–OMZ. *Potamogeton pusillus* demonstrated the most evident distribu-

tional shift from the inner to the outer parts of the area, mainly to IZ. It is noteworthy, that *Callitriche hermaphroditica*, *Ceratophyllum demersum*, *Drepanocladus* sp., *Fissidens fontanus*, *Fontinalis* sp., *Lemna trisulca*, *Myriophyllum spicatum* s. lato, *N. obtusa* and *Utricularia* sp. colonized the more oligotrophic Sjösång area in the northern part of PZ (see Fig. 1), while *Alisma plantago-aquatica*, *Equisetum fluviatile*, *Isoëtes lacustris*, *Persicaria amphibia*, *Ranunculus reptans*, *Sagittaria sagittifolia*, *Schoenoplectus* sp. and *Typha angustifolia* became less frequent there. From the species exclusive to the 1930s–1940s surveys, *Isoëtes echinospora* and *Potamogeton gramineus* × *perfoliatus* had 50%–60% of their total occurrences in the Sjösång area.

Most of the species whose frequency and distribution decreased between the surveys, and the majority of the species exclusive to the 1930s–1940s surveys, occurred only in PZ and MZ. *Eleocharis parvula*, *Ranunculus peltatus* ssp. *baudotii* and *Stuckenia filiformis*, which have their distribution centres in OZ–IZ, declined in IZ. The two last mentioned species were among the most abundant species of the zone in the 1930s–1940s.

Significant inward spreading of species was not found in this study. Only *Zannichellia major* occurring in OZ and OMZ advanced slightly inwards within OZ.

Ellenberg indicator values

The Ellenberg nitrogen and light values for the transects were calculated as means of their vascular plant species. When comparing the historical and contemporary transect mean indicator values, it was evident that between the surveys the nitrogen values increased (t -test: $t_{89} = -7.731$, $p < 0.0001$), and the light values (t -test, data square-root-transformed: $t_{88} = 8.903$, $p < 0.0001$) decreased significantly. A significant difference in nitrogen indicator values was found (one-way ANOVA: $F_{5,176} = 4.406$, $p = 0.014$) between PZ and the middle parts of the study area (MZ–IZ) (Tukey post-hoc test: $p < 0.05$). The nitrogen values increased from PZ (median 1930s–1940s = 5.2, median 2005/2007 = 5.9) towards MZ–IZ (median 1930s–1940s = 5.6, median 2005/2007 = 7.0) in both the historical and contemporary data sets. In OZ–OMZ, the 2005/2007 nitrogen values decreased again (median = 6.5), whereas the 1930s–1940s values (median = 5.6) had been similar as those in MZ–IZ. Concerning light indicator values, all zone groups differed significantly from each other (one-way ANOVA: $F_{5,174} = 24.155$, $p < 0.0001$): PZ and MZ + IZ ($p < 0.0001$), PZ and OZ + OMZ ($p = 0.020$), MZ + IZ and OZ + OMZ ($p < 0.0001$). As opposed to the spatial distribution of the nitrogen values, the light values declined from PZ (median 1930s–1940s = 6.8, median 2005/2007 = 6.6) to MZ–IZ (median 1930s–1940s = 6.6, median 2005/2007 = 6.0) in both the historical and contemporary data sets, and rose again in OZ–OMZ (median 1930s–1940s = 6.8, median 2005/2007 = 6.4).

Turnover

The temporal change in the species composition of the transects is expressed as absolute turnover values (T_{abs}). They were highest on the transects of PZ and MZ (mean $T_{\text{abs}} = 0.1$), and declined

towards the outer zones (mean $T_{\text{abs}} = 0.04$). The transect species composition remained more similar in the archipelago than in the inner zones. Our mean turnover values can be considered low as they do not exceed the values of a subtropical island presented by Herwitz *et al.* (1996).

Discussion

The overall species number remained fairly unchanged in the study area during the last ~70 years. One colonization by the lemnid *Spirodela polyrhiza* was found in Pojoviken. Probably, the species colonized the area through the rivers Svartån or Fiskars å. Extinctions could not be detected in our study due its design: the species exclusive to the 1930s–1940s surveys have probably not completely disappeared from the area, but declined seriously and were missed during the 2005/2007 surveys. According to Luther (1951b), species found only in the 1930s–1940s prefer oligotrophic conditions (*Isoëtes echinospora*, *Myriophyllum alterniflorum*, *Potamogeton alpinus*, *P. gramineus*, *P. gramineus* × *perfoliatus*) or are inferior in competition with the reed and mats of detached algae (*Chara baltica*, *Elatine hydropiper*, *E. triandra*, *Ranunculus confervoides*, *Schoenoplectus maritimus*). Species that were exclusive to the 2005/2007 survey (*Fissidens fontanus*, *Spirodela polyrhiza*) benefit directly or indirectly from higher nutrient levels (Luther 1951b, Toivonen 1985, Vanderpoorten & Klein 1999). Most of the species with an unchanged frequency either occurred ubiquitously in the area or were limited to the Pojoviken and mainland zones.

Long-term frequency changes are common in the study area, as frequencies of over half of the species found in both surveys changed significantly between the 1930s–1940s and 2005/2007. Some of these changes were probably natural, others induced by humans, and reasons are presumably many (Sculthorpe 1967). In the estuary area of the Pojoviken–Ekenäs archipelago, salinity is the major factor affecting the distribution of species (Luther 1951a). The long-term monitoring data from the outer archipelago show that salinities in the 1930s–1940s and 2005/2007

were similar. Hence, species frequency changes require alternative explanations.

Eutrophication

The rise in the Ellenberg nitrogen and decline in light values throughout the study area indicate that species of productive and turbid habitats comprised a larger portion of the transect vegetation in 2005/2007 than during the 1930s–1940s. Declining transparency in the Baltic Sea (Sandén & Håkansson 1996) is also evident when comparing the autumn transparencies measured in the study area. During a study period from the 1970s to the beginning of the 21st century, Munsterhjelm (2005) observed a replacement of charophytes by species with lower light requirements, e.g. *Ceratophyllum demersum* and *Myriophyllum spicatum*, in shallow bays (flads) in the Pojoviken–Ekenäs archipelago area, subjected to human-induced increased turbidity. In the geolittoral zone of islands in the archipelago of SW Finland, an analogous increase of vascular plant species with high nutrient indicator values was shown by von Numers and Korvenpää (2007).

Majority of the species whose frequencies increased are favoured by nutrient-rich conditions and are considered indicators of eutrophication (Fig. 2) (Kurimo 1970, Toivonen 1984). They include several non-rooted pleustophytic vascular plants (*Ceratophyllum demersum*, *Lemna trisulca*, *Utricularia* sp.) and bryophytes (*Drepanocladus* sp., *Fontinalis* sp.) that are dependent on the nutrient supply from the water column (Toivonen 1985). *Nitellopsis obtusa*, whose frequency clearly increased, is an exception among charophytes as it tolerates and even benefits to some extent from eutrophication (Penning *et al.* 2008). The outwards spreading of species, such as *N. obtusa*, *Potamogeton obtusifolius*, *P. praelongus* and *Lemna minor*, implies that it is driven by direct or indirect nutrient enrichment. The scarcity of the outermost occurrences of these species may indicate that they occur at their extreme salinity limit on particularly favourable sites. According to Luther (1951a), eutraphent and salinity-tolerant species *Ceratophyllum demersum* and *Potamogeton pusillus* were particularly abundant

in the shores surrounding the town of Ekenäs, the main source for nutrient enrichment in the 1930s–1940s (Häyrén 1944). By 2005/2007, the distribution of both species expanded clearly towards the archipelago.

Several species whose frequencies decreased and several species exclusive to the 1930s–1940s surveys have a rooted, bottom-dwelling or rosette-like growth habit. They are, thus, sensitive to alterations in light supply due to e.g. increase in phytoplankton and epiphytes or thriving life forms such as pleustophytes, and mechanical perturbations (Phillips *et al.* 1978, Hough *et al.* 1989, Sass *et al.* 2010). This concerns especially small species (e.g. *Elatine hydrophiper*, *E. triandra*, *Eleocharis acicularis*, *E. parvula*, *Ranunculus reptans*, *Stuckenia filiformis*) and isoetids (*Isoetes echinospora*, *I. lacustris* and *Plantago uniflora*) (Fig. 2). Filamentous algae decrease the light supply (Valiela *et al.* 1997) and detached, decaying algae mats generate hypoxia and anoxia (Norkko & Bonsdorff 1996, Vahteri *et al.* 2000). Also taller species, such as *Ranunculus peltatus* ssp. *baudotii*, suffer from algae deposits, e.g. in the seedling phase (Idestam-Almquist 1998), or when drifting algae are entangled in the surface-rising inflorescent, thus exposing them more severely to the tearing effect of waves (H. Pitkänen unpubl. data). The charophyte *Chara baltica* was exclusive to the 1930s–1940s surveys, and the frequencies of *C. globularis*, *C. tomentosa* and *Nitella* sp. decreased between the surveys. A particularly clear decline was that of *C. tomentosa*. *Chara globularis* and *Nitella* sp. seem to have persisted better in the area. They tolerate somewhat nutrient-enriched waters (Luther 1951a, Sinkeviciènè 2003, Penning *et al.* 2008), although high levels of eutrophication are deleterious to both species (Toivonen 1984). Charophytes are generally recognized as indicators of good water quality (e.g. Krause 1981, Svanbäck 1982, Schubert & Blindow 2003, Munsterhjelm *et al.* 2008), hence they react faster than vascular plants to alterations in water quality (Blindow 1992). As it is possible that species whose frequencies decreased could have been present in-between the transects, we emphasize that the actual population reductions may not be as drastic as the ones found in this study.

Several studies reported a similar increase in occurrence of eutrangent and decline in oligotrangent vascular plant, charophyte and bryophyte species, both in Finnish (Uotila 1971, Toivonen 1985, Toivonen & Bäck 1989, Rintanen 1996, Nurminen 2003) and in European lakes (Blindow 1992, Sand-Jensen *et al.* 2000, Arts 2002 and references therein, Mäemets & Freiberg 2005, Penning *et al.* 2008, Mäemets *et al.* 2010, McElarney *et al.* 2010). Long-term results concerning the impact of eutrophication on benthic vegetation in the Baltic coastal areas originate from studies on hard-bottom macroalgae (Kautsky *et al.* 1986, Eriksson *et al.* 1998, Bäck & Ruuskanen 2000). Also, recent declines in occurrences of charophytes were observed within the coasts of the Baltic Sea (Blindow 2000, Schubert & Blindow 2003). Munsterhjelm *et al.* (2008) reported that *Chara tomentosa* has disappeared from 88% of its localities in the mainland zone since the 1930s–1940s as a result of eutrophication and mechanical human impact (dredging, shore construction and motor boat traffic). Studies comparing historical and contemporary occurrences of aquatic vascular plant species are noticeably scarcer in the Baltic Sea. Boström *et al.* (2002) showed that *Zostera marina* meadows in more marine conditions in Tvärminne, SW from our study area, persisted from the 1960s without significant changes. Nonetheless, Munsterhjelm (2005) found that the abundance of *Myriophyllum spicatum* along with other macrophytes increased in these *Zostera*-stands indicating enhanced nutrient inputs over the past decades. Unpublished field data of Riggert Munsterhjelm from 1979–2005 support the observed increase and expansion of several eutrangent and decline of several oligotrangent species in our study area. Studies on changes in marine seagrass distribution implicate the anthropogenic sources (nitrogen loading and mechanical perturbations) and the eutrophication-induced increase of filamentous algae as the causes for global seagrass decline (Short & Burdick 1996, Valiela *et al.* 1997, Duarte 2002). To use some aquatic plant species (*Ceratophyllum demersum*, *Myriophyllum spicatum*) as indicators of eutrophication in the Baltic coastal areas in a similar way as in lakes, may be more complicated because of the electrolyte compensation by the brackish water

(Luther 1951a, Munsterhjelm 2005). Nonetheless, the strong and parallel frequency and distribution changes concerning especially several eutrangent species point to an intensified eutrophication process in our study area during the last 70 years. This is supported also by the long-term shift in the transect Ellenberg indicator values. The Ellenberg values have been used for terrestrial vegetation, but according to our experience they seem to work well also for the aquatic plant species of the Baltic Sea. When comparing the Ellenberg nitrogen and light values to the trophic characteristics of the aquatic plant species present in our study and their relation to nutrient enrichment (Luther 1951a, 1951b, Uotila 1971, Wallentinus 1979), they are acceptably correspondent.

The reed overgrowth

The formation of reeds is especially vigorous on the soft and sheltered bottoms in the inner parts of the area, while the harsher conditions limit the growth of *Phragmites australis* in the archipelago. In the Pojoviken and mainland zones, the spatial reed growth has accelerated in the absence of cattle grazing that was generally practiced on the shores until the 1960s (Luther 1951a, Luther & Munsterhjelm 1983, H. Luther unpubl. data). In the archipelago, reeds have colonized new sites besides becoming denser and wider (own data). This is most probably caused by the increased productivity of the shores. Expansion and (outwards) spreading of *P. australis* was observed in the SW archipelago of Finland (von Numers 2011) and in the Estonian lake Peipsi (Mäemets & Freiberg 2004) due to eutrophication and cessation of shore pasturing. In the North-American Chesapeake estuary, *P. australis* invasion was linked to increasing human impact on the shores and increasing N-levels (King *et al.* 2007). The process of primary land uplift (3 mm/year, Kakkuri 1987) is enhanced by sedimentation, which can increase the overgrowth mainly in narrow sounds between islands and close to the mainland where some temporal vegetation changes could be seen even during the 1930s–1940s (Luther 1951a).

The optimal growth depth of the majority of the species whose frequencies decreased is < 2

m: e.g., *Alisma plantago-aquatica*, *Eleocharis acicularis*, *E. parvula*, *Nymphaea alba s. lato*, *Persicaria amphibia*, *Ranunculus reptans*, *Sagittaria sagittifolia*, *Schoenoplectus* sp., *Stuckenia filiformis*, *Typha angustifolia*, *T. latifolia*. Also, 80% of the species found exclusively during the 1930–1940s was limited to very shallow waters. These weak competitors and annuals are often outcompeted by *P. australis* as reed stands can occupy the shore down to 2 m depth (Luther 1951b), and thus benefit from the open and shallow water area created as a result of different kinds of natural or human-induced disturbances, e.g. grazing (Uotila 1971, Luther & Munsterhjelm 1983, Toivonen & Nybom 1989). By contrast, *Typha* species increased in European and North-American lakes (Uotila 1971, Nurminen 2003, Egertson *et al.* 2004) and in rock pools in the archipelago of SW Finland (von Numers 2011). An explanation for the difference with our results may be offered by the fact that especially *T. latifolia* is able to supersede *P. australis* in eutrophied and sheltered small freshwaters (Toivonen & Bäck 1989), but *P. australis* can be a superior competitor in brackish and more exposed coastal areas, even at the nutrient-richer sites. According to von Numers (2011), *Schoenoplectus tabernaemontani* increased on the shorelines and in rock pools of the Finnish SW archipelago. The species is probably favoured by the eutrophication-induced productivity in the archipelago, but suffers from the extensive reed overgrowth evident in the inner parts of our study area. Generally, the other emergent species are favoured by grazing, especially in the Pojoviken and mainland zones, as they are more capable of vegetative regeneration after grazing by animals than *Phragmites australis* (Luther 1951a, 1951b). Besides overgrowth, also small-scale shore construction and dredging, as well as boating activities may locally contribute to the decline of species restricted to shallow waters (e.g. *Nymphaea alba s. lato*).

The distributions of several species, e.g. *Eleocharis acicularis*, *Schoenoplectus* sp., *Stuckenia filiformis* and *Typha angustifolia*, became fragmented. Currently, habitat fragmentation is considered to have a strong negative influence on the distribution of terrestrial plants of, for example, heathlands and old forests, which is a major

threat to worldwide biodiversity (Hanski 2005, Piessens *et al.* 2005, Helm *et al.* 2006). Throughout the study area, the most likely factors causing fragmentation were the decline in oligotrophic habitats and the increase in competitive pressure, following eutrophication and reed overgrowth. In addition, shoreline construction can alter or destroy habitats which became rare as the large-scale environmental changes have processed.

In conclusion, our results show long-term distribution and frequency changes that occurred in the aquatic vegetation of the northern Baltic Sea: decline of oligotrophent and (outward) expansion of eutrophent species took place in all parts of the study area during the last 70 years. The reed overgrowth, accelerated by increased productivity and cessation of shore grazing, limit the space for shallow-water species. The vegetation changes are most intensive in the more enclosed inner parts of the area, from Pojoviken to the inner archipelago. The long-term, multi-species floristic comparisons provide the overall picture of change in the aquatic plant community over time. This information is valuable also for conservation purposes, especially as many of the changes found in this study are human-induced.

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