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Natural succession and human-induced changes in the soft-bottom macrovegetation of shallow brackish bays on the southern coast of Finland

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II Munsterhjelm, R.: What does the vegetation map tell us? – A methodological study and a visual analysis of the macroscopic water vegetation of shallow brackish water bays in SW Finland. (Submitted to Memoranda Societatis pro Fauna et Flora Fennica.)

III Munsterhjelm, R., Henricson. C. & Sandberg-Kilpi, E.: The decline of a charophyte – occurrence dynamics of *Chara tomentosa* L. at the southern coast of Finland. (Submitted to Hydrobiologia.)

IV Henricson, C., Sandberg-Kilpi, E. & Munsterhjelm, R.: Experimental studies on the impact of turbulence, turbidity and sedimentation on *Chara tomentosa* L. (Submitted to Hydrobiologia.)

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PREFACE

Panta rhei

There are two ancient statements that well illustrate the problems involved in our attempts to develop a configuration of reality, in particular when approaching it from an ecological point of view. One is Chinese: “in nature and in life, everything depends on everything”. This illustrates the difficulty for the researcher confronted with the complexity of nature at the stage when he first chooses the subject of his research. The other statement is Greek. It illustrates the insight a field researcher achieves having faced the variability of nature and finally is forced to submit to “the only unalterable principle of nature”, a principle according to which everything is involved in a process of moving or floating around: “*panta rhei*” (Heracleitus c. 540 – c. 480 B.C.).

We must believe in these expressions if we truly are the logical thinkers we consider ourselves to be. This also means that the aspects of the nature we study and the methods we use are products of our own highly selective choices, which are dependent on our educational background and individual subjectivity. Logically, our understanding of the environment is subject to limitations, and the real reasons for study are always questionable. Our choices are only defendable from a practical and organisational point of view.

Facing these restrictions and the uncertainty considering the research theme I was given in 1978 by my professor in botany Hans Luther, I decided to use a purely descriptive, phenomenological approach. I was supposed to investigate the flora and vegetation of the flads, shallow and sheltered brackish water environments on the border between sea and land. My initial grasp on the theme was natural because these habitats were almost completely unclassified. Only a few ecological descriptors are usually used for understanding the function of ecosystems, but I did not know what these would be. And, I did not want to use the wrong approach to an unknown theme. Thus, I first classified the localities and their vegetation from an organisational point of view. Classical classification studies, however, were already out of date at that time. Other types of biotopes, forests, mires, archipelagoes, rock-pools and lakes had already been classified at least half a century beforehand. I was therefore quite alone with my work.

The Master’s thesis students of my professor were given subjects that sometimes formed the essential materials of their future PhD theses. My work became prolonged as I gradually became interested in the questions it offered. New sensations waited around every next corner. My final goal was to define the differences and similarities between the localities studied to create an understandable picture of the system. But the environment was so complex and variable, that I had to wait for a long time to accomplish this. Since I originally was a pure zoologist interested in birds and their behaviour, the studies finally led me to the concept of successional behaviour of the flad vegetation. But at that stage, I had already started to focus on my future profession in art, thus, effectively shelving my work in botany.

In 1997 I returned to my old botanical material full-time for a shorter period. Revisiting my former study areas, I hoped to examine the successional model that I had produced in the 1980s. By then interest in and knowledge of the topic had developed considerably and I became involved in different projects. A problematic situation gradually developed: The new methods were not really comparable with the old ones. Gradually it also began to look as if the information obtained during the new visits to the old sites did not always support the original model. Thus, the significance of my own methods and conclusions had to be re-evaluated; completely new research had to be done.

As a consequence of this situation, one of the main goals was to study how much information, theory and conclusions could be achieved by simply observing nature as I had originally done by sampling and looking. My old instinct to preserve a close contact to the original material was kept as a leading principle throughout the work. Gradually, it became clear that human disturbances were the reasons for the unexpected changes in direction of succession. These indications were finally tested experimentally. In the end, the new studies of shallow bays that I planned to complete in one and a half year finally required seven years that also included other studies connected with ecology, environment and even environmental medicine.

CONTRIBUTIONS

Supervised by	Prof. Carl-Adam Hæggström University of Helsinki
Reviewed by	Dr. Olof Rönnberg Åbo Akademi University
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Natural succession and human-induced changes in the soft-bottom macrovegetation of shallow brackish bays on the southern coast of Finland

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The brackish water soft-bottom macrovegetation of shallow bays was studied in the west part of the coastal area of southern Finland. The emphasis was laid on the succession of the vegetation in the different isolation stages of flads, which represent a regional type of coastal lagoons. They develop towards more isolation through land uplift processes. The concept of succession was first outlined through comparative studies of localities in a present perspective. As the main period of study lasted from 1978 to 2003, also real changes could be observed. Historical information from the end of the 19th century prolonged the view 100 years back in time from today. The method of study can be described as phenomenologically descriptive and comparatively classifying. Observations of the conditions in reality and visual images, vegetation maps, were largely used as a substantial information source. Aquatic plant occurrences and their environments are obviously constantly changing, not only varying and fluctuating. The change occurs in many scales, both spatial and temporal ones. The successional model created was supported by numerical analyses. The succession along the isolation stages of flads was compared with the succession along the general environmental gradient in the entire region, i.e. that from the outer to the innermost parts of the very diverse coastal area. The relative importance of the environmental factors seems different along the two gradients. In the isolation gradient change in salinity is less important than in the regional one. The environmental causality behind the changes is thoroughly discussed. The successions of the vegetation may be both natural and human induced. The stonewort *Chara tomentosa*, the decline of which is documented in detail, is seen as an important indicator for human-induced environmental changes. Its response to factors (turbidity, sedimentation and water circulation) that increase in importance after mechanical disturbances of its typical habitats, sheltered bays and flads, was tested experimentally. The results supported the analysis based on observations in the nature. The value of knowledge of the natural conditions and processes for understanding the nature of changes is emphasised. The study invites to both practical studies for future management of shallow soft bottom environments and more principal studies of successional mechanisms.

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CONTENTS

INTRODUCTION

The Baltic Sea and its coastal areas belong to the most carefully investigated brackish water areas of the world. However, an increased knowledge of the coastal environment and its vital ecological processes is still needed. Notable environmental changes take place in the open Baltic Sea and in the connected waters along the coasts, consequently creating new environmental problems and subsequent questions. Increased knowledge of the environmental requirements, sensitivity and indicative reactions of the aquatic organisms is needed. Mechanisms of the changes ruled by nature or by man have to be carefully separated from each other, and described. Their complex interactions have to be analysed. In addition, further information regarding the importance of different habitats in relation to the larger ecosystems must be gathered. First, however, a general image of the various habitats has to be created.

This thesis focuses on shallow bays, and especially coastal lagoons, in the northern Baltic Sea. Coastal lagoons are special morphological formations resembling shallow lakes or deltas. Biologically they owe a significant similarity to estuaries, mangroves, marshes and coral reefs. Typical coastal lagoons of the Finnish and Swedish coasts consist of different developmental stages of so called flads, small shallow waters being cut off from the Baltic Sea by the land uplift processes (Lundegårdh-Ericson 1972, Ingmar 1975, Munsterhjelm 1985a, 1997, Tolvanen *et al.* 2004). They are unique in the world and have consequently been given priority on the EU-level (Airaksinen & Karttunen 1998, Bäck & Lindholm 1999). Coastal lagoons are sensitive to nutrient enrichment, and are affected by it worldwide (Sfrizo *et al.* 1992, Taylor *et al.* 1995, 1999). The flads are no exception (Wallström & Persson 1997, 1999, Wallström *et al.* 2000). Also mechanical disturbances such as dredging works and motor boat traffic influence these formations and their biota (Schubert & Blindow 2003, Eriksson *et al.* 2004). Shallow bays are today threatened by both exploitation of and increased pressure on the drainage area (Sandell & Karås 1995, Hästbacka 1995, Andersson *et al.* 2000, Eriksson *et al.* 2004).

Shallow and sheltered coastal habitats, like flads, are far more complex and diverse than the open sea. Among others, they exhibit a special and interesting macrovegetation covering their shallow soft bottoms and obviously interacting with the plankton community of the water. They are important not only as contributors to the general diversity of the Baltic coastal landscape, but for the coastal ecosystem as a whole. Stoneworts, i.e. charophyte species that today may be threatened in more open localities form conspicuous meadows in the flads (Schubert & Blindow 2003). Shallow bays function as breeding areas for fish, including economically important species such as pike (*Esox lucius*) and perch (*Perca fluviatilis*; Karås 1999). Their most important qualities for fish are high water temperature, dense macro-vegetation that offers shelter for the larvae and juveniles, and in certain cases, fresh water influence attracting originally fresh water fish species to breed. Their clear water makes finding food easier for the fish larvae (Urho *et al.* 1990, Karås & Hudd 1993, Karås 1996a, 1996b, Karås 1999). They are also foraging and resting areas for birds (Koivula *et al.* 2000, von Numers 2002).

Until the last fifteen years, the research of these areas has been minor (Häyrén 1902, 1910b, Cedercreutz 1937, Lundegårdh-Ericson 1972, Ingmar 1975, Ingmar & Willén 1980, Blomqvist 1982, 1984, Svanbäck 1983, Hästbacka 1984, Bonsdorff *et al.* 1985, Munsterhjelm 1985a, 1985b, 1987a, 1987b). During the 1990s the investigation of shallow bays and problems associated with these finally developed into a broad field of research in Finland and Sweden, however, still mostly presented in the "grey" literature (cf. Ekebom 1990, Bäck & Lindholm 1999, Länsstyrelsen i Stockholms län 1991, 1997, Lindholm 1991, 1998, Sandell & Karås 1995, Giegold *et al.* 1996, Munsterhjelm 1997, Rinkineva & Molander 1997, Wallström & Persson 1997, 1999, Dahlgren 1997, 2001, Dahlgren & Virolainen 1998, Lehtinen 1998, Nurminen 1998, Grundin 1999, Karås 1999, Numminen 1999, Andersson *et al.* 2000, Appelgren 2000, Wallström *et al.* 2000, Anderson 2001, Dahlgren & Kautsky 2001, Hansson 2001, Ojala 2001, Tobiasson 2001, Degerlund 2002, Henricson 2002, Kautsky & Dahlgren 2002, Meriläinen 2002, Munsterhjelm & Ekebom 2002, Hirvonen 2003, Lehtinen 2003, Dahlgren *et al.* 2004, Londesborough 2004, Tolvanen *et al.* 2004).

The investigation presented in this thesis was performed in the southwest coast of Finland – at the mouth of the Gulf of Finland (Fig. 1A). The Tvärminne Zoological Station (University of Helsinki) served as a base for the survey. The main investigations be-

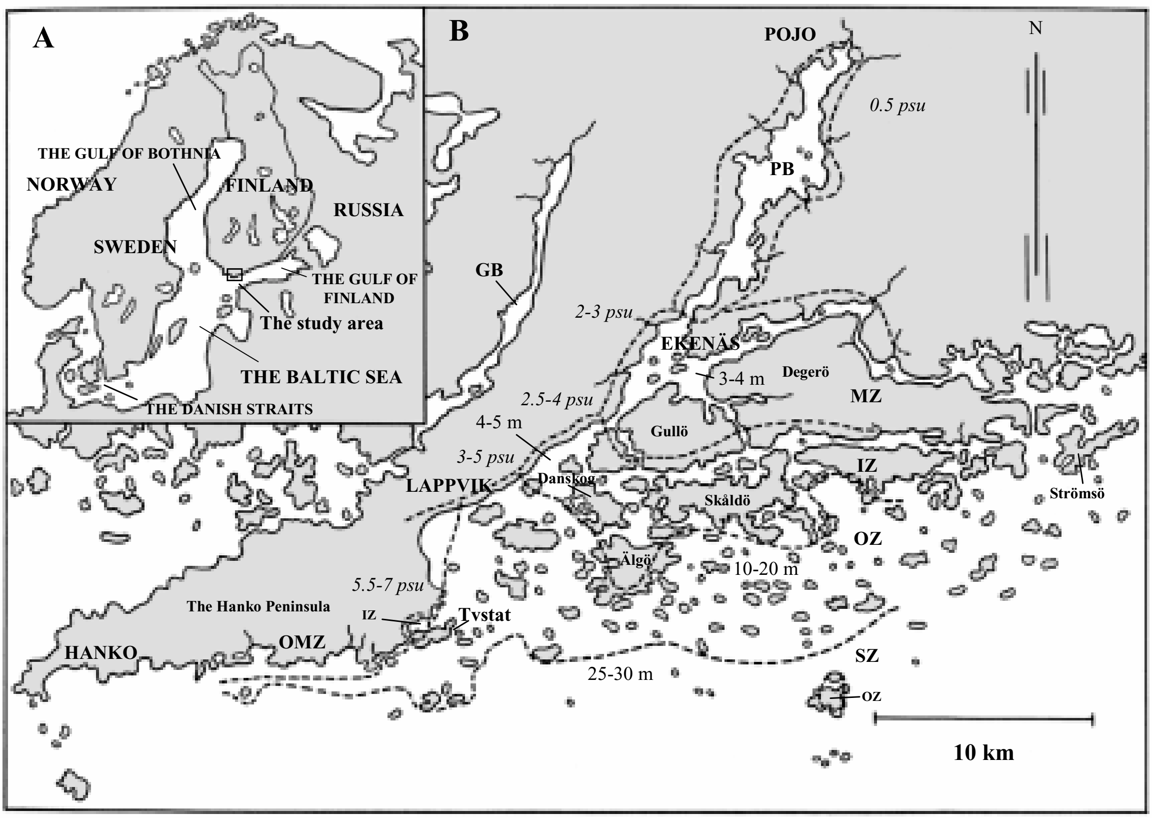


Figure 1A-B. A) The position of the study area in the Baltic Sea. B) The study area. Abbreviations: GB = Gennarby Bay, IZ = Inner archipelago zone, MZ = Mainland zone, OMZ = Outer mainland zone, OZ = Outer archipelago zone, PB = Pojo Bay, SZ = Sea zone, Tvstat = Tvärminne Zoological Station. Main depths (in m) and main summer salinities (psu) are given.

gan in August 1978. The purpose was initially to study the macrophyte vegetation of the flads around the island of Danskog, east of Tvärminne in the archipelago of the town Ekenäs (Fig. 1B). It was decided, that the main goal of the investigation should be to create a descriptive outline of the observable elements of these distinctive ecosystems on the border between the open sea and land. Later, as a consequence of the observations made, it seemed possible to define some occurrence and successional patterns of the various macrophyte species and typical assemblages of vegetation they create. This was done by interpreting, "reading" and comparing the descriptive or visual images achieved. The study can, thus, be regarded as phenomenologically descriptive. This also means that the observed causalities discussed may still remain to be tested.

Seven main goals of this study developed during the work. Initial goals were to: 1) map the vegetation of shallow bays in the area, thus filling a gap in the distributional information of aquatic plants (paper I) existing before (Luther 1951a), and 2) classify and describe the habitats according to their morphology and vegetation (papers I and II). Additional goals which developed during the investigation were to: 3) increase the understanding of the developmental and successional processes of the archipelago (papers I, II and III), 4) test the relevance of the indicated mechanisms (paper I and IV), 5) contribute to the information needed for nature protection of the coastal area (papers I-IV), 6) analyse the possibilities of descriptive methods in aquatic plants research (paper II) and finally 7) contribute to a framework of historical and recent information for future, and specified research of the different parts and mechanisms of the shallow bay ecosystem (papers I-III).

THE STUDY AREA AND ITS RESEARCH HISTORY

The Baltic Sea is one of the largest brackish water basins of the world. It differs from the other large brackish water bodies, i.e. the Black Sea and the Caspian Sea, by being shallow (mean 55 m), cold and geologically young, but its salinity is about the same as in the Caspian Sea (Wallentinus 1991, Snoeijs 1999). A gradual and relatively stable gradient from less than 0.5 psu in its innermost parts to 35 psu in its opening area towards the North Sea (brackish water < 0.5 psu to 30 psu) is one of the main characteristics of the Baltic Sea (Wallentinus 1991, Snoeijs 1999). The water exchange with the North Sea and thereby with the Atlantic Ocean is highly restricted by the narrow and shallow Danish Straits (Fig. 1A). The coasts of the northern Baltic are slowly rising from the sea. In the Northern Baltic Proper including the present study area the land uplift is approx. 3-4 mm/year and in the northernmost part of the Baltic approx. 9 mm/year. In the south the land is sinking, approx. -1 mm/year (Ekman & Mäkinen 1996). Natural changes of the environment and biota are typical for the Baltic Sea. The organisms are of both marine and lacustrine origin, and may occur side by side (Snoeijs 1999). Their distributions are largely ruled by the salinity gradient. The macroalgal flora, with the exception of certain prominent green algae and stoneworts, is mainly of marine origin. By contrast, the phanerogams are mostly, and originally, freshwater species. In Finland, however, some of the freshwater macrophytes occur as brackish water species (Luther 1951a, Langangen *et al.* 2002).

The organisms of the Baltic Sea are under physiological stress because of the unusual environment, and are therefore sensitive to additional environmental disturbances from pollution sources along the coasts, and internal nutrient loading (Wallentinus 1991, Snoeijs 1999). The long winter period with ice cover exerts also stress on the environment. Oxygen depletion at the deeper bottoms – “dead bottoms” – cyanobacterial blooms at the surface and increased filamentous algal blooms at the coasts account for the most prominent problems of the Baltic Sea.

The Finnish and Swedish coastal areas of the northern Baltic Sea are characterised by a mosaic of islands and skerries with an extremely prolonged shoreline in comparison with the more open coasts in the south (Bonsdorff & Blomquist 1993). The archipelago has a filtering function, thus creating accumulation bottoms closer to the surface in the direction of increasing wind shelter towards the inner or more sheltered parts of the area (Luther 1951a, Persson *et al.* 1993). In the present study area (Fig. 1B), the coastal areas of SW Finland, all typical features of the northern Baltic Sea are present. These are decisive for the birth of the environmental entireties presented in this study, the shallow bays and coastal lagoons or flads. The salinity of the study area exhibits a gradient of almost fresh water conditions in the innermost parts of the area to the full salinity of the Northern Baltic in its outermost parts (6-7 psu) and is parallel to the gradient from the northern Baltic to the inner part of the Gulf of Bothnia.

The study area is conveniently reached from the Tvärminne Zoological Station (Fig. 1B). It comprises the archipelago south and east of the Hanko peninsula and the archipelago and the mainland shores south of the town of Ekenäs. The basic geological structure of the area consists of an Archaean bedrock, which forms a gently southwards sloping peneplane with a characteristic surface structure. A formation dividing the SW archipelago area of Finland and separating the Archipelago Sea (N side) from the Gulf of Finland (S side) is the Salpausselkä I end moraine forming the Hanko Peninsula. Other characteristic formations strengthening the impression of zonation are the fault valleys extending in a W-E direction or in SW-NE direction. The latter ones form the deep furrows of the fiord-like Pojo and Gennarby Bays at both sides of the end moraine.

Different morphological and environmental features of the study area, e.g. the archipelago zones, the different environmental gradients and the environmental dynamics have been described (Häyrén 1900, 1902, 1931, Luther 1951a, Niemi 1973, 1975, 1978, Hällfors *et al.* 1983).

The earliest angiosperm aquatic plant samples of the study area which are found in the collection of the Botanical Museum in Helsinki were collected in the second half of the 19th century. E. Hisinger collected *Myriophyllum sibiricum* in 1852 and *Ceratophyllum demersum* in 1854. The first species of the herbarium collected by the first devoted aquatic plant researcher of the area Ernst Häyrén was *Hippuris tetraphylla*. It was collected in 1892 in a locality he called “Fladan” (“The Flad”) at the island of Danskog (Fig. 1B). In 1893 he collected *Ranunculus peltatus* ssp. *baudotii* at Danskog.

Ernst Häyrén (1878-1957) was the first botanist to adopt the Tvärminne Zoological Station as a base for continuous botanical field research. He specialised in plant geography and sociology and started his life-long systematic plant collecting and excursion activities in the Tvärminne-Ekenäs area in the end of the 19th century.

During his excursions the concept of the archipelago zones was born (Häyrén 1900, 1931, 1948, Luther 1951a, paper I). Häyrén described, in a very perspicacious way, the gradual transition from the open sea to land, how naked and wind exposed rocks rise from the sea and towards the inner parts of the archipelago, grow into wooded islands, which in turn fuse to larger islands and finally with the mainland (Fig. 1B). He focused on geomorphology and the biological gradients which are a consequence of the physical conditions. Also changes under the water surface were described. His work became a basis of the regional geographic classification of the archipelagos of the Baltic Sea and directed research attention towards the archipelago (Luther 1960).

Häyrén's concept of zonation offers an on-the-spot account of the geological postglacial land uplift process. The importance of this phenomenon is also presented in a study describing the primary (rising of the bedrock) and secondary (accumulation of material) land upheaval processes which together increases the speed of the rising bottom (Häyrén 1902, 1910b). The transporting power of water movements and aquatic plant production and their filtering mechanisms (e.g. reeds) are involved in the secondary process. Information of the typical zonation and communities of flads and successive patterns can be extracted from his many small documentary publications (e.g. Häyrén 1902, 1912, 1924, 1936a, 1936b, 1958).

In 1929, the student C.A. Borgström investigated the shore vegetation of the Pojo Bay (Borgström 1930). This work also included aquatic vegetation. Hans Luther (1915-1982) was the son of Alexander Luther, professor in zoology and head of the Tvärminne Zoological Station. H. Luther's first aquatic plant sample, *Ruppia cirrhosa*, from brackish water found in the herbarium collection of the Botanical Museum in Helsinki was collected in 1925 near Tvärminne. Like Häyrén, Luther paid much attention to the knowledge of species and on the field research. Luther began a comprehensive autecological study of the aquatic plants in the area in 1936-1937. His study comprised the soft bottom macrophytes, both phanerogams and algae, along the gradient from more marine and exposed outer soft bottom areas to almost lacustrine and wind sheltered innermost environments along the Tvärminne – Pojo Bay stretch, the general environmental gradient of the area. During the years of study (1936-1939 and 1945-1947), he investigated 3820 sampling stations along a 250 km long shoreline. His material was summarised in his classical study (Luther 1951a, 1951b), one of the most comprehensive regional ecological studies of soft bottom macrophytes in the Baltic area.

In the late 1970s and in the 1980s two soft bottom macrophyte investigations at Tvärminne Zoological Station, initiated by H. Luther completed the picture of aquatic plant distribution of the area. One was performed west (Heinonen 1986) and the other east (Munsterhjelm 1985a, 1985b) of Luther's area. The latter concentrated upon morphological development and successive processes of the water vegetation during the isolation process of shallow sheltered bays, flads and gloes (Munsterhjelm 1985a, 1985b, 1987b, paper I). In 1986 and 1987 the environmental change during this process was studied (Ekebom 1990).

In 1998 and 1999 an EU co-operation project ("Environmental state of shallow bays", Interreg IIA) between the Tvärminne area (University of Helsinki), the Åland archipelago (Åbo Akademi University) in Finland, and the Uppland coastal area in eastern Sweden (Uppsala University) was performed. The localities studied in Tvärminne were documented and compared with localities from the other regions (Wallström *et al.* 2000). The project focused upon testing methods and evaluating the environmental state in shallow bays on the basis of some environmental parameters and the occurrence of macrovegetation and bottom- and epifauna. An interdisciplinary approach to the flad ecosystems was born. The new methods taken into use (Wallström *et al.* 2000) were later compared with the old ones used for this thesis (paper II). At the same time, studies concerning the changes of charophyte occurrences were started within a Baltic Marine Biologist project "Charophytes of the Baltic Sea" (Schubert & Blindow 2003). All available historical and recent records from different types of localities, and regions of the whole study area were put together and analysed in a Baltic perspective. One result of this work concerns historical occurrence data of the stonewort *Chara tomentosa* (paper III). The initial results of the study inspired experimental testing of the impact of abiotic disturbances on the species in 1999 (Henricson 2002, paper IV). Later, in 2001 and 2002, several studies were performed within a project focusing on the faunal and phytoplankton community structure and the function of the developmental stages of flads (Meriläinen 2002, Hirvonen 2003, Lehtinen 2003, Londesborough 2004). A new EU project ("Production of fish larvae in shallow bays", Interreg IIIA, conducted by Johan Persson, Uppsala University) was performed in Tvärminne in 2001 to 2004 (M. Kilpi, O. Mustonen, M. Westerbom, A. Lappalainen, L. Urho). Distribution of the submerged vegetation was also included in the project.

MATERIALS AND METHODS

The present study is mainly based on an inventory field material of macroscopic aquatic plants collected between 1978 and 2003 (papers I, II and III). The water vegetation of more than 100 shallow localities, for example many bays and flad stages was studied. The localities and locality types visited and studied are shown in Fig. 2. Most of the lo-

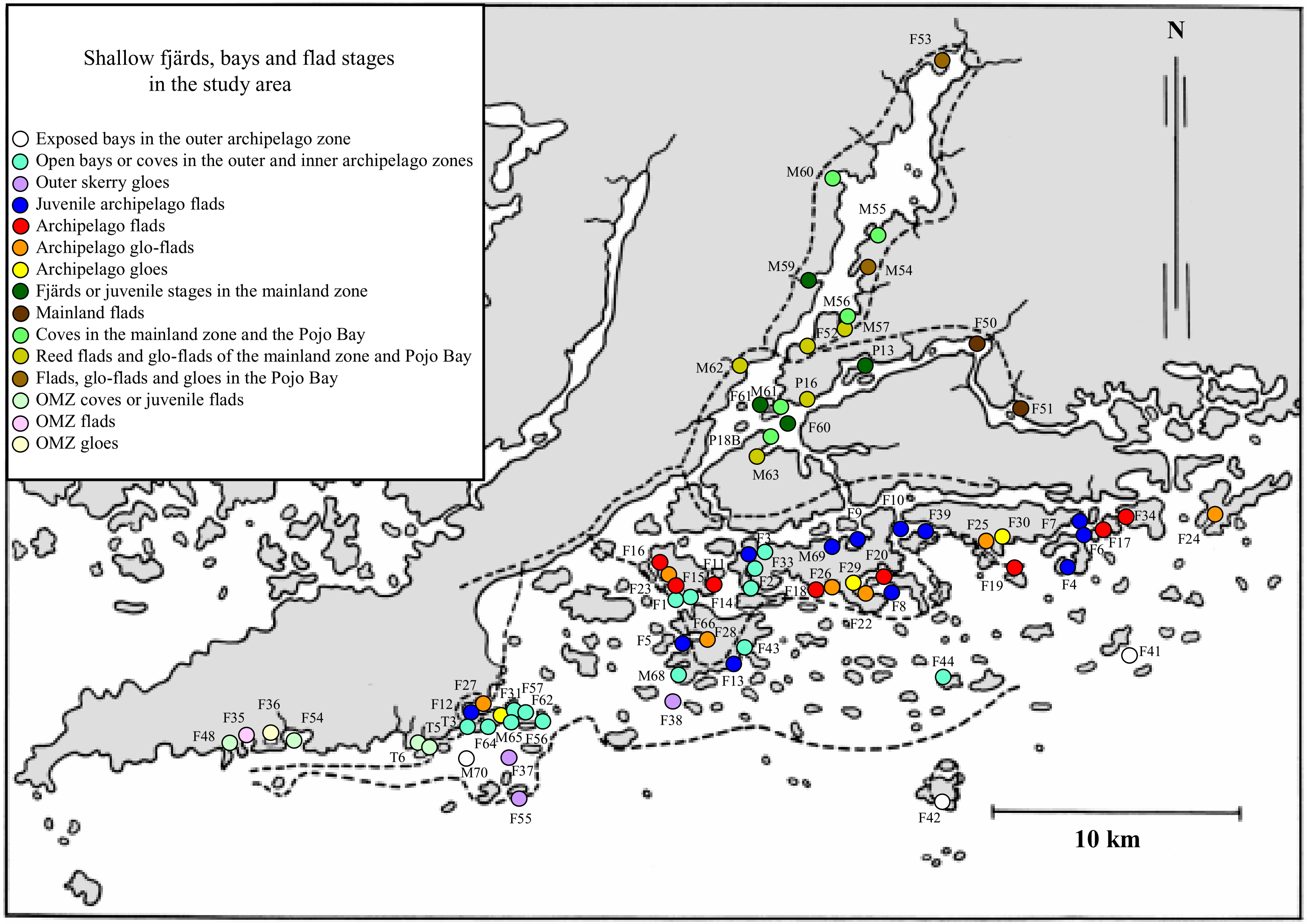
Figure 2. Shallow bays of different types studied in the coastal and archipelago area of the Hanko Peninsula, Ekenäs archipelago and Pojo Bay. The information about the localities is based on Paper I, III, Munsterhjelm 1985b, 1986 (F-, P-localities), Heinonen 1986 (T-localities), and on field investigations performed by M. Westerbom, O. Mustonen and M. Kilpi (M-localities). Many of the localities were also studied by Luther (1951a).

F1 = Mörnäs cove, F2 = Sommarö cove, F3 = Notholmen cove, F4 = Knipholmsfladan, F5 = Älgö flad, F6 = Storfladan II, F7 = Lillfladan I, F8 = Kopparöfladan, outer part, F9 = Brändöfladan, F11 = Gyltviken, F12 = Byviken, F13 = Verkfladan, F14 = Danskogfladan, F15 = Björkviksfladan, F16 = Ekholmsfladan, F17 = Västerviken, F18 = Åkernäsfladan, F19 = Ytteröfladan, F20 = Kopparöfladan, inner part, F22 = Simmet, F23 = Solbacksfladan, F24 = Strömsö Gloet, F25 Storfladan I, F26 = Nabbfladan, F27 = Namnsholmssundet, F28 = Verkviken, F29 = Kopparöfladan gloes, F30 = Lillfladan I, F31 = Tvärminne Gloet, F33 = Sommarö Gloet, F 34 = E Växär flad, F35 = Västerfjärden, F36 = Österfjärden, F37 = Lillhamnen glo, F38 = Gloholmen glo, F39 = Fåfängöfladan, F41 = Bystfladan, F42 = Söderfladan, F43 = Södergårdsfladan, F44 = Krokgloet, F48 = Kattrumpan, F50 = Totalfladan, F51 = Persöfladan, F52 = Prästviken, F53 = Gumnäsfladan, F54 = Täktbukten, F55 = Långskär flad, F56 Brännskär cove, F57 = Krogarviken, F60 = Båssafjärden, F61 = Ekenäs stadsfjärd, F62 = Jovskärsviken, F64 = Kallvassen, F66 = Snärjeviken.

P13 = Dragsviken, P16 = Snäcksund cove/reed flad, P18B = Notholmen.

M54 = Baggby Fladan, M55 = Sjöbodviken, M56 = Lillvik, M55 = Huluvik, M60 = Sunnanvik, M61 = Blindsund, M62 = Trollböle, M63 = Gårdsvik, M64 = Potten, M65 = Klobbviken, M68 = Potten, M69 = Backfladan, M70 = Vindskär.

T3 = Sikhalsen, T4 = Kyrkgrunden, T5 = Österviken, T6 = Västerviken.


Shallow fjärds, bays and flad stages in the study area
○ Exposed bays in the outer archipelago zone
● Open bays or coves in the outer and inner archipelago zones
● Outer skerry gloes
● Juvenile archipelago flads
● Archipelago flads
● Archipelago glo-flads
● Archipelago gloes
● Fjärds or juvenile stages in the mainland zone
● Mainland flads
● Coves in the mainland zone and the Pojo Bay
● Reed flads and glo-flads of the mainland zone and Pojo Bay
● Flads, glo-flads and gloes in the Pojo Bay
○ OMZ coves or juvenile flads
○ OMZ flads
○ OMZ gloes
N
10 km
F53
M60
M55
M54
M59
M56
M57
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P13
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F42

calities were visited several times during different years. Additional information about aquatic plant occurrences was also obtained from literature and other sources. Older field notes, aerial photographs (papers I, II and III), as well as information given orally by field researchers and local inhabitants (paper I and III), were also gathered.

About 120 aquatic macrophyte taxa (108 in Luther 1951a) may be found on soft bottoms in the study area if also loose lying macroalgae are included. All species of which the individual plants can be viewed with the naked eye were regarded as macrophytes, i.e. macroscopic plants. Most of the taxa investigated for this study were soft bottom species. The division of the aquatic plants into lifeforms, e.g. helophytes and hydrophytes, is in accordance with Luther (1949, 1951a, 1983). Benthopleustophytes are not rooted species occurring close to the bottom. Haptophytes, mainly macroalgae, are species that are attached to hard substrates. When forming macroscopic mats loose lying benthopleustonic algae were recorded. In certain investigated soft bottom bays there were also rocky shores with haptophytic macroalgae which also were included in the data.

Angiosperm plant nomenclature is in accordance with Hämet-Ahti *et al.* (1998). Regarding charophyte nomenclature, Schubert & Blindow (2003), and for other algae, Tolstoy & Österlund (2003) are followed.

A bay can be considered as a topographically discernable depression in the shoreline. Thus, bays always provide shelter from certain wind directions and can therefore, accumulate materials brought by the sea – in more exposed bays above the shoreline and at water levels deep enough not to be reached by the waves, and in more sheltered ones also between these levels. The description of the principal development of flads (paper I) is presented in Fig. 3.

The limit between shallow and deep areas may be defined according to the depth amplitudes of the vegetation. The red alga, *Furcellaria lumbricalis*, is the deepest extending attached macrophyte in the area and has been found on rocks to a maximum depth between 18 and 21 m depth (A. Ruuskanen and M. Westerbom pers. obs.). Loose lying specimens of macroalgae may be found at even deeper levels. Rooted soft-bottom macrovegetation (*Zostera marina*, *Tolypella nidifica*, *Ruppia cirrhosa*) has been found down to depths between 6 and 7 m in the clear water of the outer parts of the archipelago (OZ and OMZ) (Luther 1951a, 1951b). In open bays with bottoms continuously sloping towards deeper levels the vegetation could reach depths of 6-8 m (Häyrén 1958). A minor, 23 %, of 84 macrophyte taxa (Luther 1951a: Table 7), exhibited occurrences down to 4 m depth or deeper. 69 % occurred only on depths shallower than 3 m. In the flad stages investigated for this study the main deep limit of the vegetation was observed between 3 and 4 m. Flads are considered shallow. Concerning the main depths of localities in this study the limit between shallow and deeper bays is suggested to be 4 m.

Quantitatively large, but spatially, temporally and qualitatively diverse, environmental materials have been collected from the study area. The conception of the environmental conditions of this summary is based on these partly unpublished materials. During the field work period of the author, measurements of temperature, Secchi-depth and salinity were performed. In 1986 and 1987 the development of the environment of different flad stages and a reference station in an open *fjärd* of the archipelago was studied by comparing the conditions in four different localities (Ekebom 1990, R. Munsterhjelm & J. Ekebom, unpubl.). The localities were investigated five times from October

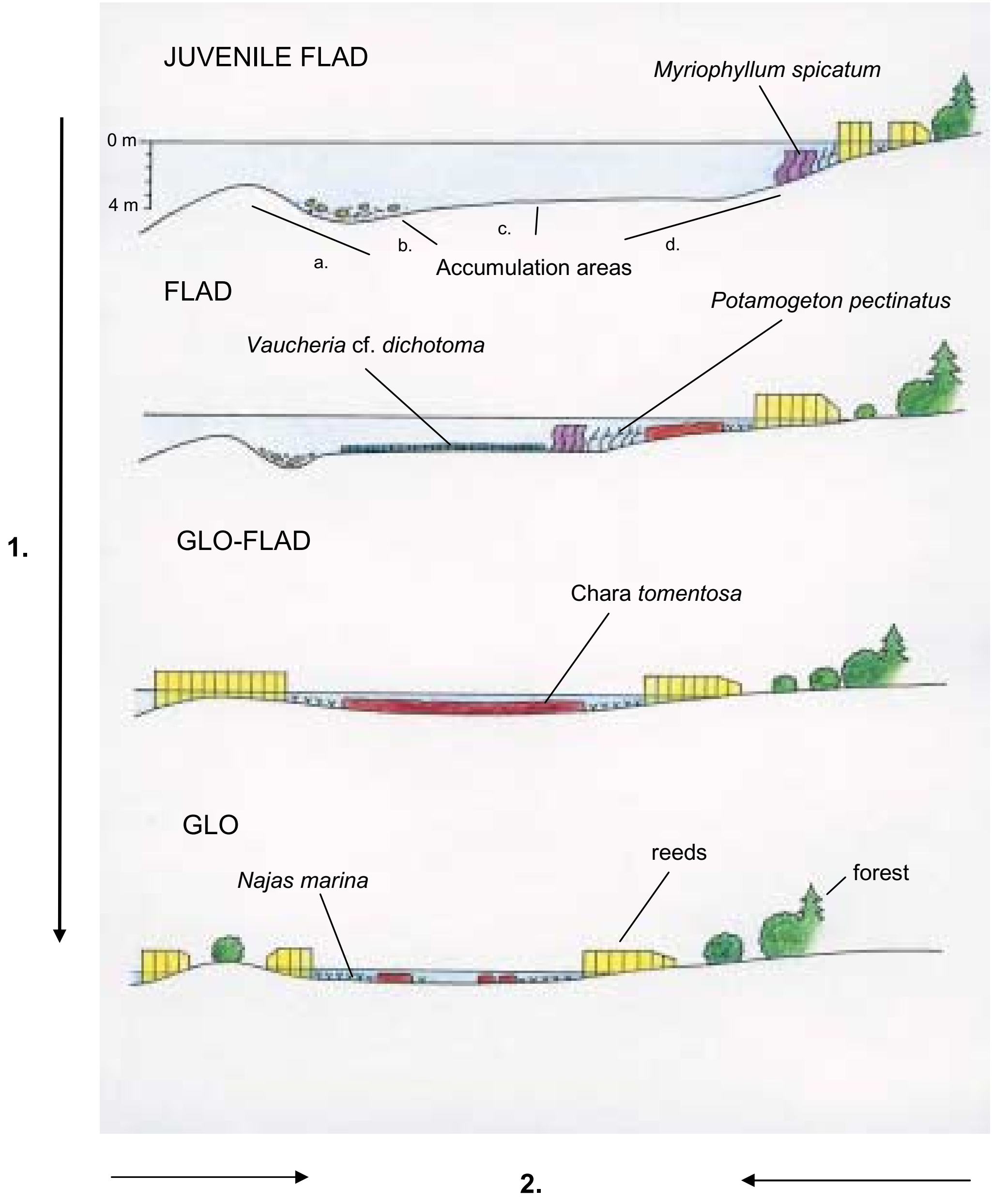
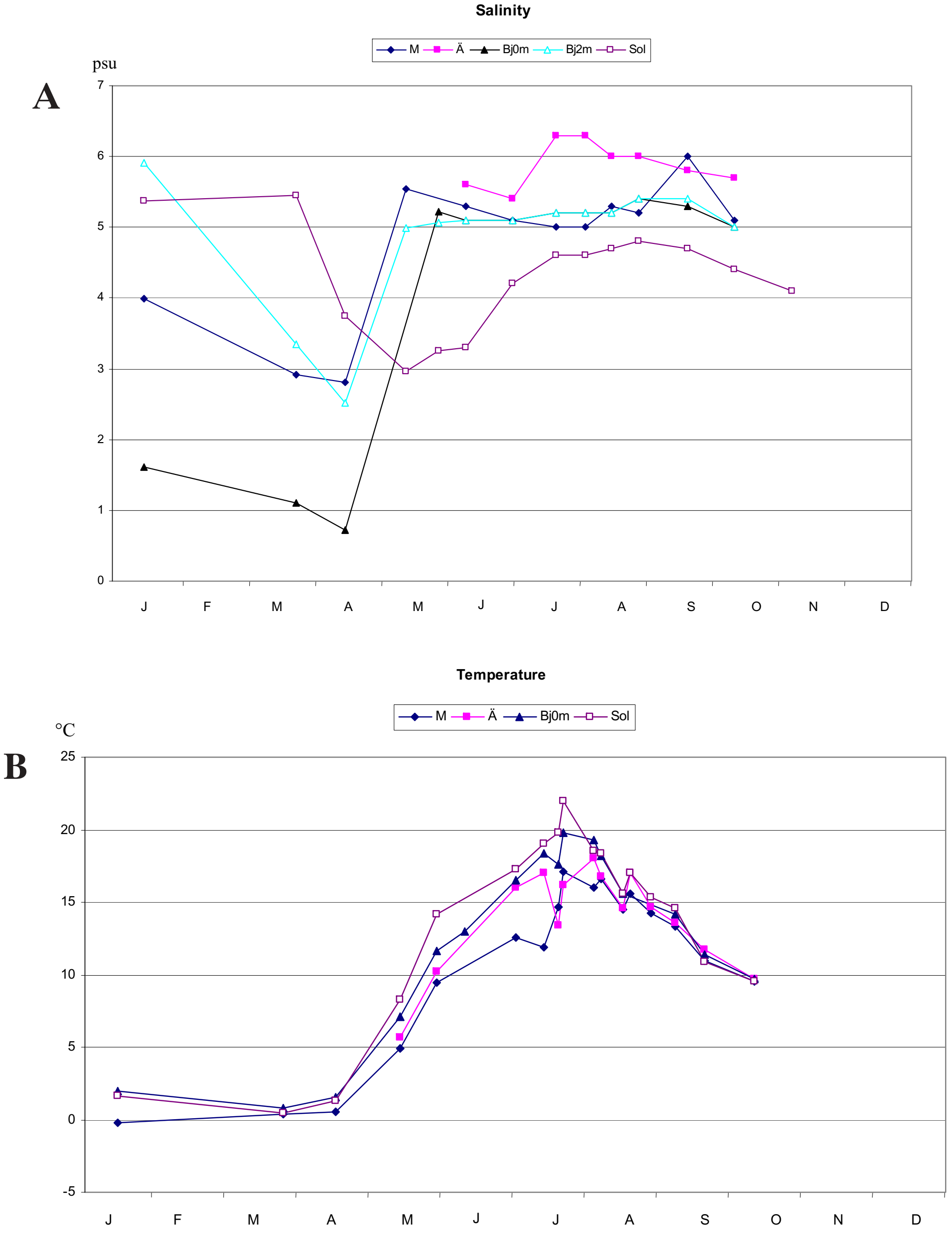


Figure 3. Principal model of the morphological flad development and the succession of the vegetation. 1. The isolation gradient along which for example following changes occur: reduced water exchange, increased shelter, decreased salinity, depth of water and decrease of the area of localities. 2. Succession of reeds and terrestrial vegetation. Accumulation of material in different degrees of shelter: a. If not a permanent feature of topography (e.g. rocks) the sill of the opening area may develop where the transporting ability of the waves carrying heavier material ceases and e.g. sand is deposited. b. Accumulation of detritus, e.g of *Fucus vesiculosus* and other macroalgae. c. Accumulation of sediments transported into the flad or d. formed in the flad.

1986 to April 1987 and 15 times from May to November 1987. Some of the results from 1987 are presented in Fig. 4A-D. One late developmental stage, a glo was investigated less intensely. Salinity, Secchi-depth, pH, oxygen, nutrients (total phosphorus, orthophosphate, total nitrogen, nitrate and ammonium) and chlorophyll-a concentrations were studied. These materials are referred to in papers I and III. In 1998 and 1999 additional environmental information was collected from three pairs of undisturbed and disturbed localities in different stages of the flad development (Wallström *et al*. 2000). During the



summers 2002 and 2003, suspended material, turbidity, pH, oxygen and total nutrients were investigated in shallow bays, flad stages, and archipelago areas; five localities in 2002 and 13 in 2003 (C. Henricson unpubl.). This information is referred to in paper III.

During the field work, environmental factors (e.g. turbidity, colour of the water and filamentous algae covers) were also visually registered. It is considered that these observations provided valuable indications of the environmental state of the localities. They

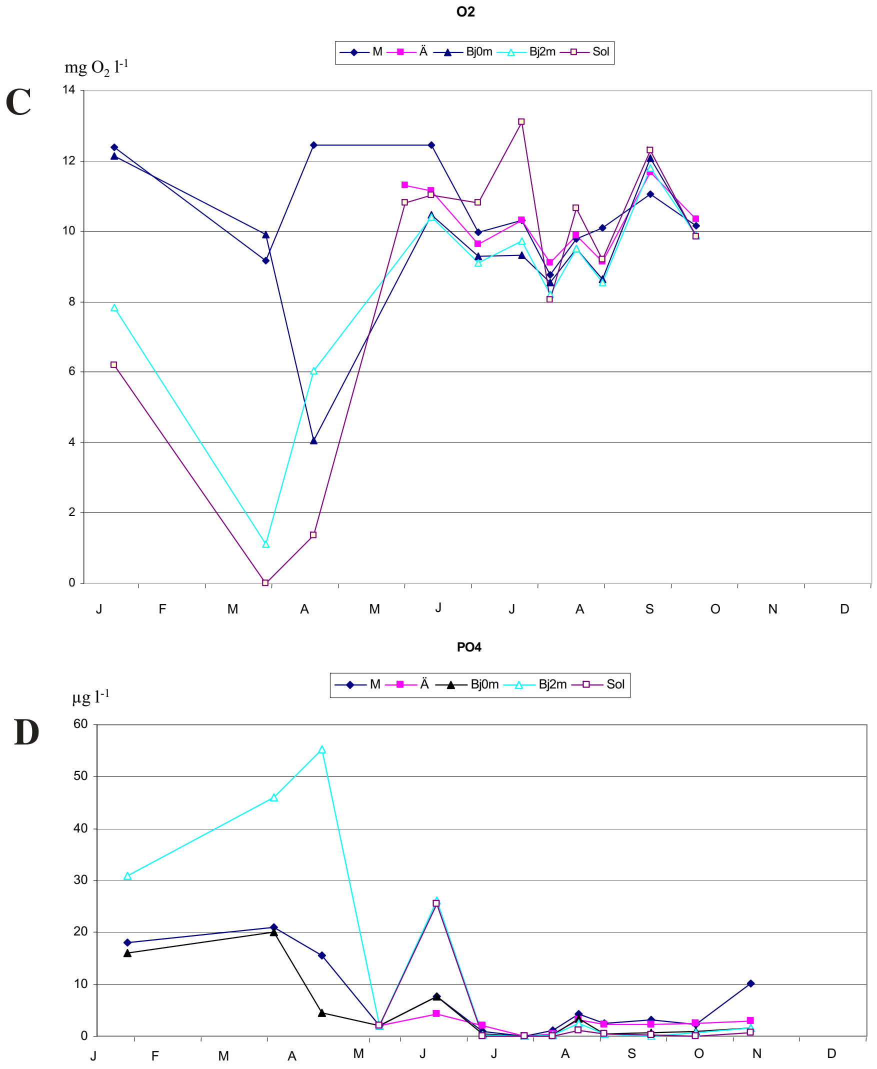


Figure 4A-D. The dynamics of the environment in the sea and in three flad stages during the year 1987. M = Mörnäsfjärden, an open archipelago water area; Ä = Älgö flad, a juvenile archipelago flad; Bj = Björkviksfladan, an archipelago flad; Sol = Solbacksfladan, a glo-flad. A) Salinity; B) Temperature; C) Oxygen; D) Phosphorus. In Björkviksfladan the samples were taken from 0 and 2 m water depth and in the other localities between 0 and 0.5 m. The figures are based on Ekebom (1990) and on unpublished material (R. Munsterhjelm & J. Ekebom).

were largely used to support the descriptions and definitions of the localities (papers I, II and III). The main bottom types – gravel, sand, clay and organic mud or *gyttja* – were determined visually, too.

The main inventory field work of the present study were performed by means of a transect method (papers I and II). The transects were placed in order to give a representative cut of the morphological variety of the investigated localities. The investigations along the transects were performed from a boat or by diving.

The abundance of the species was mainly determined with the 7-degree abundance scale of Norrlin (Luther 1951a, papers I and II). Later, simplified 5-degree scale was used (paper II). The terms "covering", "abundant", "scattered", "sparse" and "very sparse" in the scale of the sampling from the transects (about 20 m wide), represent classes clearly distinguishable from each other in the field. A simple 4-degree scale based on the typical occurrence habit of *Chara tomentosa* was applied on the historical material of its occurrences in order to make the very heterogeneous information from different types of sources treatable in a uniform way (paper III).

The abundance scales used in the field can be regarded as subjective, but they provided good relative information when performed by the same investigator (papers I and II). In the presentation of the results, for example in vegetation maps, the subjectivity is also decreased by the application of less detailed scales than those used when the material originally was collected.

The advantages and disadvantages of the traditional and new methods were evaluated (paper II). One result was that the traditional methods (paper I) allowed at the same time detailed and relatively fast field work.

The vegetation and distribution maps (papers I and II) were based on basic maps (1:20 000) or photographs (1:20 000 and 1:2 000) and the inventory material. They were drawn by hand and completed by means of computer programs. Different species and environmental variables obtained in the field work were placed on different transparent sheets of the map. The correlation between different elements of the ecosystem (e.g. the depth information or bottom material and species distribution) was visually analysed by combinations of the sheets. Maps from different localities were also compared. The method provided considerable information, otherwise difficult to obtain. The concept of competition and succession is based on such data (papers I and II).

An experiment (paper IV) based on the indications obtained in the other studies (papers I and III) was performed in a controlled situation. It aimed to confirm the effect of water turbidity, sedimentation and turbulence, which are typical disturbances following mechanical interferences in wind-sheltered bays.

In classification and organisation of environmental (e.g. geomorphological features) and botanical information great flexibility was aimed to achieve. Although the picture may become more diffuse, it is still closer to reality than having too fixed classifications. The classifications and indicative significance of species based on the descriptive material were also tested numerically (paper I). This supported the achieved concept in great detail.

The general methods of this study can be described as comparative as in traditional anatomy and evolution research. Based on the similarities and differences in the obtained botanical and environmental evidence from different localities a model of movement and development was built up (paper I and II). However, also a real temporal change supporting the concept could be documented (paper I and III).

NATURAL CHANGES OF THE ENVIRONMENT AND THE VEGETATION

Environmental and biological developmental processes in the archipelago

Organisms respond to environmental gradients. One example is the largely light-dependent zonation of macroscopic algae on rocky substrates. On the seacoasts, four gradients are considered the most crucial for the presence and abundance of aquatic vegetation – light, temperature, wave exposition and salinity (Raffaelli & Hawkins 1996). The general aquatic environmental gradient of the study area directed from its outer towards its inner parts is expressed as zonation of the environment (Fig. 1B) as well as of the organisms (Häyrén 1900, 1948). Its hydrobiological changes are connected with various factors of increasing shelter and influence of fresh water (Häyrén 1900, 1948, Luther 1951a). Favourable opportunities to study ecologically and biologically important, as well as restricting, conditions for the organisms are offered. Most of the aquatic organisms of the area attain some environmental limits along the gradient (Luther 1951a, b, Koli 1961, Niemi 1973, 1975, 1978, Hällfors & Munsterhjelm 1982, Hällfors *et al.* 1983). The environment is also modified by the organisms themselves (Raffaelli & Hawkins 1996), e.g. in the development of organic sediment bottoms in the more sheltered parts of the archipelago, where organic material is accumulated (Häyrén 1902, paper I).

The gradients and the zonation of the archipelago (Fig. 1B) are an expression of a temporal historical process of land upheaval (Häyrén 1900, 1902, 1910b, 1948). The present distributions of species, e.g. of macrophytes (Luther 1951a), can be seen as on-the-spot accounts of the ongoing distributional successions of organisms. Phytoplankton and epiphytic algae also exhibit successions on the regional plane (e.g. Niemi 1973, 1975, 1978, Hällfors & Munsterhjelm 1982, Hällfors *et al.* 1983).

Other aquatic gradients in the coastal area are created through a process of isolation by *rock-pools* (Hällfors 1984), i.e. small depressions in the bedrock, and *flads*, i.e. coastal lagoons typical for the Northern Baltic archipelago areas (Tolvanen *et al.* 2004, paper I). Also these gradients are directed from brackish towards fresh water, and finally terrestrial conditions, and both are characterised by the succession of organisms. The flads, as well as the rock-pools, exhibit successions on a smaller, more local, spatial scale than does the general gradient.

The rock-pools are the first bodies of water to become isolated from the sea during land uplift. They occur mainly in the outer archipelago zone (OZ) and outer parts of the inner archipelago zone (IZ), (Fig. 1B). They are invaded by opportunistic phytoplankton and filamentous algae, which manage to survive in their ephemeral or strongly fluctuating environmental conditions (e.g. freezing, drought, heat, salinity and nutrients; Hällfors 1984). They are finally absorbed by terrestrial vegetation (Hällfors 1984, Hæggström & Skytén 1987).

The occurrence of various types of bays and flads is presented in Fig. 2. The outermost fladlike localities, *the outer skerry flads and gloes*, are larger than the rock-pools. They are developed in the OZ between rocks that provide enough shelter for sediments to accumulate on the bottom (paper I). As a consequence of the geological structure of the bedrock the outer skerry flads and gloes are small compared with other flad types. The *archipelago flads* are mainly developed between islands, from more open typical archipelago waters called *fjärds*, or from sounds or bays in the middle parts of the archipelago (in the OZ and IZ; paper I). The *beach flads* develop on the sandy shores of the outer mainland zone (OMZ) (paper I). In contrast to the rock-pools the shallow flad ecosystem is characterised by soft-bottoms and soft-bottom macrophytes (paper I). In the mainland zone (MZ) the *fjärds* turn into large, shallow *mainland flads* (cf. Häyrén 1902, paper I).

Fjärds may also turn into lakes during the land-uplift process, if they are deep enough. Their development will slow down after their transition into the lake stage, which is more permanent than the shallower flad stages. In contrast to shallower basins, many pass through a meromictic stage with a stratified water column (Lindholm 1975, 1991, Weppling & Lindholm 1983).

Environmental development of flads

The development of flads (Munsterhjelm 1985a, 1985b, 1985c, Lehtinen 1998, Numminen 1999, Tolvanen *et al*. 2004, papers I and II) begins with 1) shallow *fjärds* or 2) shallow *open bays* and proceeds towards more sheltered and isolated stages. These include 3a) *juvenile flads*, 3b) the more isolated *flads* and 3c) the even more closed *glo-flads*, in which the openings are choked with reed or other emergent vegetation and through which the water can only slowly percolate. Finally, they proceed to 3d) the *glo* stage, which is already topographically but not completely hydrologically cut off from the surrounding waters (Fig. 3). These localities remain open and turn into lakes isolated hydrologically and biologically from the sea, turn into swamps or are choked by reeds and colonised by subsequent terrestrical vegetation (Ingmar 1975, Ingmar & Willén 1980, paper I).

The prerequisite for initiation of the isolation process of true flads is the formation of a submerged sill in the opening. Sills may be dependent on the original topographical features of the underwater landscape, e.g. rocks, but are also commonly formed at sites where the sediment-transporting power of the water ceases, i.e. where the circulation becomes too weak to carry the materials in question. Depending on local water circulation conditions the sills can be developed at different stages of bay isolation. At a certain stage the soft-bottom sills are overgrown by reeds and the glo-flad is born. The sill can also be formed by a reed belt accumulating filtered material or material produced by the reed itself (Häyrén 1902). Sandbanks, *tombolos*, may be formed in shallow, sandy, coastal areas on the lee sides of islands, connecting them with the shore (Tolvanen *et al*. 2004); the beach flads of OMZ are born in this way (paper I). Very sheltered bays and flads become traps for inorganic and organic material flowing in from the archipelago or coming from the drainage area, or for material produced in situ under to the highly productive conditions in the flad (Häyrén 1902, Tolvanen *et al*. 2004, paper I).

During morphological development the localities gradually become shallow enough to offer benthic microalgae and macrophytes favourable light conditions over large bottom areas (Ekebom 1990). I suggest that the border between juvenile and flad stages under natural conditions should be defined by their deepest benthic macrovegetation limits which occur mainly at 3-4 m depths (papers I and II). If the vegetation-free bottoms below this depth limit represent the predominant bottom type of a flad locality, it should be a juvenile flad. The macrovegetation in the juvenile flad will only form a fringe along the shores (paper II). The maximum water depth is usually 4 m or more in the juvenile stage, less than

3.5 m in flads and usually less than 2 m in glo-flads and later stages. Use of this classification should, however, not be too rigid, since there are turbid flad-like localities that are shallower than 3-4 m, but that are still characterised by vegetation-free bottoms. It is probably the stage of isolation that is more decisive for the type of vegetation than the depth (paper I). Additional features separating the stages from each other include the number and size of openings and the proportion of rocky shores compared with shores covered by reeds (paper I). The later the stage the more complete is the reed coverage and the fewer and smaller are the openings.

The connection between coastal lagoons and the sea is restricted also elsewhere in the world. The lagoons show closer couplings with the bottom sediments than does the sea (Nixon 1982, Kjerfve & McGill 1989, Taylor *et al.* 1999). In contrast to the situation in the open bays and estuaries where phytoplankton predominate, the coastal lagoons exhibit complex assemblages of sea-grasses and drifting algae (Taylor 1983, Thorne-Miller *et al.* 1983, Nixon *et al.* 1984, Oviatt *et al.* 1986).

The stages in the flad development represents environmental factors that are only partly the same as those in the surrounding sea and which differ in relative importance, thus offering additional opportunities to study the ecological importance of various factors for organisms. The hydrological and hydrobiological conditions in a morphologically representative set of bays, flad-like localities and stages in the flad development in the northern Baltic Sea have been examined since the 1960s (Forsberg 1965a, 1965b, Willén 1962, Lundegårdh-Ericson 1972, Ingmar & Willén 1980, Kuosa 1985, 1986, Ekebom 1990, Wallström *et al.* 2000, R. Munsterhjelm & J. Ekebom unpubl., M. Viitasalo *et al.* unpubl., R. Munsterhjelm & C. Henricson unpubl.). One example is given by the juvenile stage complex in, the Tvärminne Byviken Bay (Kuosa 1986). Here, changes in phytoplankton species composition, biomasses and chlorophyll-a indicate a transition from open sea conditions to inner flad conditions. A generalised outline of the natural environmental dynamics of and development between various stages is given below.

The environmental conditions and fluctuations of the archipelago waters of the study area are highly dependent on the open Baltic Sea, e.g. on salinity fluctuations, and are for example clearly influenced by storms (Hällfors *et al.* 1983). They are also affected by freshwater flow from the innermost parts of the area, the mainland shore and estuary area of Pojo Bay. In many respects juvenile flads and flads follow the environmental changes of the sea during the year (Fig. 4A-D). The juvenile flads exhibit more immediate reactions to the events in the outer waters, whereas the flads may show a temporal delay in their reactions, as a result of further developed isolation (Ekebom 1990, R. Munsterhjelm & J. Ekebom unpubl.). Juvenile flads and flads are also affected by the freshwater layer emerging beneath the ice in winter from the inner parts of the area (Hällfors *et al.* 1983; Fig. 4A). Glo-flads are more independent on events in the sea. However, during periods of high seawater level in autumn and winter, brackish water becomes trapped in the glo-flads for the winter (Fig. 4A). This causes a considerable delay in the general process of water becoming fresh during isolation. At the time of snowmelt, from April to May, salinity decreases. In glo-flads this fresh water becomes locked in for the summer part of the year. The gloes may be close to freshwater conditions. They are dependent on the frequency of contacts with the sea and their salinities may considerably vary between different localities and time periods.

The salinities of the flad development vary between different times of the year, different stages and different localities. The observed summer salinities of juvenile archipelago flads varied from 5.0 to 6.5 psu. In the archipelago flads they remained between 5.0 and 6.0 psu. In glo-flads they varied between 3.0 and 5.5 psu and in gloes between 0.5 and 4.5 psu.

Opposite to the *fjärds* and open bays, oxygen deficiency develops below the ice in winter in the flad stages and in later stages (Fig. 4C). The amounts of nutrients increase to higher levels than in the sea through anaerobic processes, but they are consumed by phytoplankton immediately after the ice break-up as in the sea (Fig. 4D). A nutrient and subsequent phytoplankton peak (high chlorophyll) not as conspicuous in other localities has been observed in the summer in the flad and glo-flad stages. This was probably a result of the late decay of the hibernated *Chara tomentosa* community dominant in these stages.

Secchi-depth, turbidity and/or suspended material measurements show that the light conditions in the sea fluctuate considerably more and exhibit larger amplitudes than in flads and later stages. The water is less turbid in the flad stages than in the more open, wind-exposed, shallow environments outside the flads (Häyrén 1912) and in juvenile flads. The clearest water is found in connection with dense macrovegetation in flads and glo-flads, especially over the *Chara* meadows (paper III).

The deepest limits of the vegetation, mainly seen in the open bays or juvenile flads, are clearly determined by the light conditions. In flads of a natural state the vegetation normally reaches the maximum depth of the locality. Beyond competion from other species (e.g. reeds) important factors regulating the occurrence of the vegetation in its upper levels are sea-level fluctuations exposing the vegetation to the atmosphere (Luther 1951a, Fletcher *et al.* 1985, paper I), ice-scarping and freezing of the bottom (Luther 1951a, Rich *et al.* 1971, paper I, III) or all combined (paper I).

The last stage in flad development is a vegetation-poor stage that may be compared with very shallow lakes (Thomasson 1955). In the shallow lakes the upper sediment surface becomes diffuse in a late stage of the bottom development and its availability for colonisation of benthic organisms decreases. The stabilising effect of deeper waters is lost and the water climate becomes totally dependent on the more dramatic climatic fluctuations. The environment becomes increasingly poor in diversity of organisms and ecological niches. In this situation epipelic microalgae mainly predominate production in the flads (Ekebom 1990).

Development of reed vegetation

The dynamic development of reed (*Phragmites australis*) vegetation is a decisive factor affecting development and distribution of the vegetation of shallow open bays and flads (Fig. 3, papers I and II). In the innermost parts of the archipelago, in the PB and MZ, reed colonises most of the shorelines and reaches its deepest limit of 2.1-2.2 (max. 2.25) m depth (Luther 1951a). It also colonises a considerable part of the soft-bottom shorelines in the IZ. Further out in the archipelago, the reed colonises mainly the most sheltered bays in the OZ. Here it does not completely cover the shores and extends to depths between 1 and 1.5 m. In sheltered IZ coves and bays and in the juvenile flad stages it may reach approx. 1.5-2 m in depth, and occasionally its deepest limit. During flad development it expands towards greater depths, mostly reaching its deepest limit in flads. It can be asked why these flads and later stages, where large bottom areas are shallower than 2.25 m, are not overgrown by reeds? In the flads reed exhibits an elevation of its deepest limit towards the most sheltered shores, a process that may already begin in the outer stages. In sheltered bays and juvenile flads, reed-free ice-pressed glades in the reed belt (Luther 1951a, 1951b) are formed at approx. 0.5-0.8 m depths. These reed-free areas develop mainly on soft gyttja bottoms. Here the rhizomes of the reed lose their hold on bottoms eroded by the ice. During every growth season reeds attempt to colonise the shallow bottoms in a horisontal zone up to several metres, but is every winter torn up from the bottom by the ice. Finally, as the critical depth becomes free from reed, inner and an outer reed belts may be formed. The deep limit of the inner belt will finally withdraw to 0.2-0.3 m depth. The outer belt will disappear at the latest when its bottom has risen to the critical level. The effect of this process increases with the rising of the bottoms and becomes more prominent towards later stages in the flad development. Thus, the flad stages will not primarily become overgrown by reeds. The total colonisation of reeds does not occur until the locality has become shallow enough for the movements of the ice to decrease, i.e. less than 0.2-0.3 m. Of course there is a shrinking of the area of the entire locality as the shore-line gradually moves towards the middle (Fig. 3). Forming belts and reed-turf, giving shelter from winds and water movements, and filtering and accumulating material the reed substantially participates in creation of the flad environment (Häyrén 1902, paper I, II).

Succession of submerged vegetation in the development of archipelago flads

The concept of succession of the archipelago flad vegetation suggested below is based on regional distribution data of aquatic plants (Luther 1951a, 1951b, Heinonen 1986, R. Munsterhjelm unpubl.), comparative studies of the successional stages of flads (Munsterhjelm 1985b, Lehtinen 1998, Nurminen 1999, papers I and II) and on regional and historical information (Luther 1951a, 1951b, Luther & Munsterhjelm 1983, Munsterhjelm 2000, R. Munsterhjelm unpubl., paper III). Models of the succession of flad species and vegetation are presented in Figs. 5, 6A-J and 7A-B.

The starting point of flad development seems diverse. The first soft-bottoms colonised by macrophytes in the archipelago are the sandy bottoms of open, shallow, clear-water *fjärds* in the OZ and OMZ. Here *Zostera marina* and closer to the shore also *Ranunculus peltatus* ssp. *baudotii* may predominate. The group of species is composed of species that either require circulating water (*Zostera marina*, *Ruppia cirrhosa*) or are favoured by it (*Potamogeton perfoliatus*, *Myriophyllum spicatum*) or that can withstand circulating conditions (*Potamogeton pectinatus*). If the bottoms are shallow enough and surrounded by a suitable topography, they may directly develop to more isolated vegetated flad bottoms. If they are deeper, the clear-water macrovegetation will decline during the transition towards the more turbid IZ waters. When topography permits, such bottom areas may develop into the vegetation free deeper floors of juvenile flads.

Development at shallower depths (approx. 0.2-1.0 m) begins in the open bays in the OZ or OMZ with sandy bottoms, which may develop directly into vegetated shallow flads of the beach flad type or to shallower vegetation zones on shores above the deeper bottoms in archipelago juvenile flads. The nearshore belt of dwarf hydroamphibionts is tolerant to sea-level fluctuations (e.g. *Potamogeton filiformis*, *Zannichellia palustris*, *Chara aspera*, *C. canescens*, *Tolypella nidi-*

fica and small plants of *Potamogeton pectinatus*; Figs. 5 and 6A, E, J). In more exposed sites on gravel or stony substrates *P. filiformis* often predominates. These are all brackish water species. From depths about 0.3 or 0.6 m downwards, *P. pectinatus* gradually begins to predominate. The brown alga *Fucus vesiculosus* and filamentous brown, red and green algae that may accumulate in the outer bottoms also accumulate in the bays, at different depths depending on the exposure.

In the most sheltered shallow OZ bays where *gyttja* is formed, *Potamogeton pectinatus* is likely to predominate (Fig. 6E). In shallow reed free-areas *Ruppia maritima* (*R. maritima* var. *maritima* and in flads mostly *Ruppia maritima* var. *brevirostris*) may partially replace the belts of the more exposed shores and bays. *Myriophyllum spicatum*, *M. sibiricum* and *Potamogeton perfoliatus* extend to deeper levels (Figs. 5 and 6B-D). Some other species establish or become more established in the sheltered bays (e.g. *Ranunculus circinatus*, *Callitriche hermaphroditica*, *Ceratophyllum demersum*).

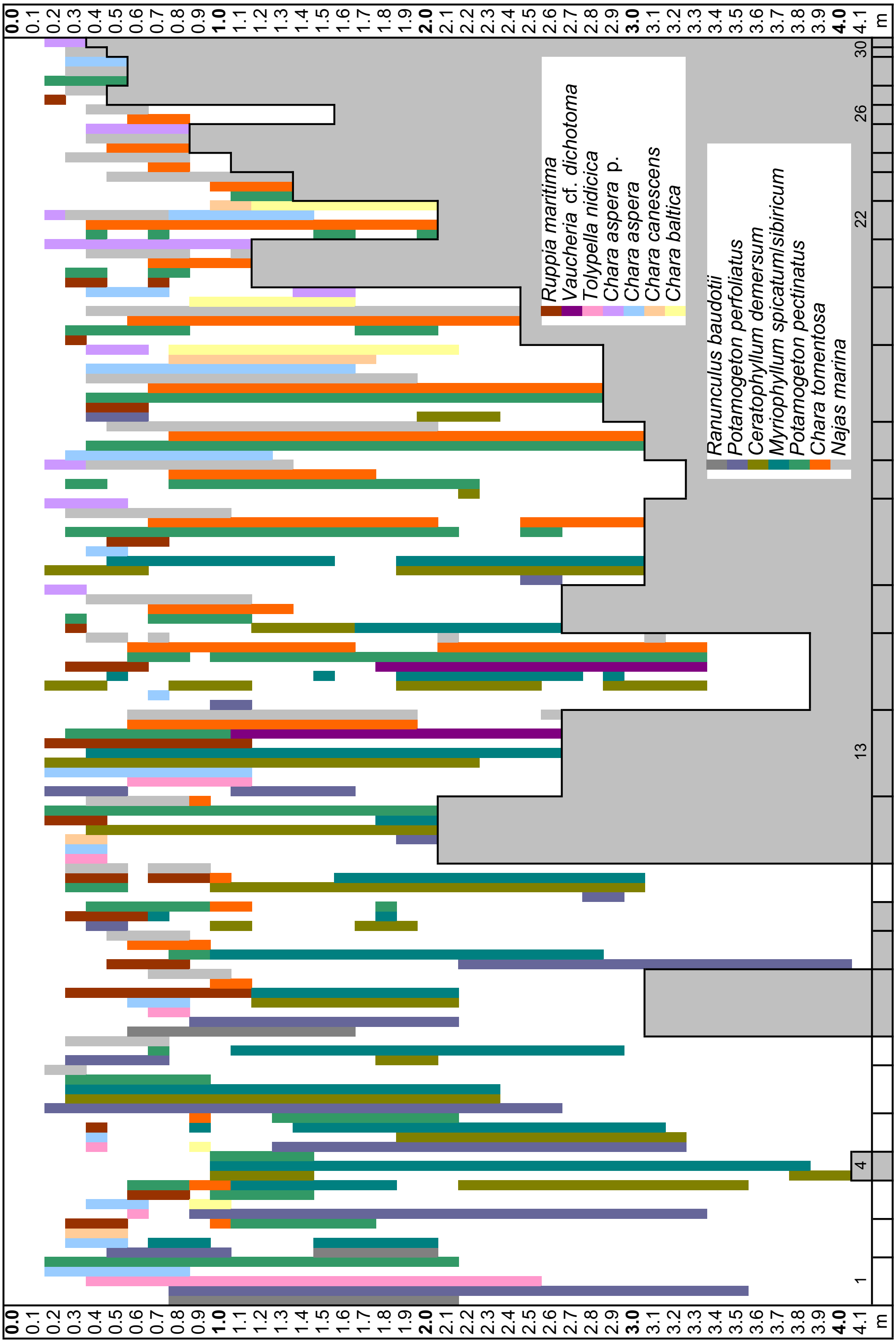
Further inwards in the archipelago, in IZ, some typical species at deeper levels reach their inner salinity limits (*Zostera marina*, *Ruppia cirrhosa*). The shallow belt of hydroamphibionts is mostly replaced by reeds. The dominant species in bays are, however, the same as in the outer bays. These are species widely distributed in the area, comprising the typical ubiquitous species (e.g. *Pota-*

Figure 5. A model of the natural succession of the main species along the gradient from open coves via juvenile archipelago flads, archipelago flads, archipelago glo-flads to archipelago gloes in the outer and inner archipelago zones of the study area. The succession is expressed as changes in occurrence and depth distribution along the isolation gradient. The borders between the localities used for the model are given at the horizontal axis of the figure. 1-3 = Open bays, 4-12 juvenile flads, 13-21 flads, 22-25 glo-flads, 26-30 gloes. The grey field indicates the increasing shallowness during the isolation and is based on maximum depths of the localities.

The localities: 1. Kalvön bay, 2. Sommarö cove, 3. Notholmen cove, 4. Storfladan II, 5. Kopparöfladan, outer part, 6. Älgö flad, 7. Brändöfladan, 8. Mörnäs cove, 9. Knipholmsfladan, 10. Gammelbyfjärden, 11. Gyltviken, 12. Byviken, 13. Danskogfladan, 14. Björkviksfladan, 15. Västerfladan, 16. Ekholmsfladan, 17. Åkernäsfladan, 18. Ytteröfladan, 19. Kopparöfladan, inner part, 20. Tronsböle flad, 21. Simmet, 22. Solbacksfladan, 23. Strömsö Gloet, 24. Storfladan I, 25. Verkviken I, 26. Sommarö Gloet (Gloet II), 27. Lillfladan I, 28. Tvärminne Gloet (Gloet III), 29. Verkviken II, 30. Kopparöfladan gloes.

The figure is based on field notes and is modified from Figs. 14 and 23 in paper I, Fig. 3 in paper II (Älgö flad) and App. 2 in paper III. On the basis of botanical features the Mörnäs cove has in this picture been placed among the juvenile flads. Only scattered to very abundant (covering) occurrences are depicted (paper I). Only localities from which complete distributional data was available and which were considered in a natural state or close to natural state at the time of investigation are included. The localities were investigated between 1978 and 1985. In case of the Älgö flad information from 1999 (paper II) is used. The occurrence of *Chara tomentosa* in Gyltviken is taken from an aerial photo from 1962.

N.B. The figure illustrates how predominance of earlier species is exchanged to predominance of later species and how the diversity of species decreases towards the latest stages.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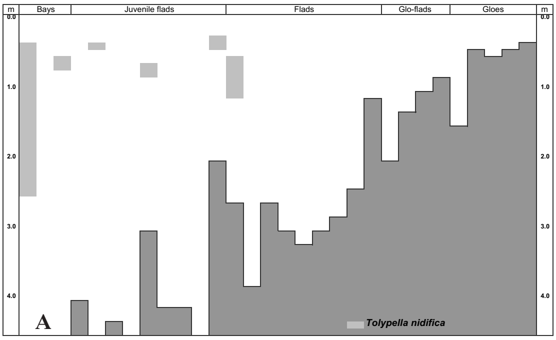
Tolypella nidicica
Chara aspera p.
Chara aspera
Chara canescens
Chara baltica
Ranunculus baudotii
Potamogeton perfoliatus
Ceratophyllum demersum
Myriophyllum spicatum/sibiricum
Potamogeton pectinatus
Chara tomentosa
Najas marina


m
Bays
Juvenile flads
Flads
Glo-flads
Gloes
m
0.0
1.0
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3.0
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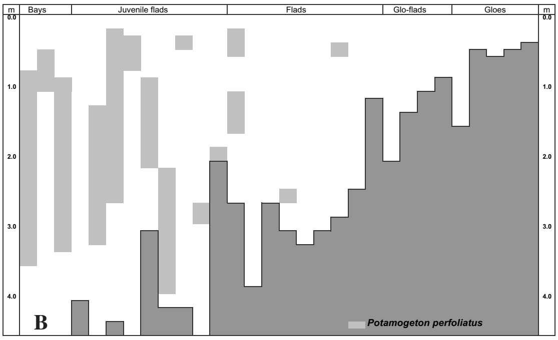
A
Tolypella nidifica


m
Bays
Juvenile flads
Flads
Glo-flads
Gloes
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0.0
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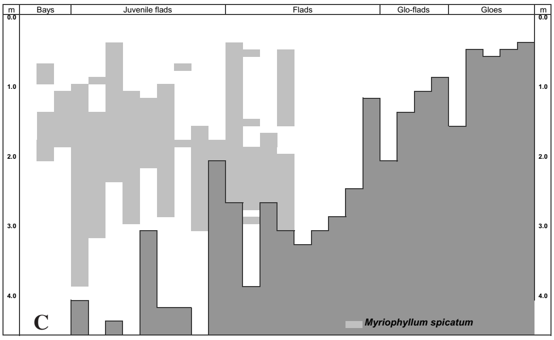
B
Potamogeton perfoliatus


m
Bays
Juvenile flads
Flads
Glo-flads
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0.0
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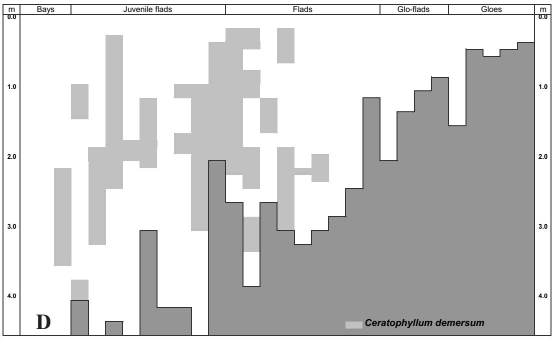
C
Myriophyllum spicatum


m
Bays
Juvenile flads
Flads
Glo-flads
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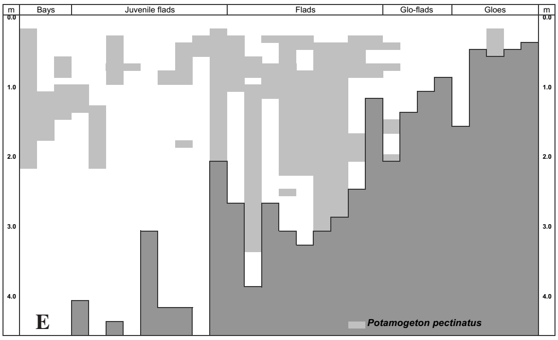
D
Ceratophyllum demersum


m
Bays
Juvenile flads
Flads
Glo-flads
Gloes
m
0.0
1.0
2.0
3.0
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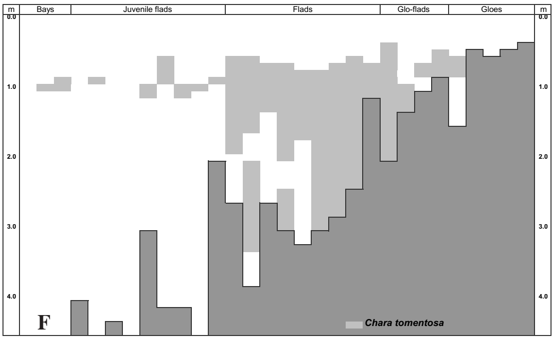
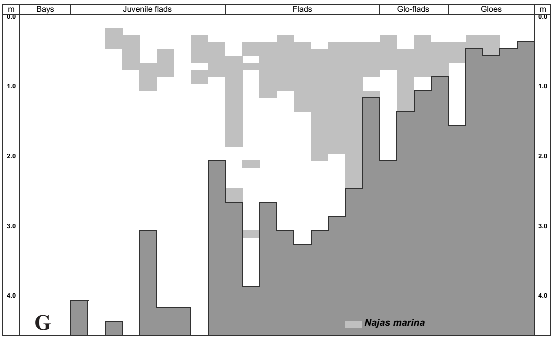
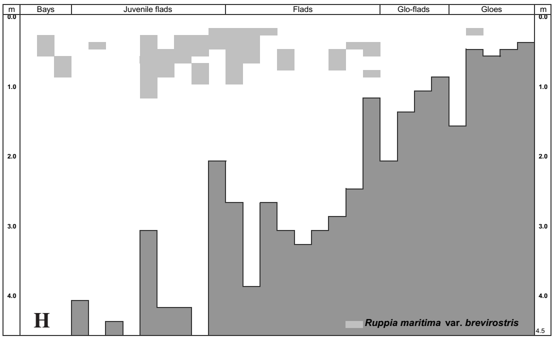
E
Potamogeton pectinatus


m
Bays
Juvenile flads
Flads
Glo-flads
Gloes
m
0.0
1.0
2.0
3.0
4.0
F
Chara tomentosa


m
Bays
Juvenile flads
Flads
Glo-flads
Gloes
m
0.0
1.0
2.0
3.0
4.0
G
Najas marina


m
Bays
Juvenile flads
Flads
Glo-flads
Gloes
m
0.0
1.0
2.0
3.0
4.0
4.5
H
Ruppia maritima var. brevirostris

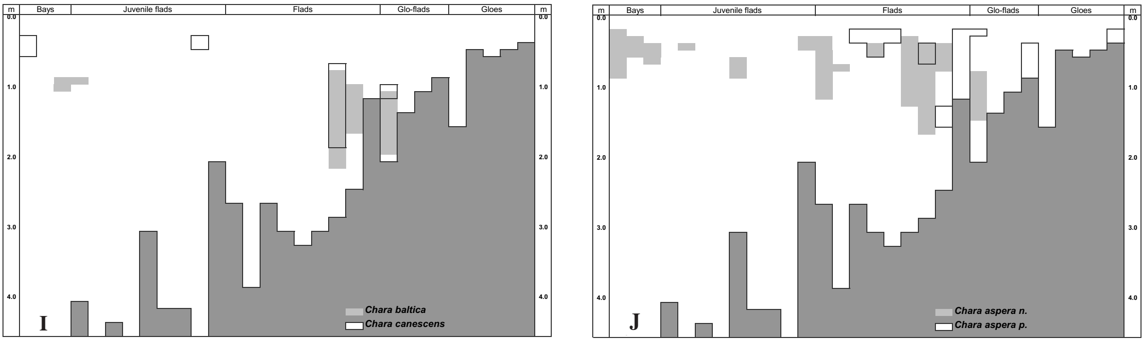
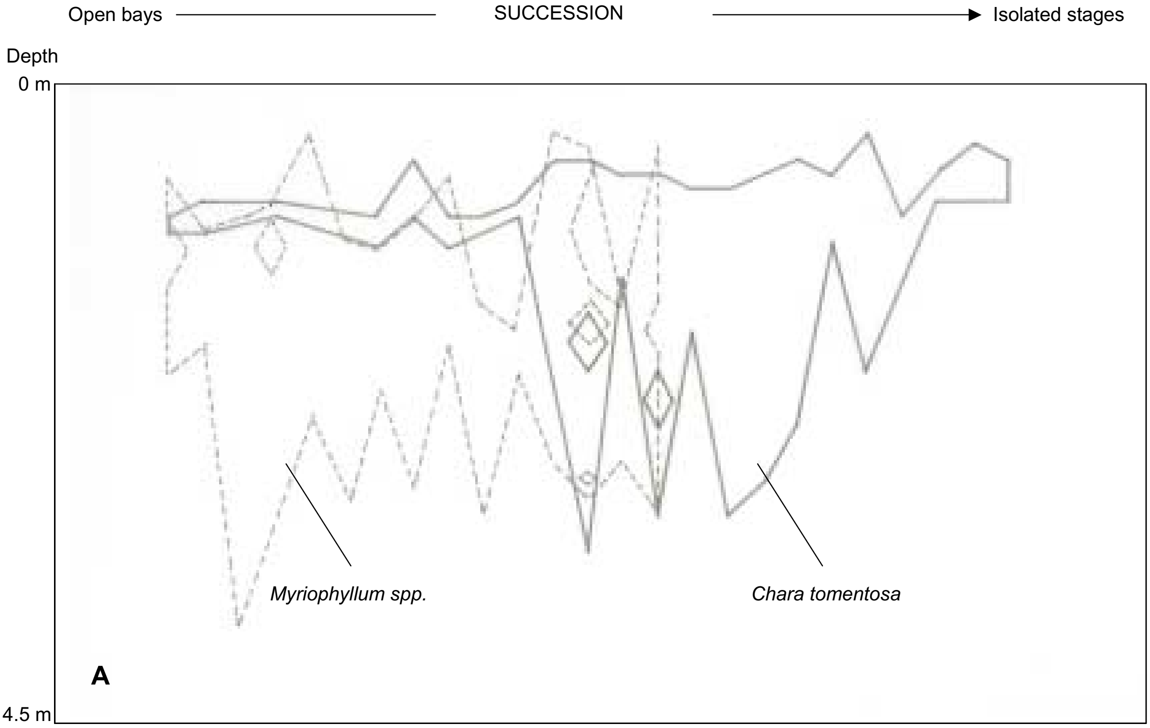


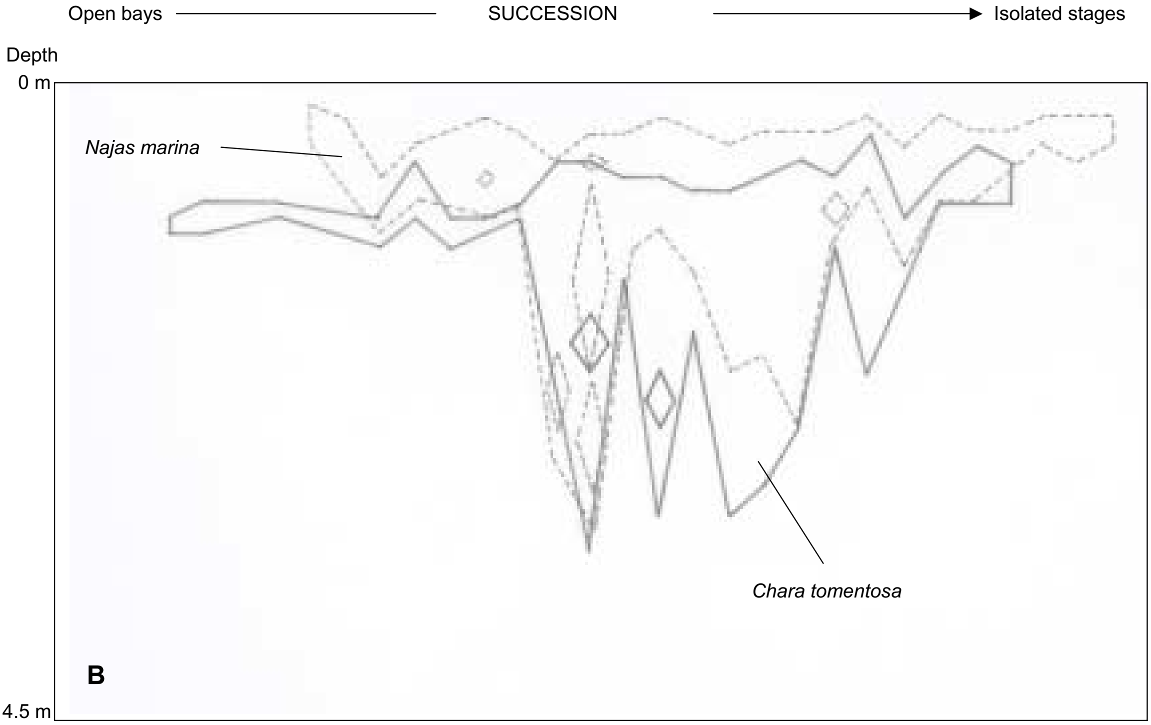
Figure 6A-J. Models of the natural succession of some species common in the archipelago of the study area or important in the archipelago flad development. The dark grey fields represent the decreasing shallowness and are based on the maximum depths of the investigated localities. The figure is extracted from Fig. 5.

A-D) "Early" species decreasing in occurrence and distribution towards early flads (*Tolypella nidifica*) or declining in the intermediate flad stages (*Potamogeton perfoliatus, Myriophyllum* spp. and *Ceratophyllum demersum*), E-G) "Early to intermediate" (*P. pectinatus*) and "intermediate to late" species (*Chara tomentosa*, *Najas marina*) increasing in horizontal and depth distribution along the flad gradient. H) "Intermediate" species (*Ruppia maritima*), I-J) "Early and late" charophyte species (*Chara canescens*, *C. baltica* and *C. aspera*) exhibiting a divided distribution along the flad gradient. *C. aspera* occurs in a normal form (n.) and a cortex cell free form (p.). The cortex free *Chara aspera*, very diffucult to detect in the field, is probably more common in the late stages than indicated by the figure.

N.B. *Potamogeton perfoliatus* is a very common species outside flads, often predominating in open bays and juvenile flads. Towards later stages the occurrences lose their former distributions and have to resort to the few sites and levels not occupied by other species (Fig. 6B). First it appears to be excluded by dense *Myriophyllum* spp. (Fig. 6C) and *Ceratophyllum demersum* (Fig. 6D). Later *Chara tomentosa* seems to hinder its continuity (Fig. 6F). In later stages also the *Myriophyllum* and *C. demersum* occurrences become fragmented in the same way. *C. tomentosa* establishes its first communities at a narrow depth level in sheltered bays and juvenile flads. *Potamogeton pectinatus* (Fig. 6E) establishes earlier than *C. tomentosa* but both species may reach maximal amplitudes in early flads after which *C. tomentosa* expansion continues and *P. pectinatus* declines. The bottoms becoming shallower causes narrower depth amplitudes for the communities towards later stages. *C. tomentosa* establishes also deep communities in early flads. In later stages space is given to other charophytes in the *C. tomentosa* community (Fig. 6I-J). The *C. tomentosa* community cannot form permanent communities at shallower bottoms areas (mainly < 0.6 m depth). At these levels *Najas marina* predominance increases the most during the succession (Fig. 6G). *C. tomentosa* is finally excluded from the deeper bottom areas and only *N. marina* and the cortex free form of *C. aspera* (Fig. 6J) may be left.

mogeton perfoliatus, Myriophyllum spicatum) and species typical of sheltered coves (*M. sibiricum* and *Ceratophyllum demersum*). The depth amplitude at which the submerged vegetation occurs may become narrower due to the reeds and the permanently more turbid water. The submerged vegetation forms a fringe parallel with the shoreline. This is also the typical condition of the starting point of the succession in juvenile archipelago flads. In the juvenile flads at more exposed reed-free sites on small stones and


Open bays
SUCCESSION
Isolated stages
Depth
0 m
4.5 m
Myriophyllum spp.
Chara tomentosa
A


Open bays
SUCCESSION
Isolated stages
Depth
0 m
4.5 m
Najas marina
Chara tomentosa
B

gravel, the typical vegetation of open seashores may still predominate in a narrow belt. The belt of the filamentous alga *Cladophora glomerata* typical of the OZ, OMZ and IZ still occurs on the hard bottoms just below the shore-line, but is narrower. Through spatial competition benthopleustonic *Fucus vesiculosus* may form a conspicuous structuring element for other vegetation in juvenile flads.

The most vigorous and diverse vegetation of the flad succession occurs in the early flad stage (Fig. 5). The shallow, well illuminated, nutrient-rich *gyttja* bottoms create conditions that favour the development of the largely distributed meadow like flad vegetation (Figs. 6F and 8). The relative dominance of the distribution of species suggests that localities of different successional stages can be distinguished, but the transition between these types is mostly gradual. From the flad stage to the glo-flad stage, however, a leap occurs (Fig. 8) as the opening becomes overgrown by reeds. This results in a successional type that differs strongly from the former type. All the species of the complex vegetation of the opening are excluded.

The vegetation of the opening and the area just inside it in the early flad stages is similar to that of slightly exposed OZ bays. It may contain species that require (*Ruppia cirrhosa, Chorda filum* and haptophytic *Fucus vesiculosus*) or are favoured by circulating water (*Potamogeton filiformis, Zannichellia palustris, Callitriche hermaphroditica*) and that mostly do not occur inside the opening area. Some of the species extend further inwards in the flads (in deeper levels *Myriophyllum spicatum*, *Potamogeton pectinatus*, in shallower levels *Chara aspera*). A change in species composition from the opening towards the most sheltered parts is developed and may be both gradual and exhibit sharp limits of the species distribution. Different communities predominated by one or a few species can be distinguished along the change.

Inside the opening vegetation the filamentous bottom-covering alga *Vaucheria* cf. *dichotoma* may characterise a certain stage in the early succession. The charophyte *Chara tomentosa* established at shallow depths in the most sheltered open bays of the archipelago or of juvenile flads, forms conspicuous

Figure 7A-B. The succession and relations between three important species in the succession of flad vegetion. A) Comparison of the occurrence and depth distribution of two mostly not associated species in the flad succession, an “early” taxon (*Myriophyllum* spp.) and a “late” species (*Chara tomentosa*). B) Comparison of the occurrence and depth distribution of two late and often associated species (*Chara tomentosa, Najas marina*) in the succession of the flad vegetation. The information is based on figure 6.

N.B. The canopy-forming *Myriophyllum* species (mainly *M. spicatum*) shade the bottoms and may form a competional hindrance for the expansion of the bottom-dweller *Chara tomentosa* in earlier stages of the succession. In the earliest stages of the succession *C. tomentosa* has to resort to levels not occupied by *Myriophyllum* or levels at which it can compete. Fragmentation of the distribution of both species is seen in the stage of the succession where their depth-amplitudes overlap. The main occurrences of *Najas marina* are found on a level shallower than the levels of *C. tomentosa* probably as a result of the competition from the dense charophyte community.

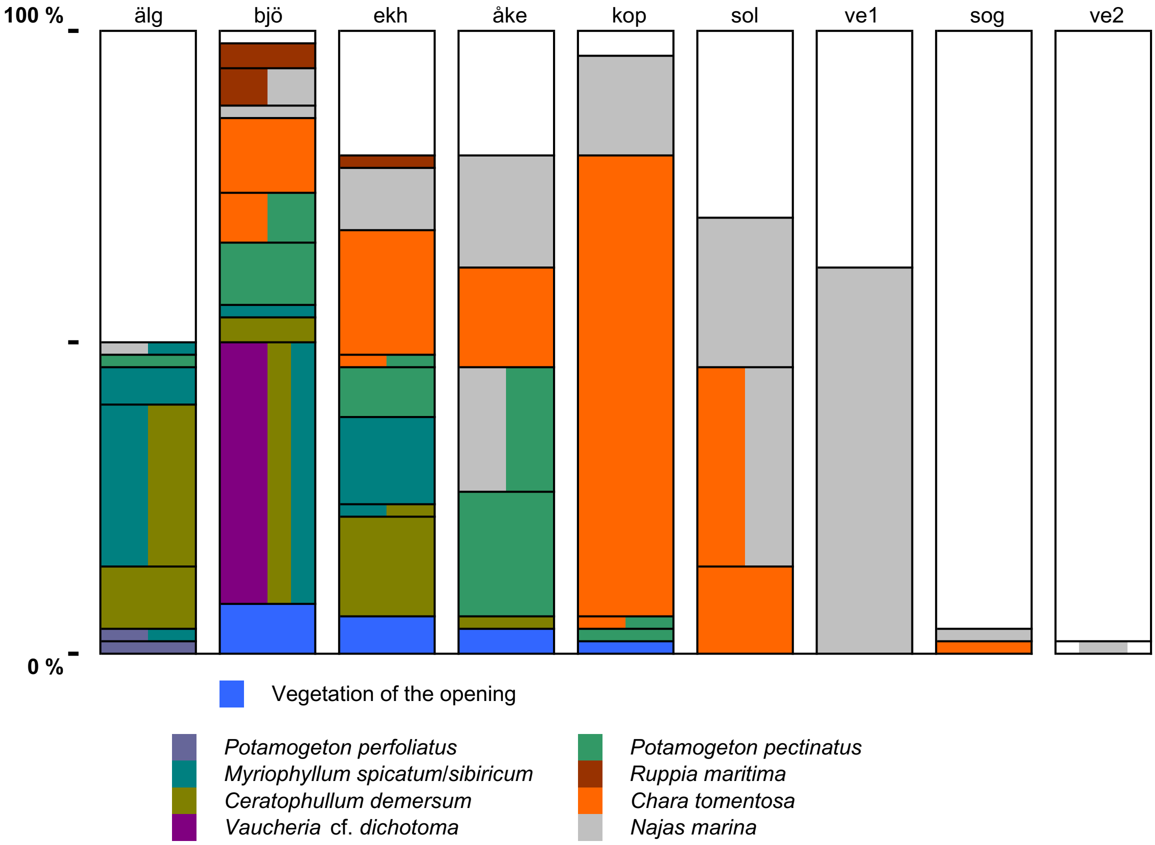


Figure 8. Model for the natural succession of coverage of the main macrophyte communities along the flad development. Coverages are given in percentage of the entire investigated localities. älg = the E bay of the juvenile Älgö flad, bjö = the "early" flad stage Björkviksfladan, ekh = the "early" flad stage Ekholmsfladan, åke = the intermediate flad stage Åkernäsfladan, kop = the late flad stage Kopparöfladan (inner part), sol = the glo-flad Solbacksfladan, ve1 = the glo-flad Verkviken I, sog = the glo Sommarö Gloet (Gloet II), ve2 = the glo Verkviken II. The figure is modified from Fig. 22 in paper I and completed with the information from the Älgö flad in 1999 (Fig. 4c in paper II). In ve2 the coverage of *Najas marina* was very low.

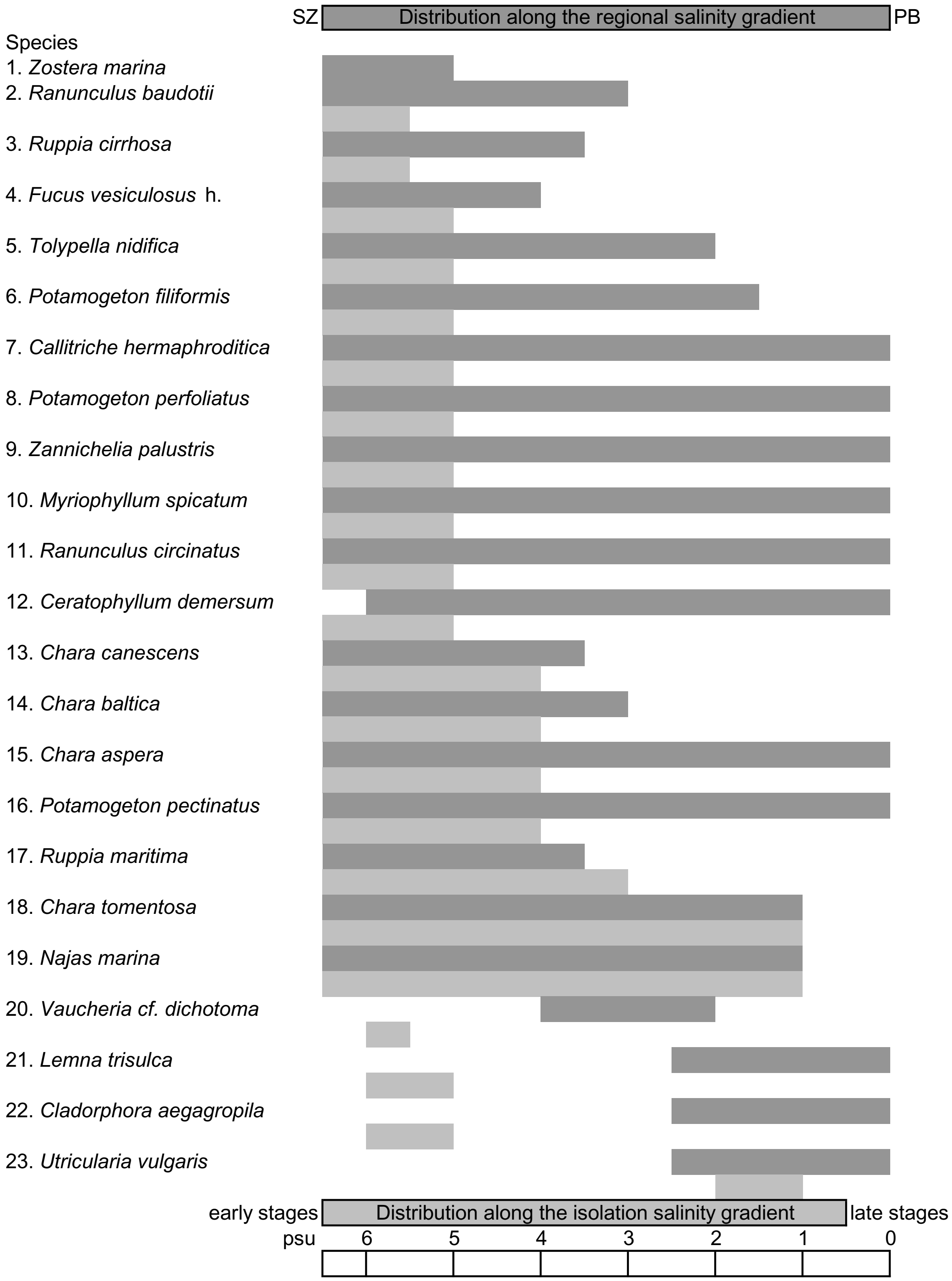
belts in the most sheltered parts of early archipelago flads at levels deeper than 0.5 m. Here *Potamogeton pectinatus* often forms an intervening belt between the *Chara tomentosa* and the deeper vegetation (e.g. *Myriophyllum spicatum*, *M. sibiricum*, *Ceratophyllum demersum*, *Vaucheria* cf. *dichotoma*). At shallower levels the dominance of species follows the changes in exposition, exhibiting belts mostly dominated by *Chara aspera* in the more exposed sites, *Ruppia maritima* in more sheltered and *Najas marina* in the most sheltered sites. Thus, one succession is characteristic of shallow depths and another for deeper depths. The limit between these levels, between 0.6-1.0 m, coincides with the uppermost limit of permanent *Chara tomentosa* communities. The distributions of the species of these levels may of course over-lap.

During flad development, the vegetation of the opening area shrinks towards the opening, subsequently followed by the deeper flad communities. *Potamogeton pectinatus* and *Chara tomentosa* subsequently expand towards the deeper levels until they totally dominate the entire flad at levels deeper than 0.5-1.0 m. In certain early flad stages the *Chara tomentosa* community may also establish a community at levels deeper than those at which it first occurred (Figs. 5 and 6F). The upper and developed lower *Chara tomentosa* communities tend to grow onto each other and enclose and finally choke the intervening communities. Later, in the late archipelago flad stages and glo-flads, new space is opened for other charophytes (*Chara aspera*, *C. baltica* and *C. canescens*) by bare patches that develop in the otherwise very dominant *Chara tomentosa* community (Figs. 5 and 6I, J). Thus, charophytes that may occur in more exposed open areas and possibly disappear during the succession may later exhibit a return in the later stages of development. At levels shallower than those at which the *Chara tomentosa* community occurs, *Najas marina* is the expanding species (Figs. 5, 6G and 8).

During flad development the diversity of the vegetation decreases. In late glo-flads or in glo stages the submerged vegetation gradually declines, which occurs parallel with the bottom becoming softer and shallower. In this perspective the last species surviving on the wide shallow bottoms are *Najas marina* and a cortex cell-free form of *Chara aspera*. At deeper levels charophytes maintain their dominant positions; among these *Chara tomentosa* seems to be the most persistent. The reasons for the extinction of *Chara tomentosa* may be diverse. During development *Chara tomentosa* is finally, before it disappears, referred to the area around it as a critical upper limit. Here its abundances show strong yearly fluctuations. This behaviour must be dependent on fluctuations of water level and ice conditions. Deteriorated light conditions possibly due to increasing humic substances or production of poisonous H_2S in the water may exclude the species from deeper levels. Decreasing salinity to levels below the salinity limit (1 psu) of the species may also cause the final disappearance.

In shallow bays, juvenile flads and especially in early flad stages species groups of different origins meet (Fig. 9). Most of the species involved in the flad succession are present already in early flad stages, after which the species decrease in number. The flora of the open bays and early flads consists of marine species (e.g. *Fucus vesiculosus*, *Chorda filum*), brackish water species (e.g. *Myriophyllum spicatum*, *Ruppia maritima*, *Chara tomentosa* and other charophytes) and a few fresh water species (e.g. *Potamogeton perfoliatus*, *Ceratophyllum demersum*). Species whose distributions do not overlap in other parts of the archipelago may also meet in the flads, e.g. brackish water species restricted to the outer parts of the archipelago (e.g. *Ruppia maritima*, *Chara canescens*) and species from the innermost parts (*Lemna trisulca*, *Vaucheria* cf. *dichotoma*). Species of differing tolerance to water circulation may also occur in the same localities (e.g. *Myriophyllum spicatum* and *Chara tomentosa*).

Many species disappear during the earlier stages in the succession. This may be an indication of the importance of competition between species. Environmental conditions other than salinity, e.g. lack of oxygen in winter, may increasingly influence them negatively during the isolation. It is remarkable that the species remaining longest in the succession are brackish water species, not fresh-


SZ
Distribution along the regional salinity gradient
PB
Species
1. Zostera marina
2. Ranunculus baudotii
3. Ruppia cirrhosa
4. Fucus vesiculosus h.
5. Tolypella nidifica
6. Potamogeton filiformis
7. Callitriche hermaphroditica
8. Potamogeton perfoliatus
9. Zannichelia palustris
10. Myriophyllum spicatum
11. Ranunculus circinatus
12. Ceratophyllum demersum
13. Chara canescens
14. Chara baltica
15. Chara aspera
16. Potamogeton pectinatus
17. Ruppia maritima
18. Chara tomentosa
19. Najas marina
20. Vaucheria cf. dichotoma
21. Lemna trisulca
22. Cladorphora aegagropila
23. Utricularia vulgaris
early stages
Distribution along the isolation salinity gradient
late stages
psu
6
5
4
3
2
1
0

water species as in the succession along the general gradient of the archipelago (Fig. 9). Their presence along the gradient can be explained by the long-preserved influence of brackish water. Partially, in case of the later more freshwater influenced stages, it must be a question of physical isolation at which new species may have difficulty in colonising. The brackish water species reach their lower salinity limits in the glo-flad stage or glo stages.

Charophytes are clearly favoured by the flad development. *Chara tomentosa* and *C. baltica* may be considered to have a competitive advantage from their habit of hibernating in a fully developed form, thus already occupying the bottom in the spring before other species begin their yearly growth. Their sediment-stabilising effect, possible allelopathy (Blindow & Hootsmans 1991) and apparent tolerance to periods of oxygen depletion may also be considered as factors favouring their occurrence.

Succession of species along the general gradient of the study area

The concept of the succession of species and vegetation along the general gradient of the study area is mainly based on Luther (1951a, 1951b) and on unpublished material (R. Munsterhjelm, M. Westerbom, O. Mustonen). In the outer parts of the area (the OMZ, OZ and part of the IZ), marine (*Zostera marina*, brown- and red algae) and brackish water species (charophytes and e.g. *Myriophyllum spicatum*, *Ranunculus peltatus* ssp. *baudotii*) predominate (Luther 1951a). These are further inwards replaced by freshwater species. Some species occur in the entire area (e.g. *Potamogeton perfoliatus*). Correspondence with the vegetation and environment found in flad development is observed in the mainland zone. Here the shallow *fjärd* and bay bottoms exhibit wide expanses of submerged vegetation, e.g. *Vaucheria* cf. *dichotoma* and *Myriophyllum spicatum*. *Chara to-*

Figure 9. The main salinity amplitudes of species along the general (regional) environmental gradient of the archipelago (dark grey bars; Luther 1951a) and along the isolation (flad) environmental gradient (light grey bars; Munsterhjelm 1985a, paper I). Six species groups can be discerned: Species of open archipelago waters (1-2), species of open archipelago waters that extend into flads (3-9), species of open waters and sheltered coves that extend far along the flad gradient (10-16), species typical particularly for the middle or late stages of the isolation gradient (17-20) and species that have their main outer environmental limit in the inner parts of the area, but also may occur in the higher salinities of flads (20-22) and (23) a fresh water species colonising late stages of the gradient. Only some characteristic flad species (17-19) attain in the flad development the same lower salinity limits as in the general environmental gradient.

N.B. The figure shows that decreasing salinity cannot be the main reason for the decrease in the occurrence of most species in the flad development. Potentially decisive factors may be oxygen depletion and competion (cf. Fig. 4A, C and Fig. 7A).

mentosa also belong to the MZ vegetation and wide meadows are known from the later stages of the *fjärds*, the mainland flads (Häyrén 1902). The salinity (2-4 psu) corresponds to that of glo-flads and early gloes. The inner distribution limits of some of the brackish water species (e.g. *Ranunculus peltatus* ssp. *baudotii*, *Ruppia* spp., *Chara canescens*) and all the marine species (e.g. haptophytic *Fucus vesiculosus*) is drawn outside this zone (Luther 1951a). Some freshwater species (*Drepanocladus* spp. and *Fontinalis antipyretica* (L.) Hedw.) not participating in the archipelago flad succession, are present in the salinities of MZ. The partly natural state of eutrophy is indicated by occurrence of the rare charophyte *Nitellopsis obtusa* and extreme growth of *Myriophyllum spicatum* and *Ceratophyllum demersum*. The reeds behave as they do in the archipelago flads. Further inwards, in Pojo Bay, the predominance of brackish water species has changed to almost total predominance of freshwater species (e.g. *Potamogeton obtusifolius*, *P. praelongus*, *Nuphar lutea*, *Cladophora aegagropila* and water mosses). The submerged vegetation ends between approx. 1.5 and 2.5 m in depth as a consequence of the more turbid water (sediment and humic acids) flowing out from the rivers. The deepest macrovegetation consists of the water mosses and the green alga *Cladophora aegagropila*. The deeper bays of the zone resemble lakes with a fringe of floating-leaved vegetation (*Nymphaea alba* ssp. *candida*, *Nuphar lutea*). From these bays there is a succession towards shallower bay stages and glades in the reeds characterised by different species (e.g. *Chara globularis*, *Lemna trisulca* and *Cladophora aegagropila*). Different flad stages (Fig. 2) with an own typical vegetation (e.g. *Myriophyllum verticillatum*, *Hippuris vulgaris* and *Utricularia* spp.) may be formed in the reeds or between islands. More wind-exposed shores with harder soft-bottoms may exhibit a flora typical for oligitrophic lakes (e.g. *Isoëtes* spp.).

The factors governing the distribution of aquatic plants are complex. Local factors such as turbulence, sedimentation rate and particle size of the substrate influence the location of species along the shore and floor of lakes and largely determine the lake type (Spence 1967, Seddon 1972). The chemical composition of the water exerts a controlling influence that determines which species may occur, whatever their substrate preferences and what niches available (Luther 1951a, Seddon 1972). Bottom material and wind exposure are generally linked and difficult to analyse separately. They, however, change in pace with the composition of the vegetation. The type of bottom and topographical conditions strongly influence the local distribution of species and vegetation. The occurrence of species in the localities studied indicates that of the four main gradients at seashores (Raffaelli & Hawkins 1996), light and exposure are clearly crucial to the distributional structure of the vegetation in the local situations of shallow bays and flads whereas salinity and temperature may influence the entire developmental processes.

ENVIRONMENTAL AND VEGETATION CHANGES AS A CONSEQUENCE OF HUMAN DISTURBANCES

In the Baltic Sea a change from a nutrient-poor to a nutrient-rich, partially strongly eutrophicated situation has occurred since the early 20th century. This is expressed as increased primary production, and subsequently increased sedimentation and oxygen consumption that, in turn, lead to increased nutrient release from the deep bottoms. As a result of these phenomena, dramatic changes in the presence and distribution of hard-bottom macroalgae in the northern Baltic have occurred since the 1960s or 1970s. An increase occurred in periphyton, filamentous algae, phytoplankton biomasses and in turbidity. A striking expression of the processes was shown by the detached, fast-growing, rocky shore, filamentous macroalgal species, which also formed considerable biomasses on soft-sediment bottoms, e.g. in shallow open bays. The changes were thoroughly documented (e.g. Fonselius 1978, Nehring 1981, Niemi 1981, Kangas *et al.* 1982, Hällfors *et al.* 1983, 1984, Kononen & Niemi 1984, Mäkinen *et al.* 1984, Kautsky *et al.* 1986, Mäkinen & Aulio 1988, Elmgren 1989, Launiainen *et al.* 1989, Cederwall & Elmgren 1990, Kahma & Voipio 1990, Kautsky 1991, Wulff *et al.* 1994, Kiirikki 1996, Kautsky 1998, Karjalainen 1999, HELCOM 2001). Development of the Secchi depth in the Baltic Sea decreased since 1903 by 50 % in the Northern Baltic Sea. In the Gulf of Finland the decrease, accelerating since the early 1970s, was 40 % (Laamanen *et al.* 2004).

Another conspicuous indication of the changes was the decline in the brown alga *Fucus vesiculosus* and some other macroalgal species (Kangas *et al.* 1982, Rönnberg *et al.* 1985, Kautsky *et al.* 1986, Rönnberg & Mathiesen 1997, Ruuskanen *et al.* 1999, Bäck & Ruuskanen 2000).

Significant changes have also occurred in the rooted soft-bottom vegetation (Dahlgren & Kautsky 2002, Eriksson *et al.* 2004). A decline was shown for charophytes in the coastal areas of the Baltic Sea (Lindner 1972, Schmidt *et al.* 1996, Blindow 2000, Yousef *et al.* 2001, Hamann & Garniel 2002, Schubert & Blindow 2003). This decline tends to be concentrated more in the southern parts of the Baltic Sea region (Schubert & Blindow 2003).

Eutrophication is considered one of the greatest threats for submerged macrovegetation (Phillips *et al.* 1978). Elevated nutrient concentrations trigger the growth of epiphytes and phytoplankton, which causes shading of the macrovegetation and competes for nutrients. In general the eutrophication of the Baltic Sea is considered the cause for the recorded declines in charophytes (Schubert & Blindow 2003).

In coastal lagoons in different parts of the world increased nutrient loading causes a diversity of changes in plant communities: development of dense phytoplankton blooms, declines in coverage and biomass of sea-grass beds and development of extensive mats of drifting macroalgae (Ryther & Dunstan 1971, McComb & Humphries 1992, Sfrizo *et al.* 1992, Valiela *et al.* 1992, 1997, Taylor *et al.* 1995, 1999, Short & Burdick 1996). The coastal lagoons exhibit similarities with shallow lakes. In contrast to deeper lakes where part of the overall production is lost in the depths, degraded material is available for the productive layer in shallower lakes. They are, thus, particularly sensitive to increased nutrient loading, and easily become eutrophicated and shift to phytoplankton stages (Blindow 1992b, Blindow *et al.* 1993). Suspended sediment moving in the water column effectively inhibits the photosynthesis of bottom-living plants. When the stabilising effect of macrophytes is absent, the phytoplankton state will be maintained. Displacement of the sediments in temporary accumulation areas also inhibits the establishment of permanent macrophyte communities (Thomasson 1955). Shifts from charophyte vegetation to *Myriophyllum* dominated vegetation are typical in disturbed shallow lakes (Thomasson 1955, Blindow 1992a, 1992b).

Mechanical activities, such as dredging, shore construction activities, other engineering works and motorboat traffic, have destroyed considerable parts of the charophyte habitats in the southern parts of the Baltic (Schubert & Blindow 2003). For example, 80 % of the localities and 50 % of the species have disappeared from the Baltic coast of Schleswig-Holstein (A. Garniel pers. comm.). Mechanical disturbances have also become important causes for ecological changes in the aquatic environments of the northern parts of the Baltic (Bonsdorff *et al.* 1984, Wallström & Persson 1997, 1999, Andersson 2001, Eriksson *et al.* 2004). Many habitats on the coasts of Finland and Sweden are threatened by pollution as well as by mechanical disturbances and eutrophication (Lindholm 1991, Wallström & Persson 1997, 1999, Wallström *et al.* 2000, Andersson 2001). In a natural state these are often colonised by charophytes.

Only few reports have indicated declines of charophytes on the coast of Finland (Ihantola 1980, Svanbäck 1982a, Luther & Munsterhjelm 1983, Haldin 1993). Indications of a decline in several charophyte species were, however, observed during the fieldwork for the present thesis since 1978.

Chara tomentosa has been considered a common charophyte species along the Baltic coasts, e.g. along the coast of Finland (Migula 1897, Häyrén 1912, 1936a, 1936b, 1949, Cedercreutz 1936, Olsen 1944, Björkman 1947, Luther 1951a, 1951b, Blindow 2000, Schubert & Blindow 2003). The species occurs mainly in very sheltered sites on soft muddy bottoms (Enholm 1936, Ulvinen 1937, 1955, Björkman 1947, Luther 1951a, paper I). A decline in *C. tomentosa* was reported from various Baltic countries, e.g. from flad-like habitats in Sweden (Wallström & Persson 1997, Schubert & Blindow 2003). In the present study area, *C. tomentosa* has been widely distributed from the OZ and MZ to the southern part of Pojo Bay (Luther 1951a; Fig. 1B). On the SW coast of Finland *C. tomentosa* is today considered rare or sparse.

To document the extent and causality of the decline in *Chara tomentosa* and the time scale of the change, all available information on the species from the study area was collected and analysed (paper III). The study indicates a significant decline in regional distribution and a number of local occurrences during the 20th century. Disappearances of local populations predominated among the negative changes. They mostly concerned large communities, often measured in areas of hectares. New establishments of *C. tomentosa* concerned only minor occurrences. The species disappeared almost completely during the study period from the inner one of its two distributional centres, the MZ. In the outer zones (OZ, OMZ and IZ) the sites of the occurrence thinned out considerably and the communities shrank to only small populations in many localities.

It became clear that the decline was connected with both natural and human-induced environmental changes. These involve varying degrees and sets of factors, of which eutrophication and mechanical disturbances were the most important. Eutrophication that began before the 1960s in the study area is likely to have been responsible for some of the early declines of *C. tomentosa* in open habitats of the OZ, OMZ and MZ. The eutrophication in these areas originated from the Baltic in the outer parts (Kangas *et al.* 1982) and was of regional origin in the inner areas (Holmberg *et al.* 2003). The declines occurred before the early 1980s or earlier, most probably already in the 1960s. In open coves of the central part of the archipelago, in the outer IZ, and in the flads, *Chara tomentosa* populations remained stable in their occurrences, or even increased until the early 1980s. The flad localities apparently served as refuges for *C. tomentosa* during its decline in more open habitats.

Mechanical disturbances, dredgings, reed-cutting and subsequent motorboat traffic are considered the main factors for most of the negative development of the populations in the flads and glo-flads. To make them more available for boat traffic, dredgings were first directed towards the more isolated stages, the glo-flads, which exhibited earlier declines in *C. tomentosa*. Later, after the early 1980s, dredging and cutting of reeds in the opening areas of flads was also begun. In these stages the decline was initiated during the 1980s, occurring mainly after the mechanical disturbances.

A notable consequence of the mechanical disturbances was the increased water turbidity resulting from resuspended sediment, and subsequent phytoplankton production. Increased growth of filamentous algae, as well as sediment covering the vegetation, were other consequences of the actions. The effect of increased water turbidity by sediment resuspension may be temporary, but may also cause a more permanent change in nutrient dynamics in the habitat – a shift from macrophyte dominated to turbid phytoplankton dominated states like in the shallow lakes (Blindow 1992a, 1992b, Blindow *et al.* 1993). Alternatively, a shift may occur to a filamentous algae dominated state. Sediment turbidity may also become permanent when remote water masses are connected through canals and the water circulation occasionally changes direction. Boat traffic, which increased after the dredgings, probably maintains sediments in a resuspended state. Local eutrophication from agriculture and possibly from grazing activity of sea-birds occurred in only a few flads and glo-flads.

The localities in which *Chara tomentosa* either established new populations or increased in abundance were all in a natural state. Natural environmental changes, land-uplift and isolation processes, may have caused negative development in a minority of the recorded cases.

Turbidity, sediment cover on the vegetation, as well as covers of filamentous algae decrease the light available for the bottom vegetation. In some cases *Chara tomentosa* was replaced by species that can cope with low light, such as *Myriophyllum spicatum*, *Ceratophyllum demersum* and *Vaucheria* cf. *dichotoma* (cf. Luther 1951a, Blindow 1992a). The observations of environmental changes in the localities where a decline occurred indicated decreased light to be the main reason for the decline in *C. tomentosa.* The negative response of *C. tomentosa* to environmental factors considered crucial to the decline (increased sediment covering, water turbidity and water flow) all observed after dredgings, was proved experimentally (Paper IV). It is likely that the same factors may also play a role in the decline of other charophytes.

At deeper levels the bottoms abandoned by *Chara tomentosa* remained unvegetated or were colonised by the above-mentioned species. At shallower levels *Potamogeton pectinatus* partially replaced the *C. tomentosa* communities. Competition with other species does not appear to be involved in the decline of *C. tomentosa*. However, the return of *C. tomentosa* may be hindered by the later establishment of dense communities of other species, that forms a dense cover on the bottoms or tall canopies that shade the bottoms.

The described disturbance succession is the reverse of the natural succession. When mechanically disturbed, the localities in the flad stage may thus take a step backwards in their development towards a vegetation similar to that present in sheltered bays or juvenile flads. A model for the environmental changes of shallow bays, based on paper I and III and on unpublished material, is presented in Fig. 10.

Changes occurred also outside sheltered bays and flads. For example, the increased abundances of *Myriophyllum spicatum* and other macrophytes in the *Zostera marina* community outside Tvärminne after the late 1970s also indicate the presence of increased nutrient loading in the OZ (R. Munsterhjelm, unpubl.).

Another type of environmental change that resulted in changes in the aquatic macrophyte vegetation throughout the archipelago was the ceasing of shore pasture after the mid-20th century (Luther & Munsterhjelm 1983). Cattle graze preferably *Phragmites australis* and a reed-free zone will be created from above the shoreline to about 1 m in depth (Luther 1951a, 1951b, paper I). The vegetation of the grazed shores is more diverse than on not pastured shores (paper I), especially if they are covered by reed. Small amphibionts (e.g. *Eleocharis acicularis*, *Potamogeton filiformis*, *Zannichellia palustris*, *Ruppia maritima*) close to the shoreline are especially favoured and may be replaced by the taller *Potamogeton pectinatus* when grazing ceases (paper I).

Various shore types in Pojo Bay studied in 1945 (pastured) and restudied in 1981 (not pastured) illustrate the effects of reed succession (Luther & Munsterhjelm 1983). The reed succession had both positive and negative effects on the amphibiontic or submerged flora and vegetation of the hydrolittoral. In the most sheltered and nutrient-rich sites this vegetation was choked and in the more exposed and oligotrophic ones the increased shelter favoured newcomers. In the more sheltered sites dwarf amphiphytes around the shoreline became especially sparse. The annual species weak in competition were in danger of disappearing. *Nitella confervacea* and *Chara braunii* became extinct – the latter species apparently from the entire area.

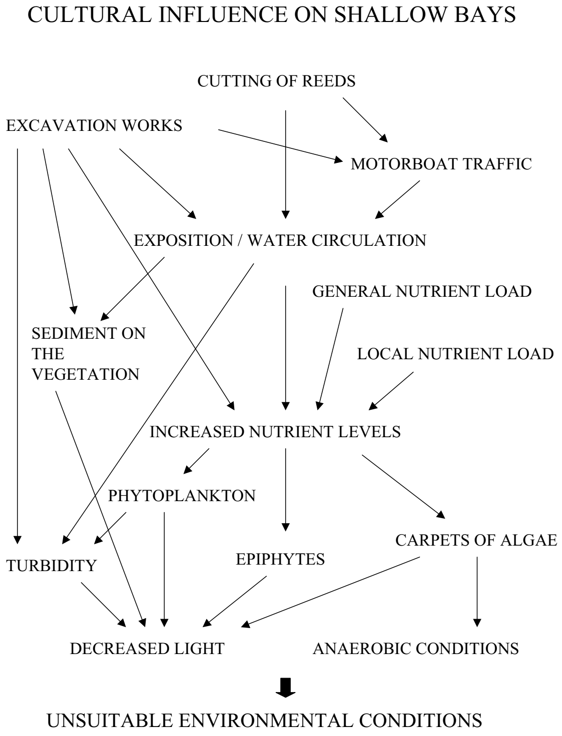


Figure 10. Proposed model of the development of unsuitable conditions for macrophytes in flads and later developmental stages caused by human influence. The model is based on Secchi-depths and turbidity, Tot-P and Tot-N measurements (R. Munsterhjelm and C. Henricson, unpublished material), observations from 1978 to 2003 (R. Munsterhjelm), Wallström *et al.* (2000), the results and discussion of paper I, III and the experimental evidence presented in paper IV.

INDICATIVE INFORMATION VALUE AND THE CONSERVATION OF AQUATIC VEGETATION – A DISCUSSION

The indicative value of freshwater flora and vegetation is well-known (cf. Kurimo 1970, Uotila 1971). In freshwater lakes plant groups indicating oligo-, meso- and eutrophic waters comprise a continuous series of taxa with progressively greater ecological tolerance (Seddon 1972). No groups are mutually exclusive and there are only a few for which the environmental ranges do not overlap. Therefore pure indicator species are difficult to define. Based on a Middle European so-called saproby system (Kolkwitz & Marsson 1902), Häyrén (1910a) developed a corresponding plant community-based system for the brackish water conditions in the coastal regions of Finland (Häyrén 1921, 1933, 1937, 1944, Hällfors *et al.* 1987). The degree of pollution in a time perspective is considered to be better reflected by the more permanent benthic communities than by solitary water quality and phytoplankton samples. A modification of Häyrén's system was later developed (Maa ja Vesi 1976, Munsterhjelm 1986, Hällfors *et al.* 1987, Lönnqvist 1990, Holmberg *et al.* 2003). Various species were given saproby values for calculations of the degree of pollution or saproby of the environments. There is, however, difficulty in investigating the relationship of species in brackish water as the brackish water partly compensates for the electrolytes of eutrophicated fresh waters (Luther 1951a, Hällfors *et al.* 1987). Some of the species typical of nutrient enrichment in fresh waters, e.g. *Myriophyllum spicatum* and *Ceratophyllum demersum*, also colonise clean brackish environments. Natural environmental and trophic changes along the Tvärminne – Pojo Bay furrow (Luther 1951a), may also confuse the interpretation of species occurrences as indications of saproby. Another possibility for misinterpretations is provided by the dense filamentous algal cover (*Vaucheria* cf. *dichotoma*) on bottoms of the mainland zone. This is not an indication of an ecological catastrophe (as believed by a consulting bureau once taking samples in the region), but a natural response on the local nutrient-rich conditions and probably an important factor in the cleaning of the water.

Charophytes are the first aquatic plants to disappear during the process of water pollution (Forsberg 1965a, 1965b, Kohler *et al.* 1971, Langangen 1974, Melzer et al. 1977, Lang 1981, Krause 1981, Svanbäck 1982b, 1983, Best 1987, Blindow 1992a). The decline in charophytes correlates in many cases with increased nutrient loading, phytoplankton production, and decreased water transparency (John *et al.* 1981, Ozimek & Kowalczewski 1984, Simons *et al.* 1994, Yousef *et al.* 2001, Schubert & Blindow 2003). Charophytes occur mostly in waters with low concentrations of inorganic phosphorus and preferably grow under oligotrophic conditions, e.g. in so-called *Chara* lakes (Forsberg 1964, 1965a, Simons & Nat 1996). In severely eutrophicated fresh waters charophytes are usually absent (Forsberg 1965a, 1965b). Good water quality and high abundance of charophytes are also positively correlated in brackish water (Forsberg 1965b, Svanbäck 1982a, 1982b, 1983, paper I).

There is a resemblance between the declines of the hard-bottom brown alga *Fucus vesiculosus* (Kangas *et al.* 1982) and the soft-bottom charophyte *C. tomentosa*. Both are sensitive to eutrophication. Due to its response to environmental disturbances, *C. tomentosa* (paper III) can be considered as an important indicator species in soft-bottom environments. However, this species also declines because of natural environmental changes, land uplift and isolation.

The initial studies of aquatic macrovegetation of the present area along the general gradient of the entire region and along the development of flads were fortunately performed at a time when these environments were still largely in a natural state (Luther 1951a, papers I and III). Different types of habitats, e.g. flads, with slightly deviating sets of environmental factors, may be seen as natural experimental situations in which the environmental restrictions for different species may be registered. However, particularly in the flad development this is complicated by the interspecific competition that apparently strongly influences the occurrence of species and communities (paper I). It is evident that without knowledge of the natural developmental patterns of the environment and the successional patterns of the vegetation, in the flads and in the entire region, indicative information may lead to confusion.

Prediction the development of the environment and the biota is difficult (Boero *et al.* 2004). Sometimes totally unpredictable single events, sudden mass occurrences of organisms, introduction of a new species to the ecosystem, or algal blooms can change the history of entire aquatic ecosystems such as the open sea (Boero *et al.* 2004). Although strongly changing, the flad ecosystem appears more predictable than the above-mentioned one. The isolation apparently induces a buffering effect against the fluctuations in the sea. In flads the macroscopic species pass through their entire life cycle on the spot, suggesting that all elements of the macrovegetation are present in those locations every year, whereas pelagic organisms are dependent on the currents. Favourable possibilities of predicting the future natural and human-induced development of flads at different environmental starting points are provided by the observational, comparative, historical and experimental data (papers I-IV).

Species richness may have a stabilising effect on the ecosystem (Kolasa & Li 2003). Early flads show greater species diversity than later stages (paper I). The vegetation of the later stages of flad development, at which the charophytes predominate, is more sensitive to disturbance. In the early stages, other vegetation may remain when the charophytes decline during moderate disturbances (paper III). The remaining species that can also cope with deteriorated light regimes (*Myriophyllum* spp., *Ceratophyllum demersum* and *Vaucheria* cf. *dichotoma*), may stabilise the sediments, thus probably decreasing water turbidity. Observations support the view that they may prepare for the return of the more sensitive species (paper III, R. Munsterhjelm, M. Westerbom & O. Mustonen, unpubl.).

A future scenario must be considered in light of the ongoing process of global warming. As a consequence of subsequent rising sea level the effect of the land-uplift process will gradually slow down (Finnish Institute of Marine Research 2005). If this trend finally results in a negative displacement of the shoreline, we will experience a future accelerated washing out of sediments trapped in the pockets of the coastal area. From the indications observed in this study it can be concluded that this would result in continuous turbidity and eutrophication. Certain macrophyte species, e.g. *Myriophyllum spicatum*, may respond to the change and filter the suspended sediments. The magnitude of the ecological catastrophe would be dependent on the rate of which the rising water level will occur.

The ecological value of shallow bays is not easily defined. Biological diversity (Bäck & Lindholm 1999) is not always a proper motivation for environmental protection. In modern management policy, the value of a given taxon is defined according to the quality and quantity of its relationships with the surrounding communities and its general importance in the ecosystem (Boero *et al.* 2004). Some late glo-flads and gloes are conspicuously monotonous regarding the diversity of the environment and macroscopic plants (paper I). Vegetation-free shallow areas of lakes, which are less available for benthic organisms, can perhaps be considered to have lost their ecological values as food sources for birds and protection areas for fish larvae (Schiemenz 1912, Thomasson 1955). Flads apparently also get old in this way.

The crucial question is what should we protect when concerned about the shallow bays on the rising coasts of the northern Baltic Sea? Environments with rare taxa are valued as single habitats, but there are mainly no real rarities, no red-listed species, in the typical flad vegetation in the SW coast of Finland. However, when not disturbed, flads and their later developmental stages serve as refuges for charophyte species (paper I and III). This increases the conservation value of them. The main value from a diversity point of view, even at low diversities in the very late stages, would be their contribution to the regional or general diversity of their surroundings. The vegetation-poor locality types must be analysed from a future point of view, e.g. as species-rich mire systems or productive pioneer stages in the succession of terrestrial vegetation. This natural loss of habitats (papers I, II and III) may, however, influence the total occurrences of localities negatively in the long run, since new suitable habitats are often already disturbed and cannot serve in the recruitment of new localities. Therefore samples of the entire developmental process must be protected.

The abundance of infauna and epifauna on charophytes is higher than on other macrophytes (Blindow 1986, Henricson 2002). Fauna associated with the vegetation is protected against predation and water movements, and is offered egg-laying sites and hiding places, while the supply of oxygen is secured. At the same time fish and bird predators are favoured. Bird abundance increases with the increases in aquatic vegetation (cf. Blindow 1986). In the clearwater state of shallow lakes the sediment is stabilised by the water vegetation, visual conditions are favourable, and fish as well as fish-eating birds are abundant (Forsberg 1969, Blindow 1986). As for shallow lakes (Blindow 1986) the protection of shallow bays should therefore include preservation of the macrovegetation.

The feasibilities of using aquatic plants as biological filters for purifying the water has been suggested by several authors (Seidel 1956, Culley & Epps 1973, Ozimek 1978). Resistance to pollution is weaker in submerged macrophytes than in helophytes, but submerged macrophytes may be more useful in situations of low pollution (Seidel 1956, 1966, Ozimek 1978). Restoration projects including biomanipulation with aquatic plants have been successfully performed in lakes (Steinman 1998, van den Berg *et al.* 1998).

ADDITIONAL REMARKS

Through our inclination for aesthetics we try to attain regularity and equilibrium and tend to look for norms and trends (Boero *et al.* 2004). The obvious risk is that we may overinterpret nature selectively, creating a conception of a priority that does not exist. On one hand, measuring nature may lead us to an exactness that gives us a false sense of security and on the other, experiments can be performed only when and where possible on scales that sometimes do not match the reality (cf. Boero *et al.* 2004). Nature changes all the time, both spatially and temporally, and in all directions from every spot and in innumerable scale categories. There is therefore always a need for a lucid picture of the systems, a picture in which the changes can be integrated. When the ecosystem is outlined, for example by simple observations, much information will already be readable from the basic material and important pieces can be picked out and analysed more closely, e.g. experimentally.

All methods, including both descriptive and numerical ones, result in symbolic expressions of the information. In contrast to reductionistic methods that analyse only parts of the whole the descriptive method may make it possible to obtain both life-like and holistic visions of systems. A visual picture of the environment is of course highly symbolic and restricted, but it has features that can be used to obtain information that closely corresponds to reality. For example, the vegetation map is both a diagram and an image true to nature. It enables us to see the correlation between the different elements of the system (cf. Sanders 1998). Some otherwise laborious measurements, can be performed directly from pictures. Pictures are seldom used as sources of information only because of traditional reasons.

In predicting the development of environment comparative and historical studies should form the first step (cf. Dayton & Sala 2001, Boero *et al.* 2004). The importance of naturalists' knowledge is emphasized (Dayton 2003, Boero *et al.* 2004). The evidence of observational field research data, e.g. on the altered distributions of marine species, supports for example the much disputed concept of global warming (Boero *et al.* 2002). Even small occurrences of a species on the vegetation map can tell much about the history of the system investigated and serve as a prediction of a possible future scenario.

The macrovegetation of shallow sheltered bays, which is partly visible from the surface and air, tempts us to a visual configuration (paper I and II, Dahlgren *et al.* 2004). However, modern visual methods for presentations of scientific information are successfully used for viewing the environmental development of the more abstract pelagic ecosystems (e.g. Kiiltomäki & Stipa, in prep.).

The value of old descriptive information obtained by the activities of field researchers and naturalists (e.g. Häyrén 1902, Luther 1951a) has turned out to be crucial for defining trends that may predict the future. To create a sustainable vision of complexity development the qualitative view of such researchers is also needed (Boero *et al.* 2004). Qualitative methods, including analytic and logic processes, may be well suited for use in parallel with quantitative ones (Lundberg & Holm 1990) as well as non-linear *systemic thinking* should be preferred in creating a vision of the not linear reality (cf. Byrne 1998, O'Connor & McDermott 1997).

This thesis emphasizes the importance of first observing and describing nature and comparing its different parts in the simplest ways (cf. Häyrén 1900). One main result of this study is inspired by the words in the preface "*panta rhei*". One should attempt to describe and understand brackish water environments on land-uplift coasts in the complex terms of changing processes rather than fixed units or viewing them as cases free from their context. My hope is that this thesis in the future will lead to co-operative teamwork between classical field researchers and modern ecologists in exploring shallow-water ecosystems. My recommendation is meant to be pedagogic: *First observe, then measure.*

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