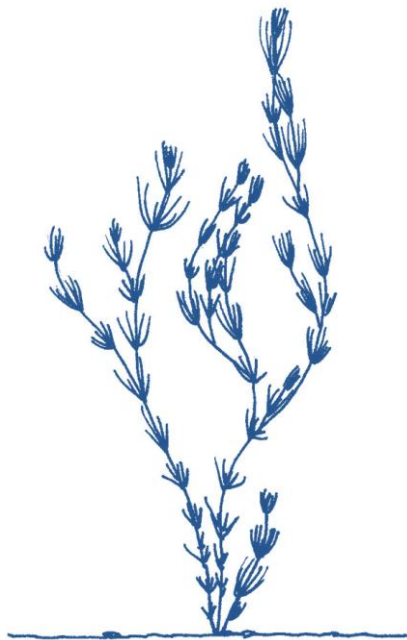


Distribution and role of macrophytes in coastal lagoons: Implications of critical shifts

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macrophytes in coastal lagoons:
Implications of critical shifts

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FRONT COVER ILLUSTRATION

Johanna Fredenberg: *Chara connivens*

BACK COVER PHOTOS

From a regional view to species level:

Husö Biological Station, Åbo Akademi University/ Martin Snickars: Archipelago

Patrik Rosqvist: Above and below the surface

Kajsa Rosqvist: *Chara tomentosa*

*Ni förstår, jag vill komma underfund med om havet har något system,
eller om det bär sig åt precis hursomhelst - det är viktigt!*

Muminpappan i Pappan och havet (Tove Jansson 1965)

ABSTRACT

Crossroads, crucibles and refuges are three words that may describe natural coastal lagoon environments. The words refer to the complex mix of marine and terrestrial influences, prolonged dilution due to the semi-enclosed nature and the function of a habitat for highly diverse plant and animal communities, some of which are endangered. To attain a realistic picture of the present situation, high vulnerability to anthropogenic impact should be added to the description. As the sea floor in coastal lagoons is usually entirely photic, macrophyte primary production is accentuated compared with open sea environments. There is, however, a lack of proper knowledge on the importance of vegetation for the general functioning of coastal lagoon ecosystems. The aim of this thesis is to assess the role of macrophyte diversity, cover and species identity over temporal and spatial scales for lagoon functions, and to determine which steering factors primarily restrict the qualitative and quantitative composition of vegetation in coastal lagoons. The results are linked to patterns of related trophic levels and the indicative potential of vegetation for assessment of general conditions in coastal lagoons is evaluated.

This thesis includes five field studies conducted in flads and glo-flads in the brackish water northern Baltic Sea. Flads and glo-flads are defined as a Baltic variety of coastal lagoons, which due to an inlet threshold and post-glacial land-uplift slowly will be isolated from the open sea. This process shrinks inlet size, increases exposure and water retention, and is called habitat isolation. The studied coastal lagoons are situated in the archipelago areas of the eastern coast of Sweden, the Åland Islands and the south-west mainland of Finland, where land-uplift amounts to ca. 5 mm/ per year. Out of 400 evaluated sites, a total of 70 lagoons varying in inlet size, archipelago position and anthropogenic influence to cover for essential environmental variation were chosen for further inventory. Vegetation composition, cover and richness were measured together with several hydrographic and morphometric variables in the lagoons both seasonally and inter-annually to cover for general regional, local and temporal patterns influencing lagoon and vegetation development. On smaller species-level scale, the effects of macrophyte species identity and richness for the fish habitat function were studied by examining the influence of plant interaction on juvenile fish diversity. Thus, the active election of plant mono- and polycultures by fish and the diversity of fish in the respective culture were examined and related to plant height and water depth.

The lagoons and vegetation composition were found to experience a regime shift initiated by increased habitat isolation along with land-uplift. Vegetation composition altered, richness decreased and cover increased forming a less isolated and more isolated regime, named the vascular plant regime and charophyte regime, respectively according to the dominant vegetation. As total phosphorus in the water, turbidity and the impact of regional influences decreased in parallel, the dominance of charophytes and increasing cover seemed to buffer and stabilize conditions in the charophyte regime and

indicated an increased functional role of vegetation for the lagoon ecosystem. The regime pattern was unaffected by geographical differences, while strong anthropogenic impact seemed to distort the pattern due to loss of especially *Chara tomentosa* L. in the charophyte regime. The regimes were further found unperturbed by short-time temporal fluctuations. In fact the seasonal and inter-annual dynamics reinforced the functional difference between the regimes by the increasing role of vegetation along habitat isolation and the resemblance to lake environments for the charophyte regime. For instance, greater total phosphorus and chlorophyll *a* concentrations in the water in the beginning of the season in the charophyte regime compared with the vascular plant regime presented a steeper reduction to even lower values than in the vascular plant regime along the season. Despite a regional importance and positive relationship of macrophyte diversity in relation to trophic diversity, species identity was underlined in the results of this thesis, especially with decreasing spatial scale. This result was supported partly by the increased role of charophytes in the functioning of the charophyte regime, but even more explicitly by the species-specific preference of juvenile fish for tall macrophyte monocultures. On a smaller species-level scale, tall plant species in monoculture seemed to be able to increase their length, indicating that negative selection forms preferred habitat structures, which increase fish diversity. This negative relationship between plant and fish diversity suggest a shift in diversity patterns among trophic levels on smaller scale. Thus, as diversity patterns seem complex and diverge among spatial scales, it might be ambiguous to extend the understanding of diversity relationships from one trophic level to the other.

All together, the regime shift described here presents similarities to the regime development in marine lagoon environments and shallow lakes subjected to nutrient enrichment. However, due to nutrient buffering by vegetation with increased isolation and water retention as a consequence of the inlet threshold, the development seems opposite to the course along an eutrophication gradient described in marine lagoons lacking an inlet threshold, where the role of vegetation decreases. Thus, the results imply devastating consequences of inlet dredging (decreasing isolation) in terms of vegetation loss and nutrient release, and call for increased conservational supervision. Especially the red listed charophytes would suffer negatively from such interference and the consequences are likely to also deteriorate juvenile fish production. The fact that a new species to Finland, *Chara connivens* Salzm. Ex. Braun 1835 was discovered during this study further indicates a potential of the lagoons serving as refuges for rare species.

Keywords Regime shift, charophytes, biodiversity and ecosystem function, habitat, succession, coastal lagoon, aquatic vegetation

SAMMANFATTNING

Grunda trösklade vikar eller laguner utgör en skyddad miljö med långsam vattencirkulation jämfört med den öppna kusten. Den snabbt stigande vattentemperaturen om våren, den naturliga näringsrikedomen som en följd av syrefria förhållanden efter vinterns delvisa bottenfrysning och den rikliga avrinningen från land erbjuder en tjuvstart för den produktiva säsongen. Dessa betingelser i kombination med att ljuset ofta tränger ända ner till botten gynnar utvecklingen av en rik och ståtlig vattenvegetation, som i sin tur är viktig för många djurarter, inte minst för en lyckad fisklek och yngeluppväxt. Framför allt gynnas kransalgerna, av vilka många arter är hotade och rödlistade i Finland. Tyvärr åtnjuter dock inte vikarna lagens skydd i tillräcklig grad och utsätts för ett ökat antropogent tryck i form av höga näringsutsläpp, båttrafik, muddringar och byggkonstruktioner som i många fall leder till att arter försvinner. Samtidigt är kunskapen om vegetationens roll för funktionen av vikekosystemet bristfällig. Målet med denna avhandling är att fastställa vilken roll mångfalden, täckningsgraden och identiteten hos vegetationen har både över rumsliga och tidsmässiga skalor för funktionen hos vikekosystemet, och att identifiera vilka styrande faktorer primärt begränsar den kvalitativa och kvantitativa sammansättningen hos vegetationen i vikar. Resultaten länkas till relaterade trofiska nivåer och det potentiella indikatorvärdet hos vegetation för fastställande av det allmänna miljötilståndet i vikar utvärderas.

Denna avhandling inkluderar fem fältstudier utförda i flador och glon i norra Östersjön. Flador och glon definieras som en Östersjövariant av vikar eller laguner som har bräckt vatten och som på grund av en mynningströskel och post-glacial landhöjning långsamt avsnörs och isoleras från det omgivande havet. Flador har ett reducerat men kontinuerligt vattenutbyte med havet, medan vattenutbytet är endast sporadiskt i glon, som med tiden antingen utvecklas till sjöar eller torkar ut beroende på vattendjupet i själva vikbassängen. Denna process som minskar mynningens tvärsnittsarea och ökar vattenuppehållstiden i viken kallas här habitatisolering. Vikarna som inkluderats i denna studie finns belägna i den åländska och västnyländska skärgården i Finland samt Upplandsskärgård i Sverige, där landhöjningen är ca 5 mm/år. Av 400 utvärderade vikar, valdes totalt 70 stycken ut för närmare inventering. Dessa vikar varierade i grad av habitatisolering, position längs med skärgårdsgradienten från inner- till ytterskärgård och graden av mänsklig störning för att täcka essentiell naturlig fluktuation. Vegetationens täckningsgrad, artsammansättning och mångfald bestämdes tillsammans med relaterade hydrografiska och morfometriska parametrar i vikarna både längs med den produktiva säsongen samt mellan ett flertal år. På en mindre skala eller artnivå, undersöktes också vilken effekt artidentiteten och mångfalden hos vegetationen har för funktionen som fiskhabitat. Detta gjordes genom att beakta fiskens aktiva val av vegetationsbestånd, samt genom att jämföra mångfalden hos juvenil fisk i enarts- och flerartabestånd av vegetation. Valet av vegetationsbestånd relaterades sedan till växthöjden och vattendjupet.

Vikarna och vegetationen konstaterades genomgå ett regimskifte initierat av den ökade habitatisoleringen som följer avsnörningen med landhöjningen. Vegetationens artsammansättning förändrades, mångfalden minskade och täckningsgraden ökade längs med processen och formade en öppnare och mindre isolerad regim, kallad kärlväxtregim och en slutnare och mera isolerad regim, kallad kransalgsregim enligt den dominerande vegetationen. Eftersom totalkoncentrationen av fosfor i vattnet, grumligheten och påverkan av regionala faktorer minskade längs med ökad habitatisolering, verkar ökad täckningsgrad och förekomst av kransalger buffra eller stabilisera förhållandena i kransalgsregimen och indikera på en ökad funktionell roll hos vegetationen för vikekosystemet. Regimmönstret var opåverkat av geografiska skillnader mellan vikarna, medan ökad antropogen inverkan splittrade regimmönster som en följd av minskad förekomst av rödsträse i kransalgsregimen. Regimmönstret var orubbligt av temporala korttidsfaktorer. I själva verket förstärkte säsons- och mellanårsmönstret bilden av den funktionella olikheten mellan regimerna och visade likheter mellan förhållandena i kransalgsregimen och dynamiken i sjöar. Som ett exempel kan nämnas att de högre koncentrationerna av totalfosfor och klorofyll *a* i vattnet i början av den produktiva säsongen i kransalgsregimen reducerades kraftigare längs med säsongen och visade ställvis till och med lägre värden i augusti i kransalgsregimen jämfört med kärlväxtregimen. Trots att vegetationens mångfald har en viktig betydelse på regional skala för mångfalden för andra trofinivåer så som fisk, verkade artidentiteten hos vegetationen få en accentuerad betydelse i resultaten i denna avhandling, framförallt då den beaktade rumsliga skalan minskade. Denna iaktagelse stöds dels av den ökade betydelsen hos kransalgerna med habitatisoleringen, dels och mera explicit av den artspecifika preferens hos juvenil fisk som verkade favorisera långa växter som växte i enartsbestånd. På artnivå, verkade långa växter i enartsbestånd ha förmågan att öka i längd jämfört med samma växter i flerartsbestånd, vilket indikerar att negativ selektion (en mekanism som får arter att prestera bättre i enarts- än i flerartsbestånd) formar habitatstrukturer (här växtlängd) som prefereras av juvenil fisk och därmed ökar fiskmångfalden.

Regimeskiftet i de undersökta vikarna visar likheter med regimutvecklingen i marina lagunmiljöer utan tröskel och grunda sjöar som utsätts för ökad näringsbelastning. Eftersom vegetationen i viss grad verkar buffra och reducera näringskoncentrationerna längs med ökad habitatisolering och ökad vattenuppehållningstid på grund av mynningströskeln, är dock utvecklingen i viss grad motsatt. Med andra ord indikerar resultaten i denna avhandling ödesdiga konsekvenser för avlägsnande av mynningen hos vikarna, tex. som följd av ett muddringsingrepp och signalerar ett behov för effektiviserad övervakning och ökat skydd av dessa miljöer. Förlust av vegetationen och förändring av vegetationens artsammansättning, frigörelse av näringsämnen och negativ inverkan på övriga trofinivåer (tex. juvenil fisk) är möjliga följder av en muddring. De rödlistade kransalgerna verkar vara särskilt utsatta för ett dylikt ingrepp. Det faktum att en ny art för Finland, kransalgen *Chara connivens* Salzm. Ex. Braun 1835 hittades i och med fältarbetet för denna avhandling understryker ytterligare att Östersjöns grunda havsvikar eller laguner har en potentiell funktion som fristad för sällsynta arter.

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LIST OF ORIGINAL PAPERS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

Appelgren, K., Mattila, J. 2005.

Variation in vegetation communities in shallow bays of the northern Baltic Sea. *Aquatic Botany* 83: 1-13. **Paper I**

Rosqvist, K., Mattila, J., Sandström, A., Snickars, M., Westerborn, M. 2010.

Regime shifts in vegetation composition of Baltic Sea coastal lagoons. *Aquatic Botany* 93: 39-46. **Paper II**

Rosqvist, K., Mattila, J.

Temporal dynamics in vegetation composition and environmental variables in coastal lagoons of the Baltic Sea. Manuscript. **Paper III**

Snickars, M., Rosqvist, K.

Diverging diversity between trophic levels – plant species interaction and identity direct the diversity of fish. Submitted manuscript. **Paper IV**

Appelgren, K., Snickars, M., Mattila, J. 2004.

Chara connivens Saltzm. Ex. A. Braun 1835 found in the Åland archipelago – a new species to Finland. *Memoranda Soc. Fauna Flora Fennica* 80: 11-13.

Paper V

The original publications have been reprinted with the kind permission of Elsevier (**paper I and II**) and Societas pro Fauna et Flora Fennica (**paper V**).

1. INTRODUCTION

Community ecology seeks to understand the manner in which groupings of species are distributed in nature, and the ways these groupings can be influenced by their abiotic environment and by interactions among each other (Begon et al. 2008). As the interaction between the environment and its biota is two-sided (c.f. Carpenter and Lodge 1986), the understanding of the direction and strength of influence is aggravated. Commonly the physical and chemical aspects of the place where organisms, species and communities exist and are distributed describe the habitat (Odum 1971, Whittaker et al. 1973, Mitchell 2005), while the added restriction set by biotic interplay is often directed to the niche concept dealing with a species functional role in trophic levels and ecosystems (Hutchinson 1957). The imposing richness of co-existing species is explained by differential living requirements corresponding to separate habitats and niches, but has further been ascribed to non-equilibrium and non-homogeneity of ecosystems involving constant change, disturbance and prohibition of complete mixing of species distributions (Hutchinson 1957, Connell 1978, *sensu* Holling 1973, Scheffer 2009). Thus, as complex interactions and context dependency seem a necessity for maintaining diversity, the effort of the ecologist forced to work with simplified models and relationships in trying to find general patterns is easily challenged and undermined. However, finding the interface where demarcation and generalization retain natural significance is intriguing, but more importantly, especially valuable and worthwhile in view of appreciation for the intrinsic value of nature in itself and in a precautionary and conservational perspective. In this thesis, I aim at finding such an interface where both ecological and management-orientated relevance is gained for coastal lagoons when studying the distribution and role of macrophytes in them.

1.1 Macrophytes as ecosystem components: definition, role and regulation

The term 'macrophyte' considers all macroscopic aquatic plants or hydrophytes including algae (or seaweeds), bryophytes and vascular plants, whereas the term 'aquatic plant' is sometimes used in a stricter sense for only higher vascular plants. When referring to the general plant ground cover of an area, not particularly the taxa, life form or other botanical characteristic the term 'aquatic vegetation' is commonly used. Macrophytes may be of rooted and non-rooted, emergent and submerged growth forms commonly sequentially related to depth on both hard and soft substrates. On soft bottoms in low-saline areas, the shoreline is occupied by emergent helophytes, such as the reeds (e.g. *Phragmites australis* Cav.) with at least the top of their shoot rising above the water surface. Moving deeper, floating leaved and entirely submerged phytobenthic macrophytes dominate, and are restricted primarily by the diminution of irradiance at greater depths where homogenous turbidity-tolerant monocultures or bare sediments are found (Chambers and Kalff 1985).

The presence of aquatic vegetation radically affects the functioning of photic coastal areas and shallow lakes (Kjerfve 1994, Scheffer 1998). As macrophytes

occupy the interface between water and sediment they function as a link between these two media and between the littoral and pelagic environment. Furthermore, macrophytes serve as habitats and mediate abiotic conditions for the biota. The direct impact of macrophytes on the abiotic and biotic environment originates from the function of added physical structure and substrate, which provide other organisms with food resources and refuge (Crowder and Cooper 1982, Schriver et al. 1995), and mechanically dampen water current velocities and decrease resuspension (Fonseca and Fisher 1986, Madsen et al. 2001). In fact, on otherwise flat bottoms macrophytes often provide the only three dimensional shaping above the sediment with importance for invertebrates, fish and zooplankton (Mattila 1992, Orth et al. 1984, Jeppesen et al. 1997). Furthermore, by reducing concentrations of macronutrients macrophytes affect primary production due to negative effects on phytoplankton and periphyton biomass (Wium-Andersen et al. 1982). Hence, the effect of macrophytes on biogeochemical cycling, productivity and general ecosystem functioning is without doubt major (e.g. Carpenter and Lodge 1986, Hemminga and Duarte 2000).

Several of the functions maintained by macrophytes are intricately related to the capacity of macrophytes to improve their own light climate (e.g. Scheffer 1998). As this trait is species-specific, alteration in species composition might affect the effect of macrophytes on other trophic levels and ecosystem functions in general. In this regard, the stoneworts or charophytes (Characeae) deserve to be introduced. The charophytes are submerged, oogamous flowerless benthic macroalgae with land plant-like habitus commonly found in freshwater and brackish environments, but marine fossils are also common (Schubert and Blindow 2003). Charophytes are distinct taxonomically in the sense that the systematic position of charophytes within the plants and the relation to other algae is controversial (Schubert & Blindow 2003, Algaebase 2010), but also ecologically due to the specific abilities and attributes detaching this group from other macrophytes especially concerning the positive effect on water transparency. Charophytes may stabilize the sediment with rhizoids and release chemical substances causing a strong and characteristic smell, which has been suggested to inhibit phytoplankton growth due to allelopathy (Scheffer et al. 1994, Van den Berg et al. 1998a, Schubert and Blindow 2003). Moreover, *Chara aspera* Willd is reported to compensate for a length disadvantage by depleting bicarbonate and thereby suppressing the taller *Potamogeton pectinatus* L. and consequently improving its own light climate (c.f. Van den Berg et al. 1998b, Scheffer 2009).

The distribution, productivity and species composition of macrophytes are directed by extrinsic forces including physical and chemical factors and by interactions among species (Chambers and Prepas 1990, Dawes 1998). These factors incorporate competition, irradiance, temperature, nutrient availability, grazing, water movement comprising wave exposure and salinity (Chambers and Kalff 1985, Bailey 1988, Berglund et al. 2003, Bergström 2005, Duarte 2005). As these factors may vary considerably, organisms are constrained to persist only within certain ranges of the gradients. Furthermore, due to variation in time and space and as an interaction of both, the relative and hierarchical order of importance of the controlling factors also alters as a consequence. For instance, in

marine temperate environments pelagic primary productivity is bound by seasonality (Lagus 2009). Similarly, macrophytes may be more productive than phytoplankton, but are restricted to littoral areas.

1.2 Regional and local framing: coastal archipelagos and lagoons

In topographically homogenous or continuous environments the tolerance of a species to its environment forms a rather abstract space, while for instance lakes or small islands make up comparably well-defined abiotic frames restricting and regulating abiotic and biotic interplay (c.f. MacArthur and Wilson 1963, Brönmark and Hanson 2005, Heinänen et al. 2008). Similarly, compared with the open sea, coastal archipelagos form topographical boundaries or hindrances of primary hierarchical importance for abiotic conditions and species distributions on a regional scale (von Numers 1995, Vahteri et al. 2009). When land to water ratio and island size increase from the outer to inner archipelago, wave exposure, average depth and overall harshness of the environment decrease (Granö et al. 1999, Ekebom et al. 2003). The approaching presence of mainland and gradual disappearance of the sea also leads to decreasing salinity and increasing land-runoff, temperature and turbidity. In the Baltic Sea, such steep gradients and rapidly changing conditions influence the distribution of many littoral organisms, such as macrophytes, invertebrates and juvenile fish (e.g. Kautsky and Kautsky 1989, Bonsdorff et al. 1996, Snickars et al. 2009). Furthermore, due to an extensive length of the shoreline and a large proportion of shallow bottoms, the littoral areas of the northern Baltic Sea constitute prolific habitats of high importance for the biota.

On a local scale, topographic demarcation and framing become further manifested in coastal lagoons (c.f. Tolvanen et al. 2004, Snickars et al. 2009). Since the framework of the lagoons is semi-enclosed, it allows for mixing of several gradients but prolongs the dilution and buffering of influences. The position of coastal lagoons on the border of land and sea further diversifies conditions in combining terrestrial and marine aquatic characteristics, which increase the heterogeneity compared with the open sea. All these aggregate features commonly result in enhanced levels of productivity and diversity of biota in the lagoons compared with the open sea (Alongi 1998). As coastal lagoons have been estimated to occupy 13 % of the coastal areas worldwide and are found on all continents (Kjerfve 1994 and references therein), the significance of this habitat type is highlighted globally.

Due to the heterogeneous conditions and global distribution of coastal lagoons, uniform defining has not always been easy or straight forward (Barnes 1980, Kjerfve 1994). Because of the requirement for their water to be marine or at least brackish, coastal lagoons are rarely completely isolated from the sea and have one or several channels through which water is exchanged with the larger adjacent water body (Barnes 1980). A workable definition presented by Kjerfve (1994) is a shallow coastal water body separated from the ocean by a barrier, connected at least intermittently to the ocean by one or more restricted inlets, and often oriented shore-parallel. The European Union Habitat Directive classifies coastal lagoons (habitat 1150) as expanses of shallow coastal salt water, of varying salinity

and water volume, wholly or partially separated from sea by sand banks or shingle, or, less frequently, by rocks; salinity may vary from brackish water to hypersalinity depending on rainfall, evaporation and through the addition of fresh seawater from storms, temporary flooding of the sea in winter or tidal exchange (Anon. 2007).

Flads and gloses make a variety of coastal lagoons in the Baltic Sea. These lagoons are cut off or isolated from the open sea due to an interaction of an inlet threshold and land-uplift. These coastal lagoon formations make well-defined habitats for a range of organisms (Anon. 2007) and occur widely in the archipelago areas of the northern Baltic Sea (Tolvanen et al. 2004). As the coastal lagoons in the Baltic are shallow, the water temperature rises rapidly in spring, while land run-off and anaerobic conditions following common bottom-freezing during the winter make lagoons naturally nutrient-rich. The coastal lagoons thereby provide an earlier or faster start for the growing season and make highly productive and vegetation-rich areas serving as important fish spawning and nursery areas, bird feeding grounds and nesting areas (Karås and Hudd 1993, Lappalainen and Urho, 2006, Snickars et al. 2009, 2010, Scheinin and Mattila 2010, M. von Numers Åbo Akademi University pers. comm.).

In a descriptive study on the south-west coast of Finland, coastal lagoons with an inlet threshold have been classified as juvenile flads, flads, glo-flads and gloses based on the morphometric habitat isolation of the lagoons from the open sea due to land-uplift and the following succession of vegetation (Munsterhjelm 1997). The juvenile flad is the most open stage, while the water exchange from the open sea to the glo-flad may not be continuous. The flad, a stage in the middle of the succession chain is defined as a shallow, clearly delimited, minor water body at the coast or in the archipelago connected to the sea by one or a few narrow inlets (Munsterhjelm 1997). On complete isolation of a glo, which has only sporadic contact with the sea, the water usually becomes fresh and the lagoon may develop into a freshwater lake or dry out depending on the water depth in the lagoon basin. Along this morphological development of the lagoons, the vegetation is described as changing due to succession from marine macroalgae and vascular plants to charophyte dominance. In **paper I**, I determine the applicability of the vegetation based classification system (Munsterhjelm 1997, 2005) to a broader geographic area incorporating coastal lagoons from the south-west mainland of Finland, Åland Islands and Sweden and test the general statistical significance of the classification system. In **paper II**, the structuring role of coastal lagoon isolation on local scale is further assessed in relation to the position along the archipelago gradient on regional scale.

1.3 System shifts

Most of the functions offered by coastal lagoons are directly or indirectly connected to the diverse and plentiful vegetation found there. Changes in vegetation composition have, for example, been shown to direct paralleled changes in diversity of juvenile fish and invertebrates (Hansen et al. 2008, Snickars et al. 2009) and biomass of zooplankton (Scheinin and Mattila 2010). The increased role of vegetation in coastal lagoons compared with deeper areas originates from the

high light penetration of the seafloor allowing for persistence of high cover of vegetation and typically higher production of macrophytes and microalgae than phytoplankton (Borum and Sand-Jensen 1996).

In marine lagoon environments entire system shifts have been reported as a consequence of dominance shifts in the composition of macrophytes. Due to nutrient-enrichment marine plants (seagrasses) and perennial macroalgae may be replaced by ephemeral, bloom-forming macroalgae and epiphytes (Duarte 1995, McGlathery et al. 2007). Ultimately, severe eutrophication may cause a dominance shift in primary producers when macrophytes are vanquished by phytoplankton (Valiela et al. 1997, McGlathery et al. 2007). Within this concept of marine lagoons reacting to nutrient loading, there is a suggestion that water residence time holds the balance of power, with longer residence times favoring phytoplankton (Valiela et al. 1997).

In shallow freshwater lakes, the vegetation may form a vegetated clear-water regime or a phytoplankton dominated turbid regime sparse in vegetation (Blindow et al. 1993). Due to a self-stabilizing mechanism of vegetation the eutrophication-induced shift from the vegetated clear-water regime to the phytoplankton regime with turbid water may be delayed. Since vegetation, as mentioned earlier, may improve its own growing conditions by several mechanisms involving nutrient reduction and provision of shelter for phytoplankton grazers, water quality and clarity may stay almost unaffected by enhancing nutrient concentrations until the critical point when the water suddenly turns turbid, submerged vegetation disappears and phytoplankton concentration increases. As well as regime shifts caused by dominance shifts of primary producers, also distinct shifts in macrophyte species from *Potamogeton* spp. to charophyte dominance affecting turbidity levels differently have been reported (Hargeby et al. 1994, Van den Berg et al. 1998b). Such shifts in composition suggest that coexistence of these two groups is unstable and that not only presence of vegetation but also macrophyte species identity (as mentioned earlier concerning especially charophytes) may be crucial in regime shifts in lakes.

Examples of regime shifts in brackish environments are scarce. In brackish coastal lagoons in Sweden, relationships between external phosphorus loading initiating shifts among different vegetative states and increased amounts of filamentous algae have been reported, while the importance of salinity is underlined for turbidity shifts in nutrient enriched lagoons in Denmark (Dahlgren and Kautsky 2004, Jeppesen et al. 2007). In both studies, the authors state that altering water exchange seems to indirectly smother shift effects or directly interact with driver variables initiating shifts. Following increasing water residence time as a consequence of an inlet threshold and land-uplift in Baltic coastal lagoons, the vegetation composition naturally changes. A diverse species composition of quite sparse growth forms of vascular plants and marine algae in less isolated lagoons turns to a less diverse assemblage of high biomass commonly dominated by charophytes in more isolated lagoons (Munsterhjelm 2005). The similarities to processes described both in marine and freshwater environments concerning vegetation state shifts are several in these lagoons. However, **paper II** in this thesis represents, to my knowledge, the first presentation of a natural regime shift in

vegetation, possibly decoupled from a nutrient induced shift but linked to the decreased water retention time in coastal lagoons due to land-uplift. The strength and stability of the regime shift pattern are further assessed in **paper III**, which determines how short-time temporal dynamics in vegetation and the abiotic environment are related to the long-term variability represented by the decreased water retention and the regime shift along land-uplift.

1.4 Biotic interaction and individual species

Although biotic interaction has been suggested to be of minor importance for the establishment of large-scale zonation of the vegetation in the Baltic Sea (Kautsky and van der Maarel 1990), the impact of vegetation might increase with decreasing spatial scale and decreasing environmental inhospitality (*sensu* coastal lagoons, c.f. Sousa 1979, Menge and Sutherland 1987). Similarly, the consideration of both α - and β -diversity (local vs. regional scale variability) has been found to confound diversity relationships, as β -diversity has been suggested to be more congruent among trophic levels than α -diversity (Kessler et al. 2009). Hence, on a smaller scale biotic interaction might crucially interfere with abiotic steering, thus influencing ecosystem functions and inducing diverging diversity patterns among trophic levels.

Inter-specific competition is one important form of biotic interaction associated with macrophytes and plants in general. It implies direct or indirect demand for the same limiting resource between species (Pianka 1981). Depending on the result of competition, a negative selection effect results when a species that perform well in monocultures (one species present) is less successful in polycultures (several species present) e.g. due to trade-offs (Duarte 2000, Hooper and Dukes 2004). On the contrary, a positive selection effect is obtained when a polyculture deviates positively from that of a monoculture for a measured variable for one species. Facilitation is one form of positive selection, and refers to one species promoting the existence of another species in a polyculture (Loreau and Hector 2001, Hector et al. 2002). Recent studies suggest that negative selection effects are common both in terrestrial (Hector et al. 2002) and marine systems (Bruno et al. 2005, 2006), implying that the identity of plant species might directly affect the survival of other organisms (Mattila 1992, Levin and Hay 1996, Hansen et al. 2010), and thereby be important for species richness of other trophic levels.

In less disturbed or exposed aquatic environments, submerged macrophytes are often subjected to two contrasting resource availability gradients of vital importance: decreasing light and increasing nutrient content in the sediment with depth (Spence 1982). As a result, macrophytes may show great plasticity in performance in terms of growth (Kautsky 1988, Weiner and Thomas 1992). As this trait varies among macrophyte species, the outcome of competition may have great influence on the habitat structure provided by macrophytes. In **paper IV**, I assess the role of plant species interaction and identity for the habitat structure function regarding juvenile fish on a smaller specie-level scale.

1.5 Human impact and species loss

The idea of defining natural and unaffected habitats most likely includes a great portion of self-deception, since the changes earth has endured from by human hand are reported sufficient to leave a global stratigraphic signature distinct from the earlier interglacial phases (Zalasiewicz et al. 2008). The effort of describing nature and its biodiversity is by no means less valuable – on the contrary, defining species and their functions as well as distinguishing among stressors is probably more important than ever. As global loss of biodiversity is recognized as the most devastating problem our planet is suffering from (Secretariat of the Convention of Biological Diversity 2010), ecologists need to price the consequences especially in relation to persistence of ecosystem functions and services. Below, a very concise description is given of the important but complex topic concerning biodiversity in relation to ecosystem functions, coastal lagoons and existing threats.

Along with species extinctions, the ecosystem functions that species provide are thought to be impoverished, with fundamental impacts on ecosystem goods and services (e.g. Constanza et al. 1997) that life depends on. Extending this reasoning, high diversity is willingly associated with high productivity based on the results from experiments when environmental steering is excluded (Naeem 1994a, b, Hector et al. 1999). Studies in nature, however, report the opposite, and most of the high productivity systems around the world have low plant diversity (Huston and McBride 2002). Nonetheless, also in nature, diversity has been seen to increase with productivity under lower productivity conditions. A partial explanation for the duality of this pattern could be that reported results address different ranges of productivity (or stages of succession) and that the response-curve of diversity is hump-shaped (Grime 1973, Huston and McBride 2002). Such a response-curve may be exemplified, for instance, by diversity-increasing (charophytes to vascular plants) and then diversity-decreasing (vascular plants to phytoplankton) changes observed in plants in lakes and in coastal areas along with eutrophication (Salovius-Laurén 2004, Scheffer 2009). High diversity is further connected to increased community stability since a diverse community likely includes species that respond differently to perturbations and thereby resist change (Yachi and Loreau 1999). Another stability-increasing notion of diverse communities is resistance towards invasion due to more thorough resource use analogous to the complementarity effect (MacArthur 1970). These statements are, however, partly watered down by a paralleled debate concerning the existence of congruence in diversity between trophic levels and between different scales (Duffy 2002, Jiang et al. 2008). Hence, another explanation for the incompatible results is certainly that studies do not (or are not able to) include ecosystems as a whole, but rather just one to a few trophic levels. Recognizing that several of the fundamental relationships coupled with the genre of biodiversity and ecosystem functioning are poorly known and that general patterns are difficult to manifest, the scientific society today agrees that global biodiversity as such is a life insurance for the present functions (Hooper et al. 2005).

Coastal lagoons in particular are vulnerable to human land use and rapidly increasing recreational activities in the coastal zone (Munsterhjelm 2005). The Habitat Directive lists coastal lagoons as a European natural habitat type in danger

of disappearance and calls for special conservation (Anon. 2007). A conservative estimate is that 35 % of the coastal lagoons in the south-western archipelago of Finland are directly threatened (c.f. Snickars and Pitkänen 2007, M. Snickars Åbo Akademi University pers. comm.). Eutrophication in particular causes deterioration of communities, which is seen as a loss of functionally important species (Rönnerberg 1991, Boström and Bonsdorff 1997) and as regime shifts (Duarte 1995). The picture is complicated by the so called estuarine quality paradox, i.e. the similarity between the features of organisms and assemblages in estuaries and anthropogenically stressed areas, both being organically rich (Dauvin 2007, Elliott and Quintino 2007, Dauvin and Ruellet 2009). The regime shift and especially the recognized natural drivers for the process described in **paper II** and **III** highlight this discrepancy in particular.

1.6 Aims of the thesis

The scientific and public knowledge on the importance of coastal lagoons in providing a diversity of functions by a diversity of organisms is rising (Anon 2007, Raunio et al. 2008). Simultaneously, the pressures on this habitat type are enhancing fast largely due to indulgent legislation, pure ignorance and increasing recreational needs. There is a lack of proper knowledge on general functioning, steering factors and the role of vegetation, and thus these are central issues in this thesis. One example of the general disregard of these environments is the encountering of a new species to Finland during this thesis work (**paper V**).

The aims of this thesis are to assess the general role of vegetation, macrophyte diversity, cover and species identity in coastal lagoons and to identify factors governing the vegetation composition both on a temporal and regional, local and small spatial scale. Further, the results are linked to patterns in other trophic levels, and the indicative potential of vegetation for the general conditions in coastal lagoons is evaluated.

In the five sections of this thesis I consider:

1. The macrophyte species composition of Baltic Sea coastal lagoons (shallow bays) under varying anthropogenic influence, and the applicability of a general classification system along isolation and land-uplift. The main focus is on spatial differences between geographically separate areas. **Paper I**
2. The drivers controlling vegetation development and regime shifts in coastal lagoons in the northern Baltic Sea on a regional and local spatial scale. **Paper II**
3. Short-time dynamics in vegetation development and the abiotic environment in coastal lagoons in relation to long-term isolation and regime shifts. The focus is set on seasonal and inter-annual temporal variability for the spatial patterns assessed in the two previous papers. **Paper III**
4. The role of species richness, identity and interaction mediating the habitat function and diversity of juvenile fish on smaller species-level scale. **Paper IV**
5. The finding of a new species to Finland. **Paper V**

An overview of the levels of focus (spatial, temporal, explanatory and response variables) of the studies in the thesis is given in **Table I**.

Table I. Spatial scale and temporal range (in years) of the main variables in the papers of this thesis. Response and explanatory variables refer to the general focus of the studies. For each paper (Roman numbers) also the number of lagoons/ number of visits to each lagoon (Latin numbers) is given. Regional refers to an archipelago-scale, local to a lagoon-scale and small to species-level.

TEMPORAL RANGE (years)	SPATIAL SCALE			EXPLANATORY VARIABLES
	Regional →	Local →	Small	
1	I (18/1), II (62/1)	II (62/1)	V (1/1)	Abiotic
4		III (10/7)		↓
2			IV (12/4)	Biotic

RESPONSE VARIABLES **Vegetation composition , cover, richness and identity**

2. MATERIALS AND METHODS

2.1 Description of study area

The studies of this thesis were conducted in the brackish microtidal northern Baltic Sea (**Fig. 1**). Several ice-ages have passed this area, but the conditions maintained today are largely shaped by the latest one, which started to move aside about 10.000 years ago. Compared with other seas, the ecosystem of the Baltic Sea has thus evolved during a very short time and has persisted in its present form only for 3000 years (Voipio 1981, Conley et al. 2009). It is a shallow sea, with an average depth of 60 m (maximum depth ca. 460 m) and characterized by naturally steep climate and salinity gradients both in a latitudinal, vertical and temporal perspective decisively shaping the biotic communities when considering distribution on large scale (Leppäkoski and Bonsdorff 1989, Hägerhäll and Hägerhäll 2007, Conley et al. 2009). The short history and the demanding environmental conditions have resulted in relatively low species diversity, which is further challenged by eutrophication slowly increasing overgrowth and inevitably changing the natural course of development (Wulff et al. 1990, Bonsdorff et al. 1997, Bonsdorff 2006).

The topography of the Baltic Sea is nuanced regionally and locally by several basins, archipelagos and islands. On a basin-scale substrate quality, depth and isolation grows in importance in structuring communities. The coastal lagoons in this thesis are located in the archipelago areas between the east coast of Sweden, Åland Islands and south-west mainland of Finland. Here the shoreline is extensive, and shallow depths (on average 23 m) dominate increasing the space for littoral processes. As an example, in the Archipelago Sea (the area between the south-west Finnish mainland and Åland archipelago) alone ca. 25.000 islands and skerries (Granö et al. 1999) and more than 450 flads and gloes (Tolvanen et al. 2004) are found. The salinity of the archipelago area of focus ranges from 3 to 6 PSU, and land-uplift, a relict process originating from the glacial period, is around 5 mm/year (Kääriäinen 1964). The vegetation on soft bottoms is characterized by pondweeds (*Potamogeton* spp.), milfoils (*Myriophyllum* spp.), reed (*Phragmites australis*) and stoneworts (*Chara* spp.), and typically bladderwrack (*Fucus vesiculosus* L.) and several filamentous algae species (e.g. *Cladophora* spp.) are attached to hard substrates, to name a few. In general, these shallow, sheltered areas rich in vegetation are important for a range of aquatic organisms, such as macroinvertebrates (Bonsdorff and Blomqvist 1993), sea birds (von Numers 1995) and coastal freshwater and marine fish species, such as roach (*Rutilus rutilus* (L.)), breams (*Abramis brama* (L.)), perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.), pikeperch (*Sander lucioperca* (L.)), sticklebacks (*Gasterosteus aculeatus* L., *Pungitus pungitus* (L.)) and herring (*Clupea harengus* L.) (Blomqvist 1984, Karås and Hudd 1993, Sandström et al. 2005, Lappalainen and Urho 2006, Snickars et al. 2009, 2010).

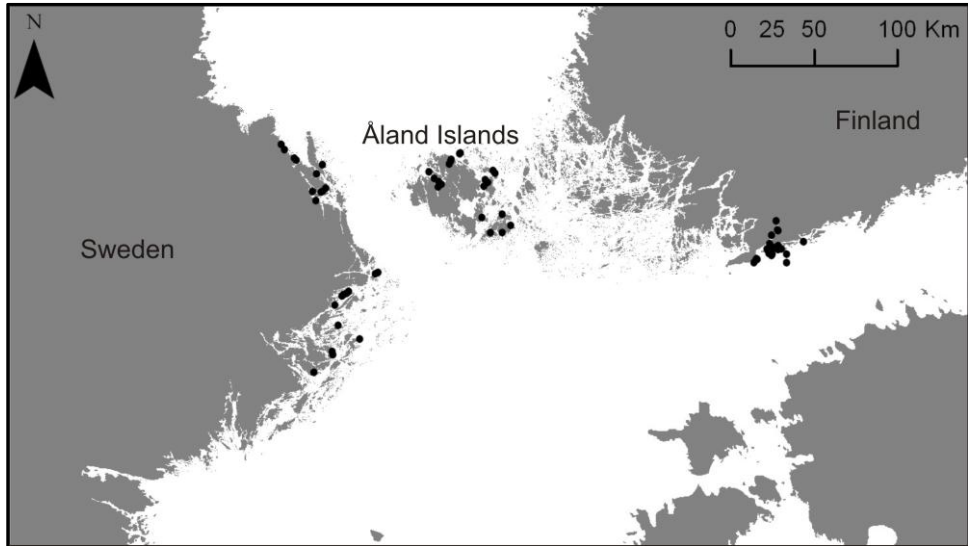


Fig. I. Study area in the Baltic Sea. The archipelago regions in Sweden, the Åland Islands and the mainland of Finland with sampled lagoons (as dots) are shown.

2.2 Biotic and abiotic variables

All studies were conducted in the field, in soft-bottom coastal lagoons during the productive season in the years 1999-2007. To maximize variability, 70 coastal lagoons of 1-20 ha in size were selected from a total of 400 evaluated sites by stratified randomization using three criteria. Firstly, the lagoons should have a threshold in the inlet restricting water inflow from the adjacent sea and thus reflecting habitat isolation. With reference to the morphological classification system presented by Munsterhjelm (1997, 2005) for coastal lagoons, stages which have continuous contact with the adjacent sea were included: the most open juvenile flad with a moderate inlet threshold, the clearly delimited flad and the glo-flad with strongly restricted water exchange (thereby excluding the glo). Secondly, the lagoons should vary in archipelago position, i.e. be found along the entire archipelago wave exposure gradient. Thirdly, in **paper I** lagoons of varying anthropogenic influence were selected, while only a limited degree of anthropogenic influence (corresponding to no observed human activity or only a couple of houses and bridges) was accepted in **papers II-V**.

In the lagoons vegetation species composition and cover (in total 100 %) as well as water depth were measured along transects using a 50 x 50 cm frame. In every lagoon when visited, the water quality variables total phosphorus and nitrogen, turbidity and salinity, as well as temperature, sediment total phosphorus and nitrogen were measured. Chlorophyll *a* was measured only in a restricted number of lagoons in the year 2003 (**paper III**). Morphometric variables determined were

average depth, shore-line length, bottom area, volume and cross-section area of the inlet for each lagoon as well as two exposure measures, i.e. habitat isolation based on lagoon and inlet size and wave exposure (Isæus 2004, Snickars et al. 2009) outside the lagoon reflecting position along the archipelago gradient. The determination of the exposure measures (habitat isolation and wave exposure) is explained in **paper II** and **III**.

2.3 Specific methods of the individual papers

In the following sections a summary of the specific methods of each paper is given. Detailed descriptions are found in the enclosed individual papers.

In **paper I** lagoons found in fairly similar wave exposure zones in the archipelago, but varying in geographic location, habitat isolation and environmental condition were selected. Focus was set on assessing the impact of geographic origin and anthropogenic influence for the development of vegetation in lagoons of varying isolation, to test the applicability of the morphological classification system developed for lagoons in the south-west mainland of Finland (Munsterhjelm 1997, 2005), and to establish which factors regulate vegetation composition during these conditions. 18 lagoons were studied for vegetation and environmental variables in the east coast of Sweden, Åland Islands and south-west mainland of Finland in August 1999. The vegetation data used as cover percentage per species of each lagoon were treated in the software CANOCO by an indirect multivariate method, DCA (Ter Braak and Šmilauer 2002), and the derived axes from the analysis were correlated to environmental data by Spearman rank correlation analysis using the software SPSS.

Paper II was a sequel to the first paper, but included a larger number of lagoons, which all were considered to be of natural condition and varied in position along the archipelago gradient. In this paper, the aim was to assess the role of habitat isolation on a local scale in relation to the archipelago gradient on a regional scale for the environmental conditions and vegetation development in coastal lagoons. Furthermore, the interacting role of vegetation, and the role of species richness and species identity in the lagoon environment were considered in the light of determining if the vegetation development and altering environmental conditions followed a succession-like and gradual course or were stepwise and reflected regime shifts along with land-uplift. 62 lagoons were studied for vegetation composition and environmental variables in the years 2002 and 2003, and the development pattern was analyzed with several multivariate techniques including CCA, DCA and MDS in the software CANOCO and PRIMER, a regime shift detection method (as an add-in for Excel) giving a regime shift index RSI (Rodionov 2004, c.f. Andersen et al. 2008), Spearman rank correlation and stepwise multiple regression in the software SPSS.

In **paper III** five less isolated and five more isolated coastal lagoons were selected based on the regimes found in **paper II**, for assessing inter-annual and seasonal variations in vegetation development and environmental conditions in relation to the degree of isolation. In addition, the buffering capacity and stability of

vegetation were evaluated in relation to isolation and potential anthropogenic induced changes. Vegetation composition and environmental variables were determined in August in the years 2002-2004 and 2007, and in 2003 seasonal sampling was conducted in May-August. Inter-annual temporal variations in the vegetation and environmental data were examined by subjecting a similarity matrix based on Bray-Curtis and Euclidian distance, respectively to non-metric multidimensional scaling in the software PRIMER. The similarity matrix for vegetation was further subjected to ANOSIM for the pre-defined regimes of different isolation. The relative extent of spatial and temporal sources of variation was analyzed for the vegetation cover and individual environmental variables with two-way ANOVA among years, and the standard deviations for environmental variables among years were studied for differences with Independent-samples t-test in the software SPSS. The seasonal development was described graphically.

The study of **paper IV** was designed to determine if macrophyte species interaction may mediate the habitat structure for fish, and further, if plant species richness and identity may influence the outcome of interaction and the diversity of fish. Preference of juvenile fish was determined for ten macrophyte species when growing in monoculture and polyculture along a depth gradient (< 4 m). As a response variable for species interaction the height of individual macrophyte species was measured in respective cultures. After the vegetation and depth survey in 2003 and 2004 (in the second and third paper) juvenile fish were monitored in July-September by point-abundance sampling using small underwater detonations, which catch small fish (15-150 mm) with well-developed swim bladders (Snickars et al. 2007). Fish sampling was randomized proportionally to macrophyte species composition and depth distribution, and Ivlev's electivity index was used to assess the selection of mono- and polycultures by fish (Ivlev 1961). To synthesize a metric for fish diversity, the Shannon index was calculated on all positive Ivlev values for each macrophyte species in both cultures. The Shannon index was also calculated for macrophyte species along the depth gradient. Fish diversity was then compared among macrophyte species, species heights and water depths in general and separately for mono- and polycultures, and further to macrophyte diversity along the depth gradient.

Paper V reports the first confirmed finding of *Chara connivens* Salzm. Ex. A. Braun in Finland during the reconnaissance of coastal lagoons for this thesis work. Appropriate environmental variables (water depth, water temperature, salinity, and area characteristics) were determined at the locality where the species was found.

3. MAIN FINDINGS OF THE THESIS

3.1 Drivers, variation and regime shift pattern for vegetation (papers I-III)

Habitat isolation was found to be a main inducing driver for vegetation development of coastal lagoons in the Baltic Sea ($p < 0.001$), illustrated by the DCA ordinations and related correlations and regressions (Fig. 1 and Table 4 in **paper I**, Fig. 2 and Table 2 and 3 in **paper II**). With increasing isolation, the species composition altered from diverse, but sparsely growing vascular plants and marine algae to dense and abundant growth forms dominated by charophytes. General geographical differences among incorporated areas (Swedish east coast, Åland Islands and south-west mainland of Finland) were not found to force the development of vegetation on a regional scale, while lagoons with apparent anthropogenic influence diverged from the pattern due to changed species composition, lower cover and especially loss of *Chara tomentosa* L. (**paper I**). The results imply that a general classification system (c.f. Munsterhjelm 1997, 2005) for natural-like coastal lagoons in the northern Baltic Sea is achievable (**paper I**).

The relationship between habitat isolation and vegetation development as well as the related abiotic environment in lagoons showed in several aspects a dual regime character. In the DCA ordination (Fig. 2 in **paper II**) lagoons were primarily arranged in increasing isolation order along axis 1 and presented divided distributions patterns for most explanatory as well as response variables. The regime shift detection method (Rodionov 2004) confirmed significant ($p < 0.01$) shifts for two major groups of variables. Firstly, increased habitat isolation, decreased average depth and increased total nitrogen appeared detrimental for a diverse but sparsely occurring group of non-dominant vascular plants and marine algae (e.g. *Ceratophyllum demersum* L., *Zannichellia palustris* L. and *Fucus vesiculosus*), which shifted negatively. Secondly, initiated by the changed conditions a shift in dominant species (e.g. decreasing *Myriophyllum spicatum* L. and increasing *Najas marina* L. and charophytes), decreased species richness and increased cover coincided with a decrease in salinity, total phosphorus in the water and turbidity (Fig. 3 and 4 in **paper II**). *Potamogeton pectinatus* was the only dominant species which presented a unimodal distribution pattern as a function of habitat isolation. Based on the significant shifts, the lagoons were considered to form a less isolated and diverse vascular plant regime and a more isolated low-diverse charophyte regime, respectively, dissociating a pure successional development and modifying the earlier classification system (c.f. Munsterhjelm 1997, 2005). Further, wave exposure (i.e. the position of the lagoon along the archipelago gradient) presented a significant relationship to (DCA) axis 2 in forms of a correlation and regime shift ($p < 0.001$ for both), while a similar relationship to axis 1 was lacking, implying that wave exposure structured vegetation development only in less isolated lagoons corresponding to the vascular plant regime (Table 2 and Fig. 2 and 4 in **paper II**). In **Fig. II A** the ordination in **paper II** is redrawn as an example of the regime shift pattern and the species encountered in this work. **Fig. II B** gives an illustration of the species cover development in regimes with habitat isolation (in ten lagoons chosen for **paper III**).

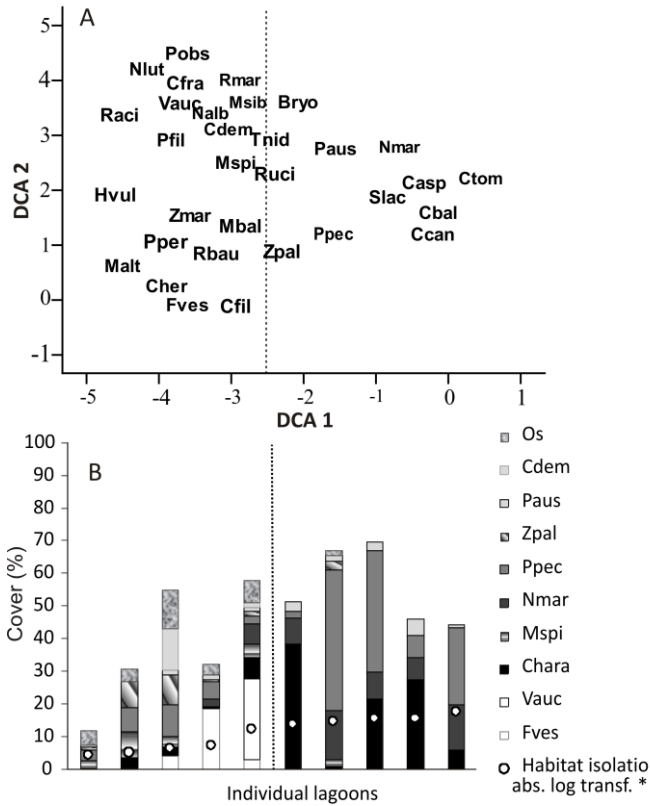


Fig. II. Regime shift and species cover development along ascending habitat isolation. **A)** DCA species ordination made on species cover (%) (redrawn according to **paper II**). **B)** Mean percentage cover for species (from four years in ten lagoons chosen for **paper III**). Here, non-dominant species are marked as other species (Os) and all charophytes as *Chara*. Habitat isolation is given as absolute values of log transformations. The dashed lines indicate position of the regime shifts in habitat isolation (based on the regime shift detection method and index). Vascular plant regime is found on the left and charophyte regime on the right of the dashed line.

Bryo=*Bryophyta*, Casp=*Chara aspera* Willd., Cbal=*C. baltica* Bruz., Ccan=*C. canescens* Loisel, Ctom=*C. tomentosa* L., Cfra=*C. globularis* Thuill. (*C. fragilis*), Cdem=*Ceratophyllum demersum* L., Cfil=*Chorda filum* (L.) Stackh., Cher=*Callitriche hermaphroditica* L., Fves=*Fucus vesiculosus* L., Hvul=*Hippuris vulgaris* L., Malt=*Myriophyllum alterniflorum* DC., Msib=*M. sibiricum* Kim., Mspi=*M. spicatum* L., Mbal=*Monostroma balticum* (Aresch.) Wittr., Nalb=*Nymphaea alba* L., Nlut=*Nuphar luteum* L. Sibth. & Sm., Nmar=*Najas marina* L., Paus=*Phragmites australis* Cav., Pfil=*Potamogeton filiformis* Pers., Pobs=*P. obtusifolius* Mert. & W.D.J. Koch, Ppec=*P. pectinatus* L., Pper=*P. perfoliatus* L., Raci=*Ranunculus circinatus* Sibth, Rbau=*R. baudotii* (Godr.), Rmar=*Ruppia maritima* L., Ruci=*R. cirrhosa* (Petagna) Grande, Slac=*Scirpus lacustris* (*Schoenoplectus lacustris*) L., Tnid=*Tolypella nidifica* (O.F. Müll.) Braun, Vauc=*Vaucheria* sp., Zmar=*Zostera marina* L., Zpal=*Zannichellia palustris* L.

The functional distinctions of the regimes were further manifested in inter-annual and seasonal differences in the dynamics of vegetation and abiotic environment (**paper III**). Apparent separation of lagoons in the MDS plot (Fig. 2B in **paper III**) and higher coefficients of variation for cover of individual species (Fig. 2A in **paper III**) implied greater inter-annual alteration in the vegetation composition in the vascular plant regime compared with the charophyte regime. The validity of the regime division in a short-term temporal perspective was additionally verified by a significant difference in similarity of vegetation composition between the regimes (ANOSIM, $p = 0.01$) and by a significant main effect of regime on vegetation cover (two-way ANOVA, $p < 0.001$, Table 2 in **paper III**) when using data from several years. Seasonally, the difference in development of vegetation cover between the regimes was not as marked. In May total cover of vegetation showed similar levels in lagoons of both regimes, but the increase along the season showed a steeper ascending slope resulting in higher mean cover values in the charophyte regime especially concerning *Chara* spp., *Najas marina* and *Potamogeton pectinatus* (Fig. 5 in **paper III**). In **Fig. III** the seasonal development is illustrated to provide a comprehensive picture of the temporal regime distinctions (vegetation variables in **Fig. III D-E**)

Short-term dynamics for abiotic variables differed from the ones for vegetation in several senses. The MDS plot for total nutrient concentrations in water and sediment presented higher inter-annual separation for lagoons of the charophyte regime than those of the vascular plant regime (Fig. 3 in **paper III**). This separation was verified by a significant main effect of year for only total nitrogen in the sediment ($p < 0.001$), and by a significant main effect for the regime division for chlorophyll *a* ($p < 0.01$), total nitrogen and phosphorus in the sediment and total nitrogen in the water, which all showed higher mean values on all years in the charophyte regime ($p < 0.001$, Table 2 and Fig. 4 in **paper III**). Mean values of total phosphorus in the water were also slightly higher in the charophyte regime than the vascular plant regime, but a main effect for the regime division was not verified. Seasonally higher values for abiotic variables were in general observed in the charophyte regime than in the vascular plant regime. Yet, the differences in total phosphorus in the water and chlorophyll *a* values between the vascular plant and charophyte regime were leveled out in August (**Fig. III A and C**), mostly due to a decrease in values in the charophyte group along the season. For nitrogen an opposite trend seemed valid in that differences among lagoons and regimes increased towards August (**Fig. III B**).

A summary of papers I-III is given as an inter-comparison of significant regime characteristics in **Table II**.

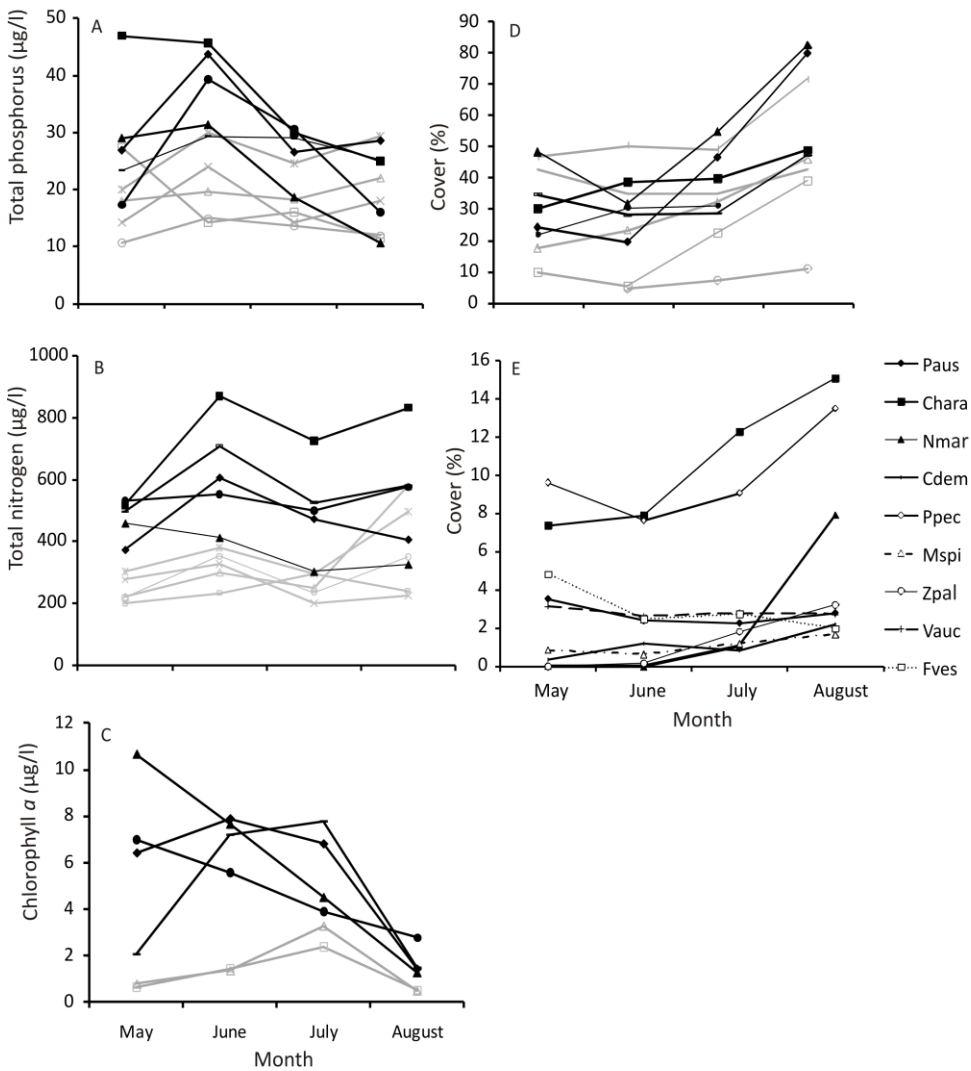


Fig. III. Seasonal dynamics (among productive months) in surveyed lagoons (redrawn from paper III). **A)** total phosphorus (µg/l) in the water, **B)** total nitrogen (µg/l) in the water, **C)** chlorophyll *a* (µg/l), **D)** vegetation cover (%) and **E)** cover of dominant species (%). Grey lines with unfilled symbols represent individual lagoons of the vascular plant regime and black lines with filled symbols mark lagoons of the charophyte regime in A-D). Chlorophyll *a* values were available only in six lagoons (out of ten in total for this study, paper III). Species abbreviations for E) in Fig. II.

Table II. Summary of significant differences in influence or value of variables, given as an inter-comparison between the described regimes (vascular plant and charophyte) with reference to **papers I-III**. * $p < 0.05$ / ** $p < 0.01$ / *** $p < 0.001$ indicate the significance level and refer to multiple separate tests (Regime shift index, stepwise multiple regression, independent-samples t-test and two-way ANOVA, of which some were applied on data derived from DCA and MDS) in the different papers.

VARIABLES	REGIME		PAPER of ref.
	Vasc. plant	Charophyte	
GENERAL CHARACTERISTICS			
Influence of archipelago position (regional factors)	Higher	Lower	II**
Habitat isolation (local factors)	Lower	Higher	I*, II**
VEGETATION			
Diversity	Higher	Lower	II**
Cover	Lower	Higher	II**
Charophyte dominance	Lower	Higher	II**, III**
ABIOTIC			
Sediment nutrients	Lower	Higher	III***
Total nitrogen in water	Lower	Higher	II**, III**
Total phosphorus in water	Higher	Lower	II**
Turbidity	Higher	Lower	II**
VARIATION IN TEMPORAL DYNAMICS			
Inter-annual in vegetation	Higher	Lower	III**
Inter-annual in abiotic variables	Lower	Higher	III**

3.2 Macrophyte species interaction mediates habitat structure (paper IV)

On a smaller scale, vegetation composition and species identity were found highly decisive for the distribution and diversity of fish in coastal lagoons. In general, juvenile fish elected plant species in monoculture, whereas bare sediment and plant species in polyculture were avoided (Fig. 1 in **paper IV**). The height of plant species differed in mono- and polycultures and for short and tall species, but in general tall plant species were taller in monoculture and short plant species taller in polyculture (Fig. 2 in **paper IV**). All plant species showed highest fish diversity values at their tallest height, i.e. in monoculture for the taller plant species (*Potamogeton perfoliatus* L., *Potamogeton pectinatus* and *Phragmites australis*) and in polyculture for shorter plant species (*Myriophyllum* sp., *Najas marina* and *Ceratophyllum demersum*). The two shortest plant species (*Chara aspera* and *C. canescens* Loisel.) were not elected at all. When there was a preference for both cultures of a species (*Chara tomentosa*), the preference was most pronounced when the plant grew in monoculture. Cover did not vary among cultures ($p = 0.14$). Neither did cover or proportion of mono- and polycultures vary across depths (Fig.

3 and 4 in **paper IV**). However, the diversity (measured by the Shannon index) of plants and fish showed contrasting trends with depth, i.e. high fish diversity at deep waters where plant diversity was low and plant height high. Furthermore, the tallest monocultures (>75 cm) increased their dominance rapidly with depth and dominated at deep waters (>2.5 m), while the shortest monocultures (<25 cm) dominated shallow water (0-0.49 m) (Fig. 4A in **paper IV**).

3.3 *Chara connivens* (paper V)

Female plants of *Chara connivens* Salzm. Ex. A. Braun 1835 (Fig. 1 in **paper V**), a new species to Finland, were found in Geta in the northern Åland archipelago in July 2004 (and confirmed by Dr Irmgard Blindow University of Greifswald). The species is rare in the Baltic Sea and has disappeared from several of the southern localities in the Greifswald/Rügen area, Gdansk Bay and Gulf of Riga (Torn 2008). Except for the new finding, recent distributions (since 1981) are reported to be restricted to the Öregrund archipelago in Sweden and the West Estonian Archipelago Sea (Torn 2008). The locality in the Åland archipelago was sheltered but had a good exchange of water. The bottom substrate was mainly silt mixed with gravel and sand. Salinity was 5.5 PSU and the water depth 0.5-1.5 m. The total area, where the species was found, was approximately 50 m * 100 m and had very clear water. As well as for some vascular plants and more common *Chara* species, also *Chara horrida* Wahlst., classified as extremely endangered (Rassi et al. 2001) and reported to be extinct in the Geta area in Åland (Torn & Martin 2003), were found neighbouring *C. connivens*.

4. DISCUSSION

4.1 The role of vegetation on different scales

4.1.1 Regime shift pattern

This thesis shows that vegetation in coastal lagoons is restricted mainly by landscape configuration driven by habitat isolation and land- uplift, while vegetation itself seems to have a strong functional role in modifying the aquatic environment especially with decreasing environmental harshness. Although the hierarchical order and direction of influence of restricting boundaries and gradients might be unclear in coastal lagoons, several studies stress the overriding structural importance of geomorphological variables for the biota (Kjerfve 1994, Frederiksen et al. 2004, Pérez-Ruzafa et al 2007).

Increased habitat isolation, i.e. a transformation from open harsh environments to sheltered low-disturbance environments, appeared to be of decisive importance in launching the shift suite of the vascular plant and charophyte regimes. Biotic interactions in harsh environments are often of secondary importance in structuring communities, but may be important when low disturbance prevails (Sousa 1979, Menge and Sutherland 1987). The decreased harshness of the environment with increased habitat isolation might thus imply both altered and increased importance of biotic interaction. Such a statement is supported by the decreased concentrations of total phosphorus and turbidity in the charophyte regime possibly due to an enhanced role of vegetation on water clarity and nutrient cycling with low disturbance. Further, also the form of biotic interaction has been suggested to vary in strength with the characteristics of the environment. Facilitation of species might render possibilities for a diverse community when harsh conditions prevail, while competition might be more important in habitats with lower disturbance (Holmgren et al. 1997, Brönmark and Hansson 2005). Thus, a diverse species composition in the vascular plant regime is probably structured strongly by environmental conditions and promoted partly by facilitation by other species, while biotic interaction (especially in forms of competition) is forming a uniform low-diverse community of abundant cover in the charophyte regime. This interpretation is supported by the structuring role of wave exposure (archipelago position) in the vascular plant regime, or foremost by the lack of a similar impact in the charophyte regime. Taken together, a switch in strength from external (topographic) steering to internally (vegetation) directed processes (Sousa 1979, Menge and Sutherland 1987) characterizes the functional and structural course of regime development with increasing habitat isolation.

In the charophyte regime the inter-annually stable species composition was combined with pronounced variability among years in abiotic variables and increased total phosphorus content in the sediment. Furthermore, an increase in cover along the productive season in the charophyte regime was combined with a great seasonal decrease in total phosphorus and chlorophyll *a* in the water. As vegetation may increase nutrient variability and phosphorus content in the sediment by participating in the bilateral recycling of phosphorus and accumulation of phosphorus in the sediment (Carpenter 1980, Van Donk et al.

1993), the temporal dynamics reinforced the interpretation of an increased functional role of vegetation in the charophyte regime. *Chara* fields in particular have been shown to store the entire annual phosphorus load of a lake (Kufel and Ozimek 1994). The amounts of nutrients stored in charophytes have further been observed to far exceed the amounts in the water, while the amounts nutrients stored in angiosperms are suggested to be lower than in the water (Blindow 1992). This further implies a buffering capacity by increased cover and by dominance of charophytes both along isolation and along the productive season (Kufel and Ozimek 1994). Total nitrogen seemed, on the other hand, to diverge from the pattern of total phosphorus and turbidity in the water and increasing in the charophyte regime (both along the season and habitat isolation). As nitrogen is less often reported as a limiting nutrient in lakes (Scheffer 1998), and as the charophyte regime showed resemblances to lake dynamics, the increased nitrogen concentrations in the charophyte regime could indicate that nutrient input increases along with habitat isolation and that foremost phosphorus limits growth in the charophyte regime. In addition, a strong ability of accumulation in the sediment does not occur for nitrogen giving reason for that nitrogen concentrations tend to respond quite promptly to changes in external loading (Scheffer 1998, Brönmark and Hansson 2005) and partly explain the observed main effect of time for total nitrogen in the sediment.

4.1.2 Species-level

On a small species-level scale, the structuring role of competition and species identity was underlined. As increasing height of individual tall species (e.g. *Potamogeton* spp.) in monocultures especially in deep water seemed accentuated in directing high diversity of fish (**paper IV**), negative selection (e.g. Loreau and Hector 2001) as a form of competition is suggested to drive preferred fish habitat structures. Concerning the active electivity of fish, tall plant species may be preferred since the height per se influences the survival of invertebrates and attracts juvenile fish as a result of better refuge from predation and more space in the vegetation canopy due to allometric relationships (Mattila 1992, Weiner and Thomas 1992, Levin and Hay 1996).

Taller narrow-leaved vascular plants (e.g. *Potamogeton* spp.) often grow sparser (compared to charophytes) and build a canopy and new biomass near the water surface (Kautsky 1988). They thus fight turbidity by increasing in length and are reported to be superior competitors in light-limited (e.g. eutrophic or deeper) environments (Goldsborough and Kemp 1988). Charophytes, on the other hand, form dense mats with high biomass per unit area concentrated near the sediment surface, and might be superior in competition for horizontal space when light is not limiting (Blindow 1992). Thus, in coastal lagoons tall *Potamogeton* spp. might be superior competitors in deeper water with decreasing light provision and provide preferred fish structures. In other words, the role of macrophyte species identity (i.e. the capacity for length increase in monocultures) and interaction, rather than richness or cover *per se* seems important in forming habitat structures for diversity of higher trophic levels.

However, a large number of studies imply a general positive effect between biodiversity and ecosystem functions, suggesting positive diversity relationships among trophic levels (Hector et al. 2002). The contradicting results of the present study might be due to a non-linear relationship between height and cover (and indirectly biomass) across depths in tall dominant species as *Potamogeton pectinatus* and *P. perfoliatus* promoting fish diversity. As *P. pectinatus* may show high morphological plasticity (Kautsky 1988) and low productivity in monocultures (Engelhardt and Ritchie 2002) and as *P. perfoliatus* presents increasing height in response to inferior light climates, an increase in the height to biomass ratio may occur across environmental gradients such as depth (Spence 1982, Goldsborough and Kemp 1988, Weiner and Thomas 1992). Such an interpretation is supported by recent studies, which state that negative selection effects are common when a species' competitive ability is not directly measured by biomass or abundance estimates (Duffy 2002, Engelhard and Ritchie 2002, Jiang et al. 2008).

4.2 Compiling signification of species richness, identity and trophic levels

As the shift described in **paper I** and **II** from high to low macrophyte diversity has been shown to direct decreases in juvenile fish and invertebrate diversity in coastal lagoons (Hansen et al. 2008, Snickars 2008, Snickars et al. 2009), the diversity pattern seems congruent among these trophic levels along the gradient of habitat isolation. Simultaneously, the identity of species also implies importance, as monocultures of individual macrophyte species (e.g. *Potamogeton* spp.) posed highest diversity of juvenile fish in **paper IV**. In accordance, species identity (e.g. *Myriophyllum spicatum*) and especially species-specific complexity of macrophytes have been shown to direct the abundance and active choice of invertebrates in coastal lagoons (Hansen et al. 2010). When is then macrophyte identity and when is richness of species important for other trophic levels in maintaining ecosystem functioning? The answer depends on the context (Hooper et al. 2005) and also on the scale (Kessler et al. 2009), as shown by the results here. Diversity patterns between trophic levels seem congruent on a regional scale when comparing among lagoons, while they diverge on smaller scale. In addition, the finding of *Chara connivens* may be seen important partly in increasing the regional species-pool, but also on smaller scale by possibly directing juvenile fish and invertebrates by its identity. The matter of both context and scale is perhaps a trivial finding from the perspective of general ecology, but is nonetheless one that often is overlooked in the genre of biodiversity and ecosystem functioning. Thus, in systems where especially disturbances and landscape configuration (*sensu* coastal lagoons) strongly modify community structure, results from e.g. small-scale experiments may be incompatible (Bengtsson et al. 2002).

Species identity may, however, also be crucial on larger scales as some species may possess key functions regarded as more important than others in an ecosystem functioning perspective, i.e. when they function as drivers rather than passengers (Walker 1992). For instance, as the brown alga *Fucus vesiculosus* is the only large perennial seaweed in the northern Baltic Sea, hard-bottom macrofauna depends on this basic habitat former, and the replacement of the species by ephemeral

algae due to eutrophication or increased traffic in the Baltic Sea, has been recorded together with changes in abundance and composition of associated invertebrates (Rönnerberg 1985, Roos et al. 2004, Wikström and Kautsky 2007). With reference to the mentioned increased impact of vegetation for conditions in the charophyte regime both spatially and temporally, a similar key function seems to hold true for *Chara* spp. as this group, and *Chara tomentosa* in particular, alone often dominated vegetation in the more isolated lagoons. The overall greater chlorophyll *a* and phosphorus concentrations in the beginning of the season, greater seasonal reduction, higher abundance of juvenile fish (Snickars et al. 2009) and higher biomass and abundance of zooplankton (Scheinin and Mattila 2010) in partly the same lagoons, further imply a higher productivity potential of the charophyte regime. Thus, it seems that a comparably low-diverse macrophyte assemblage and an increased functional role played by *Chara* spp. maintain relatively high production (Blindow et al. 2006), implying decoupling of diversity and production on a regional scale. Further, the increased functional role of vegetation with decreased diversity in the charophyte regime, could involve an increased sensitivity risk (or loss of resilience, c.f. Folke et al. 2004) as species-rich communities are believed to insure the existence of functions due to redundancy among species (Yachi and Loreau 1999).

Finally when discussing diversity related patterns in Baltic coastal lagoons the role of succession is inevitable and underlined. For example, the species composition seemed more locked in the charophyte regime among years in comparison to the naturally released niches following greater inter-annual exchange of species in the vascular plant regime (**paper III**). The resistance to new species seemed thereby higher in the low-diverse charophyte regime than the more diverse vascular plant regime, contradicting the hypothesis on greater invasion resistance with diversity (MacArthur 1970). On the other hand, when considering this pattern in the light of succession, it is hardly surprising that species exchange and richness increase in the (in sense of succession) younger vascular plant regime before stabilizing and decreasing in the more mature charophyte regime (Munsterhjelm 1997). Thus, the generality of results concerning issues related to biodiversity and ecosystem functioning (for instance the hypothesis on resistance) is in some cases ambiguous. As exemplified here, the role of natural conditions and succession is easily overlooked in the debate especially when depending on short-time empirical findings closed to their surroundings and leaving out larger spatial or temporal scales (c.f. Gunderson and Holling 2001, Bengtsson et al. 2002).

4.3 Implications for the theory on system shifts

The most important findings in this study, both from an ecological perspective and for management, are the described consequences of habitat isolation (i.e. increased water retention) for lagoon functioning and the disparities to a development described along an eutrophication gradient (c.f. the estuarine quality paradox in Dauvin 2007 and Elliott and Quintino 2007). Nonetheless, the regime shifts both in shallow marine and freshwater basins, driven by nutrient-enrichment share several resemblances between themselves as well as in comparison to brackish coastal lagoons subjected to habitat isolation.

In eutrophic marine coastal lagoons (lacking an inlet threshold) macroalgae are favored over seagrasses, and with further increases in nutrient load phytoplankton biomass will increase at the expense of macrophytes due to enhanced nutrient levels (Duarte 1995, McGlathery et al. 2007). Increased water retention has further been suggested to accelerate the process (Valiela et al. 1997). Similarly, the species composition of primary producers may change in shallow lakes from charophytes to angiosperms and further to phytoplankton dominance due to enhanced nitrogen and especially phosphorus concentrations (Scheffer et al. 1993, Blindow et al. 2006). In the described brackish coastal lagoons, however, the vegetation development seemed congruent, but reversed to marine and freshwater environments. As habitat isolation and most likely both the input and retention of nutrients increase, the vegetation turns from vascular plant and marine macroalgae to charophyte dominance, which seems to enable reductions of phosphorus and turbidity in the lagoons. Thus, charophytes favored by diminished water circulation (due to the inlet threshold) seem to buffer the negative consequences of water retention on macrophytes described for marine lagoon environments.

Hence, from a management perspective one positive implication is that especially the lagoons of the charophyte regime seem to function as a filter in trapping nutrients and counteracting eutrophication. Nonetheless, as the charophyte regime *per se* is developed following isolation (and increased water retention), the prospect of a nutrient filter seems to function only if the inlet is kept (semi-)isolated, that is undredged. From a long-term perspective, dredging of the inlet has permanent negative consequences as the lagoons may never revert to their natural developmental course again and the charophyte regime is probably in most cases entirely lost. Furthermore, due to loss of charophytes the stored nutrients in the charophyte regime would probably leak from the sediment. Indirectly this implies that if habitat isolation did not prevail (naturally or following dredging) in described brackish coastal lagoons, the development would probably be similar to the one in marine lagoons or freshwater lakes subjected to nutrient-enrichment, and angiosperms and macroalgae would be replaced by phytoplankton (instead of charophytes) (c.f. Dahlgren and Kautsky 2004).

A schematic illustration of the described courses for marine (i.e. seagrass inhabited, c.f. McGlathery et al. 2007), freshwater (Scheffer 2009) and brackish coastal lagoons is presented in **Fig. IV**.

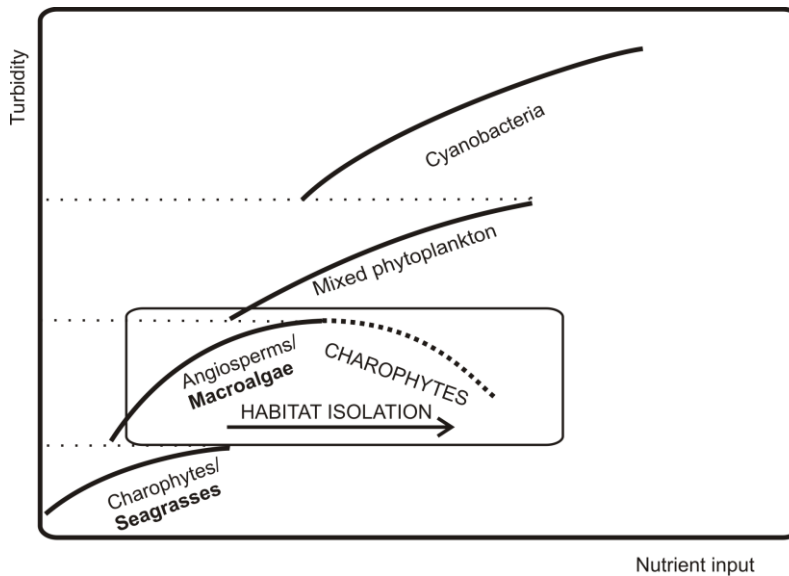


Fig. IV. Conceptual model for four different equilibria along with increasing nutrient input and turbidity. The figure is redrawn from Scheffer (2009) for conditions in shallow lakes (charophytes, angiosperms, phytoplankton and cyanobacteria), while the interpretation of marine conditions (seagrasses, macroalgae and phytoplankton) refers to the development described in McGlathery et al. (2007). In comparison, the inserted rectangular box gives a hypothesized development in brackish coastal lagoons when angiosperms and macroalgae (i.e. the vascular plant regime) are replaced by charophytes (charophyte regime) with increasing habitat isolation (and increasing water retention). This model assumes that nutrient input would increase with habitat isolation. Furthermore, decreased turbidity levels may be paralleled in decreased total phosphorus concentrations in the water in the charophyte regime.

5. CONCLUSIONS AND CONSERVATIONAL ASPECTS

In the Baltic Sea, coastal lagoons with an inlet threshold are presumed to follow a common trajectory due to increased isolation with land-uplift (Munsterhjelm 1997, 2005). The results of my thesis show that this development is stepwise rather than purely successive, and fairly radical shifts both in vegetation and environmental variables form two regimes, namely the vascular plant and charophyte regime. During the study period the separate regimes were found inter-annually and seasonally unperturbed and primarily structured by topographic factors. In fact, the distinct and regime specific temporal dynamics seemed to underline the functional differentiation between the regimes. This discrepancy between the regimes was expressed in actual values as well as in the variability among years and the steepness of the seasonal production in the regimes. The regime pattern was not dissipated by geographical differences (Sweden, the Åland Islands and the south-west mainland of Finland), while anthropogenic influence seemed to disrupt the development by harming especially the occurrence of *Chara tomentosa* (Krause 1981, Blindow 1992).

With increasing isolation, the extrinsic steering subsided and the role of internally, vegetation directed processes seemed to increase towards the more isolated charophyte regime. This development was further found to diverge from the course along an eutrophication gradient as the role of vegetation increased with enhancing water retention (**Fig. IV**). The shares explained simply by the increase in cover and the explicit identity of charophytes are not separated in this thesis, but either one or the interaction of them seems to buffer total phosphorus and turbidity levels when isolation increase. However, as charophytes have been assigned an exceptionally strong impact on their environment, especially in improving water quality (c.f. Kufel and Kufel 2002, van Donk and van de Bund 2002 and references therein) they most likely possess a key function in the more isolated lagoons. In addition, on a small scale, vegetation identity (e.g. *Potamogeton* spp.) rather than effects of richness or cover indicated signification, as monocultures and specific macrophyte species were preferred by juvenile fish. Individual traits increasing height of tall macrophyte species in monoculture seemed especially important for fish diversity, suggesting that a negative selection effect following competition might drive preferred macrophyte attributes.

The steering factors of primary importance for vegetation development seem to differ with environmental harshness, while the congruence of biodiversity patterns among trophic levels depends on the scale of observation. In rough conditions (c.f. less isolated lagoons) biotic interaction might be restrained and suppressed allowing for high biodiversity, while calmer environments (c.f. more isolated lagoons) favor a lower number of species, with an increased interaction on each other and the conditions in general. As macrophyte diversity in coastal lagoons have been connected to invertebrate and juvenile fish diversity (Hansen et al. 2008, Snickars et al. 2009), the results indicate congruence in diversity patterns on larger (i.e. regional and local) scale. On small scale by contrast, the impact of macrophyte diversity is reduced, and individual macrophyte species are able to increase fish diversity decoupling diversity patterns among trophic levels. Subsiding environmental harshness and smaller scale seem thereby to increase the

role of (macrophyte) species identity for the surrounding environmental conditions and diversity of other trophic levels. As the cover of charophytes increase with decreasing harshness, the importance of their identity is underlined and thus the finding of *Chara connivens* especially valuable.

This thesis shows the importance of coastal lagoon environments from several ecological aspects. The diversity of macrophytes (and thereby ecosystem functions and services) as such calls for conservation, but the ecological importance of macrophytes is further increased in the associated diverse juvenile fish, bird and invertebrate assemblages (Hansen et al. 2008, Snickars et al. 2009, M. von Numers Åbo Akademi University pers. comm.). The presence of low-disturbance environments seems in particular important in view of the establishment of tall monocultures nursing for high fish diversity. In addition, the finding of *Chara connivens* (**paper V**) sheds light on the general ignorance of Baltic lagoons and the potential of them acting as refuges for rare species. Thus, as coastal lagoons currently are highly vulnerable (Munsterhjelm 2005, Sandström et al. 2005) raising conservational awareness and supervision of these environments are vital. Furthermore, as the results indicate an enhanced potential of vegetation to buffer increased nutrient levels thus prolonging resilience and *status quo* of the system status with increased habitat isolation and enhanced water retention, especially dredging of the inlet would have devastating consequences (**Fig. IV**). One implication for future research is thus the need of models for predicting the presence (and abundance) of species, especially charophytes and *Chara tomentosa* (Van den Berg et al. 1999, Heinänen 2010) in order to enhance governmental preparedness in conservational issues regarding coastal lagoons. This would be important especially for charophytes, as several of them are red-listed (Rassi et al. 2001, Gärdenfors 2010) and as absence of them may indicate disturbed condition such as presented here for *Chara tomentosa*.

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Kajsa Rosqvist

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