Effects of morphometric isolation and vegetation on the macroinvertebrate community in shallow Baltic Sea land-uplift bays

Joakim Hansen
To my parents
Effects of morphometric isolation and vegetation on the macroinvertebrate community in shallow Baltic Sea land-uplift bays

Abstract – Shallow sheltered Baltic Sea bays are ecologically important habitats that harbour a unique vegetation community and constitute vital reproduction areas for many coastal fish species. Knowledge about the invertebrate community in these bays is, however, limited. This thesis examines the macroinvertebrate community in shallow sheltered Baltic Sea bays and how it is affected by: (1) the natural morphometric isolation of bays from the sea due to post-glacial land uplift; and (2) differences in vegetation types.

The invertebrate biomass and number of taxa was found to decrease with increased bay isolation. The taxon composition changed from dominance by bivalves and gastropods in open bays to a community composed of a larger proportion of insects in isolated bays. Stable isotope analysis indicated epiphytes and periphyton as the major energy resources for most of the examined consumers, but the relative importance of these in relation to larger plants decreased for some consumers with increased bay isolation.

A comparison of invertebrate abundance between plants revealed a close relationship with morphological complexity of the plants. More complexly structured plants had higher invertebrate abundance than plants with simpler morphology.

The results suggest that management of these coastal habitats should be dynamic and take into consideration the natural change in invertebrate community resulting from the slow bay isolation process. In addition, the results imply that changes in the aquatic vegetation due to anthropogenic influences could induce changes in the invertebrate community as the plant habitat structure is altered. A changed invertebrate community may in turn affect higher trophic levels since invertebrates are important food for many fish and waterfowl species.

Keywords – lagoons, macrofauna, macrophytes, hydrophytes, charophytes, ecological succession, structural complexity, habitat complexity, habitat selection, species composition, biodiversity, stable isotopes, food web

List of papers

The thesis is comprised by a summary of four papers, which are referred to by their Roman numerals:


II Hansen, JP, Wikström SA and Kautsky L (Manuscript) Taxon composition and food-web linkages in a morphometric gradient of Baltic Sea land-uplift bays. Submitted to *Boreal Environment Research*


The published papers are reprinted with permission from the publishers.
Contents

Introduction .......................................................................................................................... 11
  Where sea meets land ........................................................................................................ 11
  The importance of aquatic plants .................................................................................. 14
  Stable isotope analysis and food resource utilization .................................................... 16
  Anthropogenic influences ............................................................................................ 17

Aim of the thesis .................................................................................................................. 19

Methods .............................................................................................................................. 20
  Study area ........................................................................................................................ 20
  Field sampling ................................................................................................................ 21
  Stable isotope analysis .................................................................................................... 23
  Experiments .................................................................................................................... 24

Results and discussion ....................................................................................................... 26
  Effects of bay isolation on the macroinvertebrate community ........................................ 26
  Distribution of macroinvertebrates between macrophyte species .................................. 34

Concluding remarks .......................................................................................................... 40

Acknowledgements ............................................................................................................ 42

References .......................................................................................................................... 43

Sammanfattning .................................................................................................................. 50

Tack ................................................................................................................................... 52
Introduction

Where sea meets land

Coastal zones are among the most productive areas of the seas due to availability of light in the shallow waters and nutrient supply by water mixing and land runoff (e.g. Mann 2000). The biota of transition zones between sea and land are highly structured by environmental gradients in depth, wave action, substrate and salinity (Barnes 1980; Little 2000; Mann 2000). The brackish environment results in a habitation by a mixture of marine and freshwater organisms, and gradients in species composition from the saline sea towards land and larger freshwater influence. Among the most productive habitats in the coastal zone are plant communities consisting of algae and angiosperms (e.g. Mann 2000). These plant habitats harbour significant animal communities due to a substantial primary production and complexity in habitats.

Shallow semi-enclosed bays with abundant vegetation are common habitats along the Swedish and Finnish Baltic Sea coastlines. These wave-protected brackish habitats are naturally nutrient-rich and compared to more open coastal habitats they have a rapid warming of the water volume during spring. These features result in a productive habitat with a rich plant community of algae and angiosperms (Munsterhjelm 1997). The unique characters of the shallow bays make it a suitable habitat for reproduction of many coastal fish species (Karås and Hudd 1993; Karås 1999), and as shallow vegetated lakes (e.g. Hansson et al. 2010), the bays are important breeding areas for many waterfowl species.

The northern Baltic seascape is constantly changing due to a post-glacial land uplift (maximum 10 mm year\(^{-1}\); Påsse and Andersson 2005; Argus and Peltier 2010). Bays are continuously formed and are often gradually isolated from the sea due to formation of shallow thresholds; a process enhanced by sedimentation (Åse 1994; Berglund et al. 2009). With increased isolation, wave exposure from the sea and water exchange with the sea decreases (Munsterhjelm 1997), while the spring water temperature in the bays increases (Snickars et al. 2009; Scheinin and Mattila 2010). In addition, fresh-
water influence often increases with increased bay isolation, depending also on factors such as the size and characteristics of the catchment area. The altered hydrological conditions results in a change in the accumulation of organic particles and thereby the bottom substratum (Munsterhjelm 1997).

Altered morphometric and hydrological conditions of the bays are reflected in a succession of aquatic plants, in which the dominant form of vegetation changes with bay isolation, as described by Munsterhjelm (1997) and later tested by Appelgren and Mattila (2005) for the northern Baltic Proper. Munsterhjelm (1997) described the morphometric development of bays and the vegetation succession in a conceptual model with different stages (Table 1; Fig. 1). The development time from the first to the last stage depends on factors such as the land-uplift rate, local topography, drainage area, bay area and ice cover (Munsterhjelm 1997). The process can be rapid within a century or take centuries.

The fish community also changes with the gradient in bay isolation. The juvenile fish assemblages in the northern Baltic Proper briefly change from a stickleback-dominated community in the most open bays to a community dominated by warm-water-spawning fish species such as perch in more isolated bays, and roach and bream in the most isolated bays (Snickars et al. 2009). In addition, the zooplankton community has been documented to differ between open and enclosed bays in the northern Baltic Proper (Scheinin and Mattila 2010). Studies of the macroinvertebrate community in relation to bay isolation have not been conducted until now (paper I and II).

Table 1. Definition of four morphometric stages of Baltic Sea land-uplift bays according to Munsterhjelm (1997).

<table>
<thead>
<tr>
<th>Bay isolation stage</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile flad</td>
<td>A transitional stage between more open water and a flad.</td>
</tr>
<tr>
<td>Flad</td>
<td>A shallow, clearly delimited minor water body situated along the coast or in the archipelago connected to the sea by one or just a few threshold openings.</td>
</tr>
<tr>
<td>Glo-flad</td>
<td>A transitional stage between a flad and a glo, with overgrown threshold openings but with an almost continuous contact with the surrounding waters through reeds in the openings.</td>
</tr>
<tr>
<td>Glo</td>
<td>A similar water basin as the flad, but with openings that due to land uplift have risen above the sea water level. This leads to only occasional contact with the sea. (This stage is not examined in any of the papers in this thesis).</td>
</tr>
</tbody>
</table>
Fig. 1. Schematic illustration of benthic vegetation composition in the land-uplift induced bay isolation gradient, from open to isolated bay. Four morphometric stages are illustrated; juvenile flad, flad, glo-flad, and glo (based on Munsterhjelm 1997, data from paper I and II, and pers. obs.). The last stage, glo, is not included in any of the studies in this thesis.
The importance of aquatic plants

Large aquatic plants (macrophytes) are important habitat modifiers in littoral ecosystems as they reduce water circulation, wave exposure, resuspension of sediments (Gregg and Rose 1982; Madsen et al. 2001; Scheffer 2004) and provide habitat structure for epiphytic algae and plant-associated animals. The role of macrophytes for fauna communities has long been recognised (e.g. Moore 1915; Klugh 1926; Krecker 1939). On soft bottoms, macrophytes constitute significant three-dimensional physical structures above the sediment surface in an otherwise simply structured seascape. They are important for foraging, reproduction, predator avoidance and as a direct food resource for macroinvertebrates. Generally, animal abundance and species richness are considerably higher where macrophytes are present (e.g. Orth et al. 1984; Hemminga and Duarte 2000), as they increase the overall colonisable area and increase the structural complexity of the habitats. In addition, plant shape influences animal communities (e.g. Taniguchi et al. 2003; Warfe and Barmuta 2006). As early as 1939, Krecker noted that intricate plant structures harbour greater invertebrate abundance than does simple ones, which later have been confirmed in both marine (Hull 1997; Hauser et al. 2006) and freshwater (Jeffries 1993; Warfe and Barmuta 2006; Xie et al. 2006) ecosystems. However, the relationship is not always found (Cyr and Downing 1988; Cremona et al. 2008) and needs further exploration.

The recorded higher abundance and species number of animals found in complex versus simple macrophyte habitats (e.g. Jeffries 1993; Warfe and Barmuta 2006; Xie et al. 2006) have been suggested to depend on increased sheltering against predation (Warfe and Barmuta 2004), increased amounts of food in the form of accumulated detritus and epiphytic growth (Gregg and Rose 1982; Jeffries 1993; Warfe and Barmuta 2006), and an increase in the amount and range of exploitable microhabitats (McNott and Rypstra 2000; Willis et al. 2005).

Palatability of macrophytes can also affect macroinvertebrate distributions. Although macroinvertebrates’ consumption of fresh tissue of vascular plants and charophytes often have been considered low in relation to the consumption of epiphytic micro- and macroalgae, there are several examples of substantial herbivory by macroinvertebrates on large aquatic plants (review in Newman 1991; Kornijów 1996). For example, the Baltic Sea crustaceans *Idotea balthica* (Isopoda) and *Gammarus oceanicus* (Amphipoda), which both have broad feeding ecology, are known to feed on large aquatic plants. *Idotea balthica* has been observed to graze both on *Potamogeton pectinatus* (Boström and Mattila 2005) and *Chara* spp. (Kotta et al. 2004) in addition to *Fucus vesiculosus* and epiphytes (Jormalainen et al. 2001; Goeker and Käll 2003; Orav-Kotta and Kotta 2004), while *Gammarus oceanicus* has been
recorded to consume *Chara* spp. (Kotta et al. 2004) in addition to epiphytes (Goecker and Käll 2003). Also herbivorous insects in the Baltic Sea are known to feed on large aquatic plants. For example, the trichopteran larvae *Limnephilus marmoratus* has been reported to feed both on vascular plants and *F. vesiculosus*, apart from epiphytes (Haage 1971). Several insect species are specialised on host plants in freshwaters (McGaha 1952; Newman 1991; Sheldon and Creed 1995; Cronin et al. 1999), as in the case of the beetle *Eubrychius velutus* found in the Baltic Sea, which feeds and completes all its life stages on *Myriophyllum* (Newman et al. 2009), and species of the genus *Haliplus*, which are specialised to feed on charophytes (Holmen 1987; Schubert and Blindow 2003). In addition to fresh macrophyte tissue, decomposing macrophytes are a significant food resource for macroinvertebrates (Verhoeven 1980; Menéndez and Comín 1990; Kornijów et al. 1995; Kotta et al. 2004).

The role of macrophytes for macroinvertebrates in shallow Baltic Sea bays has been little studied. Hence there is a need to examine relationships between the macrophyte and the macroinvertebrate community, and to evaluate whether macrophyte species differ in their function as habitat, related to characteristics such as plant structure, palatability, and epiphytic load (*paper III* and *IV*, and result section in this thesis).
Stable isotope analysis and food resource utilization

Changes in abundance and species composition may alter feeding ecology and trophic relationships of consumers in an ecosystem (Fry 2006; Fox et al. 2009). The changed species composition of aquatic plants along the bay isolation gradient (Munsterhjelm 1997) represents a changed resource base for primary consumers, and these consumers may change diet when the composition of primary producers change. Apart from changes in internal primary production, the relative importance of allochtonous carbon from terrestrial sources may increase with increased bay isolation as the inflow from land runoff in relation to seawater inflow can increase. Terrestrial input can provide a considerable addition of organic material to coastal food webs (Chanton and Lewis 2002; Attrill et al. 2009), but its role in shallow semi-enclosed bays in the Baltic Sea has not been investigated.

Stable isotope ratios have frequently been used to study the often complex food webs in coastal lagoons and estuaries, with a large diversity of potential food sources (e.g. Chanton and Lewis 2002; Fry 2006 and references therein; Attrill et al. 2009; Fox et al. 2009). The stable isotope ratios of carbon and nitrogen of primary producers are affected by their habitat, their carbon and nitrogen source, their biochemical structure and the photosynthetic process. The stable isotope ratios typically differ clearly between terrestrial and aquatic primary producers and between taxonomic distinct groups of aquatic primary producers (reviewed in Peterson 1999; Fry 2006). The stable isotope ratios of consumers reflect the stable isotope composition of food sources with some predictable change due to isotopic fractionation (Fry 2006). Stable isotope analyses can therefore be used to estimate the relative importance of primary producers with different isotopic signals for consumers (e.g. Moncreiff and Sullivan 2001; Chanton and Lewis 2002; Fry 2006 and references therein), and to test for spatial and temporal variability in resource utilization and trophic position of the consumers (Fox et al. 2009; Nordström et al. 2009). In this thesis, stable isotope analysis was conducted to examine the role of different food resources for macroinvertebrates and whether the utilization of food resources changes with level of bay isolation (paper II).
Anthropogenic influences

One of the most important anthropogenic factors inducing changes in the biota of coastal zones is nutrient enrichment resulting in a set of eutrophication effects (Heip 1995; Schramm and Nienhuis 1996; Cloern 2001; Zaldívar et al. 2008). In the eutrophication process, slow-growing and perennial plant species have decreased, while fast-growing, mainly annual planktic and benthic algal species, but also some angiosperms, have increased. Among angiosperms, species that are able to concentrate much of their photoreceptive biomass near the surface are more capable to compete for light from fast-growing algae in eutrophied conditions (Barko and Smart 1981; Boston et al. 1989). High surface area to volume ratio through thin and/or dissected leaves is also common among plants that can adapt to low light conditions (Sculthorpe 1967), and this growth form is also beneficial for efficient and competitive uptake of carbon and nutrients in the water (Boston et al. 1989).

In sheltered soft-bottom areas of the Baltic Sea charophytes, such as *Chara tomentosa* and *Chara baltica*, have generally decreased during the last decades and in some areas been replaced by angiosperms more tolerant to low light conditions, such as *Myriophyllum spicatum*, *Potamogeton pectinatus* and *Potamogeton perfoliatus* (Wallentinus 1979; Blindow 2000; Schubert and Blindow 2003; Munsterhjelm 2005).

Fast-growing ephemeral algae can exhibit excessive growth in shallow soft-bottom bays, as reported from the Swedish west coast by Pihl et al. (1996; 1999). In addition, ephemeral algae on hard substrates in wave exposed areas can become detached from their substratum by wave activity, forming drifting mats that are often transported to shallow soft-bottom bays (Bonsdorff 1992; Berglund et al. 2003) where they may become trapped and entangled in larger plants (Boström and Bonsdorff 2000). These ephemeral algae can affect the performance of more slow-growing plant species due to competition for light and nutrients. In addition to effects of increased nutrient levels, overfishing is believed to be a mechanism for the increased load of ephemeral algae in the Baltic Sea through a multi-trophic cascade resulting in decreased grazing pressure on the algae (e.g. Eriksson et al. 2009).

Dredging and boat traffic are other factors affecting the vegetation community in shallow bays. Such human activities can result in uprooting and fragmentation of plants, increased water circulation, resuspension of sediments and nutrients and thereby increased turbidity. Boating activities have been suggested to negatively affect species such as *C. tomentosa*, while species such as *M. spicatum*, *Ceratophyllum demersum* and *P. perfoliatus* seems to have increased due to the influence of boating activities (Eriksson et al. 2004). In agreement, Henricson et al. (2006) experimentally showed that *C. tomentosa* is susceptible to water turbulence, turbidity and sedimentation of
particles on the plant, and Appelgren and Mattila (2005) documented that *C. tomentosa* was absent in bays subjected to severe anthropogenic influences.

In recent decades, a number of shallow soft-bottom areas in the Baltic Sea have been set aside for nature protection due to the implementation of the EU Habitat Directive (European Parliament 2000). To point out valuable habitats for conservation, mapping and evaluations of shallow coastal soft-bottom areas in the northern Baltic Sea have been conducted since the late 1990s (e.g. Wallström and Persson 1997; Andersson 2000; Johansson and Persson 2005). Monitoring of shallow coastal soft-bottom areas in the Baltic Sea has mainly focused on the submerged vegetation. The plant community is used as an indicator of ecological status (e.g. Wallström and Persson 1997; Andersson 2000; Johansson and Persson 2005; Kautsky 2008; Steinhardt et al. 2009), and high species number or high cover and depth distribution of charophytes have been suggested as indicators of conditions of low anthropogenic influence (Andersson 2000; Appelgren and Mattila 2005; Selig et al. 2007; Steinhardt et al. 2009). High cover of other taxa, such as *M. spicatum*, *C. demersum* and *Potamogeton* spp. have been suggested as indicators of low ecological status, since they are more tolerant to anthropogenic influences (Selig et al. 2007; Steinhardt et al. 2009).

Knowledge about the relationship between the plants and other biotic units in the semi-enclosed bays of the Baltic Sea is poor. Vegetation shifts are likely to affect macroinvertebrate communities, as macrophyte species harbour different faunal assemblages (Scheffer et al. 1984; Cyr and Downing 1988; Xie et al. 2006) due to their differences in morphological and chemical traits. Accordingly, there is a need to study the structure and function of the ecosystem in more detail to extend the knowledge of these habitats. Differences in the macroinvertebrate community needs to be studied in relation to the natural gradient in bay isolation, and between different macrophyte species, to provide a baseline for management of these habitats and for further studies of anthropogenic influences on this system.
Aim of the thesis

The aim of this thesis was to examine the macroinvertebrate community in shallow land-uplift bays of the Baltic Sea in relation both to the isolation gradient of bays from the sea and to vegetation in the bays. The studies were conducted on two different scales; between bays which differ in isolation from the sea (paper I and II), and between macrophyte species within the bays (Paper II and III). The following questions were addressed:

a) Does the macroinvertebrate community change in relation to the bay isolation gradient? How does it change? Is the change related to changes in the macrophyte community? Does the resource utilization by macroinvertebrates, and hence the food-web structure, change in relation to the bay isolation gradient?

b) Does the distribution of macroinvertebrates differ between macrophyte species within bays? Are such distribution differences due to differences in plant morphology, epiphyte load, plant palatability, and active habitat choices by macroinvertebrates?
Methods

Study area

The study was conducted in the northern Baltic Proper and the southern Bothnian Sea. Macroinvertebrates and macrophytes were sampled in sheltered shallow bays in four different regions within this latitudinal gradient (*Paper I* and *II*; Fig. 2). Samples were collected in late July or early August 2003, 2005 and 2007, respectively. The sampled bays were chosen to include a morphometric isolation gradient from open bays and sounds to enclosed isolated bays. Sampling and experiments were also conducted in sheltered areas near the Askö Laboratory in July 2005–2008 (*Paper III* and *IV*; Fig. 2). All sampled areas included in the study were subjected to a limited degree of local anthropogenic pressure (e.g. from agriculture, human settlement and boating activities).

*Fig. 2.* Map of the study area in the Baltic Sea. Sampled bays are marked with solid circles (*paper I*) and triangles (*paper II*). For clarification, number of sampled bays in the different geographic regions is given in brackets. Sampling and experiments in *paper III* and *IV* were conducted near the Askö Laboratory, which is marked with a solid cross.
Field sampling

Plant-associated macroinvertebrates (≥1 mm) were sampled in 18 bays to examine the effect of bay isolation on the macroinvertebrate community (biomass, abundance, number of taxa [lowest taxonomic level possible – species, genus or family] and taxon composition). Macroinvertebrates, together with macrophytes, were sampled by a free diver using a frame (0.20 × 0.20 or 0.17 × 0.17 m) with a mesh-bag (1-mm mesh) attached on top and large shears attached underneath. The sampler was pulled over a stand of macrophytes, which were cut off just below the sediment surface or just above hard bottom substrates. In each bay a total of 9 samples were collected by a stratified sampling to include much of the potential variation within bays. The 9 samples were collected along 3 transects located in the inner, middle, and outer parts of the bays. Each transect was divided into three depth intervals relative to the maximum depth of the bays; a sample was taken in a randomly selected vegetation patch in each interval. Twelve bays sampled in 2003 (0.20 × 0.20-m frame) and 2005 (0.17 × 0.17-m frame) were included in paper I and 6 other bays sampled in 2007 (0.17 × 0.17-m frame) were included in paper II. In the thesis these two data-sets are analysed together to give a general description of differences in the macroinvertebrate community between three morphometric stages along the bay isolation gradient.

To investigate distribution differences of macroinvertebrates between macrophytes within bays, samples with a dominance of Chara spp., Myriophyllum spicatum or Potamogeton pectinatus were selected for analysis (paper IV) from the data collected in paper I and II. One sample of each macrophyte per bay was selected from 6 bays, and bay was used as a blocking factor in the analysis. Additional collection of smaller samples of the four species Chara baltica, M. spicatum, P. pectinatus and Potamogeton perfoliatus was done in a small area (0.5 ha), so that the species compared were collected under as similar abiotic conditions as possible (paper III and IV). Differences in macroinvertebrate distributions were compared between C. baltica, M. spicatum and P. perfoliatus in paper III, while in paper IV macroinvertebrates distributions were compared between C. baltica, M. spicatum and P. pectinatus. Sampling was done using a plastic bag and scissors. One shoot was collected per sample by pulling the bag over a randomly selected shoot, which was cut just above the sediment surface. Samples were collected in July in two sheltered bays adjacent to the Askö Laboratory. Samples of all four macrophyte species were collected in both bays in 2007, while sampling of the three species C. baltica, M. spicatum and P. pectinatus was repeated yearly for four years (2005–2008) in one of the bays.
In addition to macroinvertebrates, macroscopic epiphytic algae (hereafter ‘epiphytes’) were identified and weighed at all sampling occasions as they can be important for macroinvertebrate distributions by increasing shelter (Hall and Bell 1988; Martin-Smith 1993) and as a food resource (Bologna and Heck 1999). Since also microscopic epiphytic algae (hereafter ‘microepiphytes’) can be important food resources for invertebrates (Skoog 1978; Sommer 1997; Råberg and Kautsky 2008), I sampled microepiphytes in 2007. This was done by shaking a sampled macrophyte shoot in a 1-L glass bottle (1 min) with 0.5 L filtered seawater (0.22 µm) and counting cells in a subsample preserved with Lugol’s solution (inverted-microscope method; Utermöhl 1931). Additionally, in 2008, a microepiphyte filtrate was filtered onto a Whatman GF/F filter (Whatman, Maidston, UK) for analysis of carbon to nitrogen ratio, as a measure of microepiphytic food quality (including both microscopic autotrophs and heterotrophs). The quantification of microepiphytes is not included in the papers, but is presented in the result section of this thesis.
Stable isotope analysis

Stable isotope analysis was conducted to examine the role of different food resources for macroinvertebrates and whether the utilization of food resources changes with level of bay isolation (paper II). I selected the numerically most dominant taxa of macroinvertebrates and macrophytes occurring in all bays sampled in 2007 for the analysis (6 bays). To achieve a more detailed picture of the food web, I additionally sampled zooplankton, juvenile fishes, particulate and sedimentary organic matter, terrestrial plants, and the emergent reed *Phragmites australis* for stable isotope analysis. The stable isotope ratios of carbon and nitrogen were measured at the UC Davis Stable Isotope Facility (University of California, Davis, CA). Possible shifts in utilization of carbon originating from epiphytes and periphyton in relation to three macrophytes was examined for four macroinvertebrates (*Gammarus* spp., Chironomidae, *Theodoxus fluviatilis* and *Radix balthica*) using a diet mixing model.
Experiments

A colonization experiment was carried out in the field in 2007 (paper III). This experiment allowed me to examine colonization of macrophytes exposed to the same abiotic and historic pre-sampling conditions. Macroinvertebrate abundance, number of taxa and taxon composition was examined on three macrophyte species; *Chara baltica*, *Myriophyllum spicatum*, and *Potamogeton perfoliatus*. In addition, three artificial macrophytes resembling the natural macrophytes in morphology were used to isolate the effect of structure from those of other biotic characteristics of the natural plants. The experiment was set up according to a randomized complete block design. A total of 96 samples in 16 blocks were placed in two bays, eight per bay, by SCUBA diving. The macrophytes were left for two weeks in the field to be colonized by fauna.

Active habitat choices by macroinvertebrates between macrophytes were examined in a laboratory experiment (paper IV). This allowed me to study short time active habitat choices by macroinvertebrates between macrophyte species in a controlled abiotic environment, also without effects of predators and epiphytes. I examined the habitat choice of four faunal species, *Gammarus oceanicus*, *Idotea chelipes*, *Theodoxus fluviatilis*, and *Bithynia tentaculata* (Fig. 3), between the three macrophytes *C. baltica*, *M. spicatum*, and *Potamogeton pectinatus*. To further investigate the effect of plant structural complexity on the invertebrate distribution, I explored whether *G. oceanicus* and *T. fluviatilis* actively choose structurally complex over simple artificial plastic macrophytes. High structural complexity was defined as high shoot perimeter and number of branches per shoot surface area. The habitat choices were compared in pairs, and were replicated 9 times with natural macrophytes (2006) and 16 times with artificial macrophytes (2007).

A feeding choice experiment was conducted to study if feeding rate of invertebrates between macrophytes differed. The experiment enabled me to examine whether differences in feeding rates could partly explain the patterns observed in macroinvertebrate abundance in the field and habitat choice in the experiment. Feeding choices of the two crustacean taxa *I. chelipes* and *Gammarus* spp. were analysed between the macrophytes *C. baltica*, *M. spicatum* and *P. pectinatus*, and an additional epiphytic green algae, *Cladophora glomerata*. The feeding rate was compared in pair-wise sets of the macrophytes in 800 mL plastic containers placed under a jetty in a sheltered sound. Containers were separated with a fine mesh (250 μm) into one section containing both macrophytes and the grazer and one section serving as a control with only macrophytes. Five individuals of the crustaceans were placed in each experimental container and allowed to feed for 72 hours in two separate experiments (*I. chelipes* in 2006, and *Gammarus* spp. in 2008). The feeding
trials were replicated 10 times for each of the crustacean taxa. The experiment is not included in the papers, but is presented in the result section of this thesis.

Fig. 3. Macroinvertebrates used in the habitat choice experiment (paper IV): (a) Gammarus sp., (b) Idotea chelipes, (c) Theodoxus fluviatilis, and (d) Bithynia tentaculata.
Results and discussion

Effects of bay isolation on the macroinvertebrate community

Results from both *paper I* and *II* showed that the macroinvertebrate community changes with the gradient in bay isolation. In *paper I*, water exchange of the bays (estimated by simple topographic openness) was used as a proxy for bay isolation. I found a hierarchical relationship between water exchange, number of macrophyte taxa and macroinvertebrate biomass and taxon number. Decreased biomass and number of taxa of macroinvertebrates were related to decreased number of macrophyte taxa, which in turn was related to decreased water exchange. In *paper II*, bay isolation was estimated by means of a combined gradient of water exchange and wave exposure. Here, macroinvertebrate biomass tended to decrease with increased bay isolation; however the most open bay had a low macroinvertebrate biomass, thereby partly contrasting the findings in *paper I*. In both studies the macroinvertebrate composition was found to change with increased bay isolation. The change in taxon composition differed to some extent between the two studies, but largely I found the faunal assemblage to change from a community dominated by gastropods and marine bivalves in open bays, to a community with larger proportions of freshwater insect taxa in isolated bays.

In Fig. 4 (p 29), I combined data from both studies and explored how the macroinvertebrate community differed between three morphometric stages along the bay isolation gradient. The taxon density decreased from about 30 taxa per bay or 13 taxa per sample in the most open bays (juvenile flads), to approximately 17 taxa per bay or 6 taxa per sample in the most isolated bays (glo-flads) (Fig. 4a). In addition, macroinvertebrate biomass was higher in the most open bays than in more isolated bays (Fig. 4b), and similar result was found for macroinvertebrate abundance. The results illustrate an impoverishment of the macroinvertebrate community with increased bay isolation. The number of macroinvertebrate species is known to increase from the open Baltic Sea towards main land due to a mixture of marine and freshwater species, variability of substrates and increased complexity of habitats.
and the number of taxa was indeed found to be high in open bays. However, my results show that as bays become more isolated from the sea, the macroinvertebrate taxon number and biomass decreases.

Species that decreased in biomass with increased bay isolation were for example the marine bivalves *Mya arenaria*, *Mytilus edulis*, *Macoma balthica*, and *Parvicardium hauniense*, and the marine crustaceans *Corophium volutator*, *Idotea balthica*, *Idotea chelipes*, *Jaera albibrons*, and *Palaemon adspersus*. Some of these species were almost exclusively found in juvenile flads, while others such as *M. balthica*, *P. hauniense*, and *I. chelipes* occurred also in flads and to a smaller extent in glo-flads. Most gastropods were found all along the bay isolation gradient and were variable in occurrence. However, all common gastropod taxa (*Theodoxus fluviatilis*, *Bithynia tentaculata*, *Radix balthica*, *Potamopyrgus antipodarum*, and *Hydrobia* spp.) decreased in biomass with increased bay isolation. Some taxa, such as the freshwater isopod *Asellus aquaticus* and the most abundant zygopteran families (Libellulidae and Coenagrionidae) had the highest biomass in flads. The most abundant anisopteran family (Corduliidae) and the trichopteran families Limnephilidae and Polycentropodidae were found in highest biomass in glo-flads. In Fig. 4c, the general change in taxon composition from dominance by bivalves and gastropods to a community with larger proportions of insects is illustrated.

The lower number of macroinvertebrate taxa found in isolated bays compared to more open bays could potentially be an artefact of lower taxonomic resolution of the taxa found here (i.e. identification to insect family rather than to species). However, in cases where taxa were identified to a lower taxonomic level, mainly one genus and one or a few species were identified per family, sample, and bay (*paper I*). Therefore the result of decreased taxon number with increased bay isolation is probably valid also at a species level, but should be confirmed by better taxonomic expertise and sampling (e.g. avoiding freezing for sample preservation as it damage the animals).
Fig. 4. (Opposite page) Mean (±CI95) macroinvertebrate and macrophyte (a) taxon density, (b) biomass, and (c) taxon group composition (biomass proportions) in different morphometric stages of shallow sheltered Baltic Sea bays; juvenile flads (JF), flads (F) and glo-flads (GF). Figures are based on data from both paper I and II; 108 samples from 18 bays (7 JF, 6 F, 5 GF). Differences in taxon density and biomass between morphometric stages were tested with mixed effects models with bay as blocking factor. Pair-wise comparisons were made with Tukkey-tests ($p<0.05$), and significant differences are indicated by vertical lines that differ in indentation. Macrophytes included macroscopic epiphytes, and macrophyte taxon density per bay was calculated from both biomass samples and visual vegetation surveys conducted using the method by Persson and Johansson (2007). Mean proportions of taxonomic groups were not examined with statistical tests, but see paper I and paper II for multivariate tests of taxon composition in relation to bay isolation.
Several factors related to the bay isolation process could cause the observed changes in macroinvertebrate community composition with level of bay isolation. Occurrence of macroinvertebrates will be affected by their dispersal limits, tolerance to environmental factors and interactions with other organisms. For example, a small opening area and limited water exchange with the open sea in isolated bays may reduce colonization rate. Although many species inhabiting the bays are highly mobile (e.g. crustaceans and gastropods), narrow openings of the most isolated bays may reduce immigration rates of invertebrates from the sea. This will be even more evident in the case of gloes (not included in the thesis) where the former opening has completely emerged above the sea level. Aquatic macroinvertebrates have long been regarded as readily dispersed by waterfowl (review in Figuerola and Green 2002; Green and Figuerola 2005). However, the actual magnitude and importance of dispersal, in contrast to the potential dispersal, of aquatic invertebrates by such vectors has been questioned (Bohonak and Jenkins 2003). Therefore, small threshold openings towards the sea may constitute a significant barrier for colonizers from surrounding waters. This will be more prominent for invertebrates with passive dispersal. In a recent study of a Baltic Sea seagrass habitat dominated by *Zostera marina*, settlement of planktophytic invertebrate larvae with long-distance dispersal (bivalves) was higher outside or along the edge of the seagrass meadow, possibly as a result of a settlement shadow and a dispersal barrier caused by reduced water movements in the seagrass bed (Boström et al. 2010). Similarly, the supply of bivalve larvae to sheltered bays may decrease with increased bay isolation due to decreased opening area towards the sea and reedbelts in the opening. Limits in distribution of these species may partly explain their decrease with increased bay isolation. Distance to freshwater can, in addition to direct freshwater inflow, affect the distribution of freshwater taxa. A large distance to freshwater can represent a dispersal barrier, especially for taxa lacking airborne adult stages. Such a barrier will, however, not be directly related to bay isolation, but rather to location of bays in the landscape.

Decreased water movements in isolated bays can further hamper permanent establishment of filtering collectors such as bivalves, since they are known to be negatively affected by very low water velocity (Lenihan et al. 1996; Wildish and Kristmanson 1997) as they benefit from a constant flow of food particles to filter out from the water column.

Mean salinity was recorded to decrease with increased bay isolation in paper I; from about 6.3 psu in open bays to 4.7 psu in more isolated bays and to 2.1 psu in the most extreme case (comparison within one region [region 4 in paper I]). Differences within this salinity range may prevent permanent establishment of some Baltic Sea invertebrates of marine origin in isolated bays, such as *P. adspersus* and *I. balthica*, which have an approximate lower salinity tolerance of 5 psu (Barnes 1994; BACC Author Team 2008). Simi-
larly, high salinity may prevent permanent establishment of some freshwater macroinvertebrates in the most open bays. The mean proportion (in biomass) of macroinvertebrates of marine origin decreased from 55% in juvenile flads to 32% in flads and 29% in glo-flads. However, mean salinity does not always decrease with increased bay isolation, as was found for the studied bays in paper II. Since the taxon composition was found to change in approximately a similar manner in both studies (paper I and II), decreased salinity with increased bay isolation cannot alone be the factor responsible for the observed changes in the macroinvertebrate community.

Salinity changes not only spatially, but also temporarily, and such variations in salinity may affect the macroinvertebrate community composition. Salinity in enclosed bays can fluctuate more than in open bays as the relative influence of precipitation and evaporation in relation to seawater influence increases. During snow melting in spring, salinity can become lower in isolated bays compared to more open areas with higher water exchange with the sea (Scheinin and Mattila 2010; J. Persson and G. Johansson, unpublished data). In summer, during shifts between high-precipitation and dry periods, salinity can change dramatically within weeks in very isolated bays, and can even become higher than that of the seawater outside bays due to evaporation (from 3 to 7 psu, pers. obs.; J. Persson and G. Johansson, unpublished data). Larger fluctuations in dissolved oxygen concentration (DO) and pH in isolated bays are also likely. In stagnant shallow vegetated waters, DO and pH often follow the photosynthetic and respiration cycle of the primary producers (e.g. Wetzel 2001; Brönmark and Hansson 2005). During daytime and photosynthesis, DO and pH are high, while at night and early morning DO and pH can be low due to respiration. High respiration rates of consumers can further lower DO, and extensive respiration rates during degradation of organic material can lead to anoxic conditions (Brönmark and Hansson 2005) and formation of toxic hydrogen sulphide (H₂S) (Wetzel 2001). Anoxic conditions are probably more frequent in more isolated bays due to a combination of organic-rich sediments, low water circulation and water exchange with surrounding waters. During winter, when an ice cover leads to decreased water mixing and gas exchange between water and air, and the ice together with a snow layer hamper photosynthetic activity by reducing light, the chance of anoxic conditions may increase. Low water exchange and often higher surface area to depth ratio in isolated bays results in a water body that responds more rapidly in temperature to changed air temperature and solar radiation than more open bays with higher water exchange with the sea. Sheltered conditions and an often shallower depth in isolated bays may further result in more frequent bottom freezing during winter. The larger fluctuations in abiotic conditions results in a harsher environment with high and frequent stress and disturbance. High such habitat harshness has long been recognized to result in decreased local biodiversity (e.g. Connell 1978; Petraitis et al. 1989; Rosenzweig 1995; Statzner and Moss 2004). The transi-
tion from more stable or intermediately harsh conditions in the most open bays to more variable and harsh conditions in isolated bays can partly explain the decrease in both macroinvertebrate and macrophyte biomass and taxon number with increased bay isolation. However, as there is a seasonal variation in the abiotic conditions in the bays, isolated bays may temporarily constitute an advantageous and less harsh habitat for e.g. juvenile warm-water-spawning fish species (Snickars et al. 2009). The seasonal and diurnal fluctuations in environmental conditions in the bays need further exploration by empirical data.

The macroinvertebrate community can also respond to changes in the macrophyte composition that accompany the morphometric bay isolation. The macrophyte community can affect the faunal community in a variety of ways. Macrophytes provide habitat structure for macroinvertebrates, facilitating shelter against predation and niche separation. They also constitute an energy resource for consumers. As macrophytes differ in habitat and food quality (paper III, IV, and results presented later in this thesis), changes in taxon composition of macrophytes with bay isolation can directly affect the faunal community as habitat structure and food resources are altered. The observed relationship between decreased macroinvertebrate taxon number and biomass with decreased macrophyte taxon number (paper I) may arise from the larger variety of structural and chemical plant properties in the diverse plant community, increasing overall niche space for invertebrates in such a habitat. The higher biomass of macrophytes in open bays also means that the colonisable area for plant-associated invertebrates was larger here, which partly can explain the higher macroinvertebrate biomass in more open compared to isolated bays.

Plant habitat permanency may also differ between bays of different degree of isolation from the sea, which can further affect the macroinvertebrate community. In isolated bays, where bottom freezing and anoxia probably is more frequent, the annual species *Najas marina* is often abundant and perennial species tend to overwinter with vegetative, more stress-tolerant propagules (bulbills, tubers or roots), rather than as full grown plants (e.g. *Chara baltica*, *Chara tomentosa*, and *Potamogeton pectinatus*). In contrast, stands of perennial species such as *Fucus vesiculosus*, *Ruppia cirrhosa*, and *P. pectinatus* (at larger depths; Idestam-Almquist 1998) are more abundant in open bays during winter. In a study of habitat permanence in a Swedish lake, Hargely (1990) found that temporal plant habitats benefit fast colonisers, such as insects with high reproductive and dispersal rates due to e.g. airborne egg-laying females (Chironomidae), while permanent plant habitats benefits slower colonizers with lower reproductive rates and mobility, such as isopods (*Asellus aquaticus*) and amphipods (*Gammarus*).
The combination of potentially more frequent disturbance in isolated bays (both abiotic and biotic through temporal disappearance of plant habitats), and increased dispersal barrier for colonizers from the sea (through decreased openness), may contribute to explain the decrease of relatively slow colonisers (bivalves, gastropods, and crustaceans) and increased proportion of faster colonisers, with high dispersal rates due to airborne life stages (insects), with increased bay isolation.

Changes in food resource composition and availability can further explain changes in the macroinvertebrate community. Species that can change resource utilization are likely more able to cope with the changed composition of vegetation accompanying the morphometric bay isolation. Results from the stable isotope analysis suggested epiphytes or periphyton as the major carbon resources for several consumers (paper II). Lower proportion of epiphytes in more isolated bays can explain the overall decrease in herbivorous gastropods and crustaceans feeding on these primary producers. Species that persists in more isolated bays must to a larger degree rely on a utilization of either fresh or decomposed angiosperms or charophytes. Accordingly, the stable isotope analysis indicated that taxa such as R. baltica and Gammarus spp., which occurred throughout the isolation gradient (but with lower biomass in isolated bays), included as much as 20–40% of angiosperm and charophyte carbon in their diet (paper II). The analysis also indicated that the relative importance of carbon from epiphytes in relation to angiosperms and charophytes may decrease for other consumers with increased bay isolation (e.g. the insect Chironomidae and the gastropod T. fluviatilis; paper II).

Macroinvertebrates can also change trophic position due to shifts in resource availability (Jephson et al. 2008; Fox et al. 2009). However, the stable isotope analysis of nitrogen indicated no change in trophic positions of the examined macroinvertebrate taxa along the bay isolation gradient (paper II). Stable isotope ratios of filter feeders (zooplankton and P. hauniense) indicated a possible utilization of food resources of terrestrial origin. But the importance of this terrestrial energy did not increase with increased bay isolation as was hypothesised (paper II).

Top-down control of shallow Baltic Sea areas has been suggested by Eriksson et al. (2009; in conjunction with bottom-up processes). As the density of macroinvertebrate-feeding cyprinid fishes is higher in more isolated than open bays, predation pressure on invertebrates may be higher in such bays. This is another possibility explaining the decrease in macroinvertebrate biomass along the bay isolation gradient.

As mechanisms for the changed macroinvertebrate community composition with increased bay isolation was not specifically tested, the relative importance of the mentioned factors (and possibly others) needs to be further explored.
Distribution of macroinvertebrates between macrophyte species

The distribution of macroinvertebrates differed between the four macrophytes I examined in detail (paper III and IV). The distribution patterns were found to be mainly related to plant morphology. Highest macroinvertebrate abundance and biomass was recorded on the most morphologically complex plant, Myriophyllum spicatum, and lowest macroinvertebrate abundance and biomass on the simplest plant, Potamogeton perfoliatus (paper III). Higher abundance was also recorded on M. spicatum than on the simpler structured Chara baltica and Potamogeton pectinatus (paper IV).

To compare the abundance between all four species of macrophytes included in paper III and IV, I combined the data from both studies and examined differences in macroinvertebrate abundance and biomass with bay and year as blocking factors (linear mixed effects model). In this way, general differences in the macroinvertebrate response variables between the macrophyte species could be examined without analysing specific effects due to variations between bays and years. To clearly illustrate the results, mean residual macroinvertebrate abundance per bay and year on the different macrophytes is presented in Fig. 5. The result shows a decrease in macroinvertebrate abundance with decreased morphological complexity of the macrophytes. The most complexly structured plant, M. spicatum, harboured both higher macroinvertebrate abundance and biomass than the two macrophytes with simplest structure ($p<0.01$).

This result is in accordance with several previous studies in other aquatic ecosystems, which have reported higher invertebrate abundance in structurally complex macrophyte habitats than in structurally simpler macrophyte habitats (McAbendroth et al. 2005; Hauser et al. 2006; Xie et al. 2006; Warfe et al. 2008). Increased invertebrate abundance with greater habitat complexity can depend on an increase of the amount and range of exploitable microhabitats (McNett and Rypstra 2000; Willis et al. 2005). Complexly structured plant habitats can facilitate coexistence of species and individuals through niche partitioning, as resources and microhabitats can be used in a greater number and variety of ways in complex than in simple structures. In addition, complex habitats can facilitate shelter from both hydrological disturbance (Gregg and Rose 1982) and predation (Warfe and Barmuta 2004).

In paper III, macroinvertebrate taxon richness was compared between the examined plants. Since the number of taxa recorded in a sample often increases with greater number of individuals in a sample (Gotelli and Colwell 2001), taxon richness (number of taxa per individuals) was computed from the original taxon density data (number of taxa per sample). Although ma-
croinvertebrate taxon density followed that of abundance and was higher on *M. spicatum* than on the other macrophytes, taxon richness was not related to complexity. The taxon richness was found to be higher on the simplest plant, *P. perfoliatus*, compared to the more structurally complex plants *C. baltica* and *M. spicatum* in one of the examined bays but not in the other. In comparison to *P. pectinatus*, which was not included in paper III, *P. perfoliatus* also harboured higher macroinvertebrate taxon richness in one of the bays (*p*<0.01) but not the other. These results contradict previous findings of higher invertebrate taxon richness on more complexly structured plants (Taniguchi et al. 2003; Hauser et al. 2006; Warfe et al. 2008). Consequently, the results imply that the relationship between structural complexity of plants and taxon richness of invertebrates is itself complex and does not always respond as predicted. A numerical dominance of a few macroinvertebrate taxa on plants with high macroinvertebrate abundance, and a more even distribution of taxa on plants with low macroinvertebrate abundance, may partly explain the higher taxon richness found on *P. perfoliatus*.

![Fig. 5.](image)

**Fig. 5.** (a) Morphological complexity expressed as mean (±CI95) macrophyte shoot perimeter per area for the species *Myriophyllum spicatum* (M.spi), *Potamogeton pectinatus* (P.pec), *Chara baltica* (C.bal), and *Potamogeton perfoliatus* (P.per). (b) Mean (±CI95) macroinvertebrate abundance expressed as mean residual log_{10} abundance per bay and per year on the four examined macrophytes. In the analyses bay and year were used as blocking factors. Pair-wise comparisons were made with Tukey-test, and different letters indicate significant differences (*p*<0.05).
In the field colonization experiment (paper III), highest macroinvertebrate abundance and biomass was found on artificial *M. spicatum*, concurrent with what was found in the field samples. However, no difference in macroinvertebrate abundance was found between natural plants. In addition, the macroinvertebrate taxon richness displayed no consistent relationship with plant structural complexity. Plants in the colonization experiment may still have been in a colonization phase at the time of sampling, two weeks after being placed in the field. This possibility was supported by lower invertebrate densities on the plants in the colonization experiment versus on the plants in the field collection. Interactions between individuals and species may have been weaker in the more sparsely occupied plants in the colonization experiment than in the more densely occupied plants in the field collection. At low invertebrate density, the effect of habitat complexity on the invertebrate community may be less pronounced; explaining why I did not find higher invertebrate abundance and biomass on more complexly structured natural plants in the experiment.

In accordance with the field results, the habitat choice experiment (paper IV) indicated that the amphipod *Gammarus oceanicus* actively chose the complexly structured *M. spicatum* over the other macrophytes. Similar, but less clear results were found for the isopod *Idotea chelipes*. *Gammarus oceanicus* was also found to actively choose complex over simply structured artificial plants as a habitat, supporting that the animal distribution was driven by differences in morphological complexity between macrophyte species and that plant structure alone can serve as behavioural stimuli for some invertebrate taxa. In addition, a higher abundance of *G. oceanicus* was recorded on *C. baltica* than on *P. pectinatus*, partly contrasting the field results. The complex surface structure of *C. baltica* with bark cells (cortex cells) and spines could have attracted *G. oceanicus* and can explain its choice of this macrophyte over *P. pectinatus*, which has a comparatively smooth surface structure.

In addition, animals could be attracted by the palatability and nutritional content of plants. In the feeding choice experiment, *Gammarus* spp. was found to consume slightly more *C. baltica* than *P. pectinatus* (Fig. 6). Apart from differences in surface structure, this could explain the higher abundance of *G. oceanicus* on *C. baltica* than on *P. pectinatus* in the habitat choice experiment. No other difference in consumption rate of *Gammarus* spp. and *I. chelipes* was found between the examined macrophytes.
The distribution differences of animals between plants recorded in the field could also have been affected by epiphytes. The biomass of attached and loose-lying macroscopic epiphytic algae differed between the macrophyte species. Such algae were observed to drift into the bays and get entangled in the macrophytes (paper III). The simply structured \textit{P. perfoliatus} accumulated the lowest biomass of macroepiphytes of the plants examined. Lower biomass of epiphytes and detritus on structurally simple than on complex plants has been found previously in other aquatic ecosystems (Gregg and Rose 1982; Jeffries 1993; Taniguchi et al. 2003; Warfe and Barmuta 2006). As epiphytes can affect invertebrate distributions, plant morphology may indirectly affect invertebrate communities through differences in their capacity to trap and accumulate drifting plant material. I suggest that complex structured plants harbour higher invertebrate abundance partly because they accumulate more epiphytes and detritus. Positive effects of epiphytes on invertebrate abundance could be caused by the transport, via drifting algae, of animals to plants (Salovius et al. 2005), by increased shelter against predators from the additional structures of algae (Isaksson et al. 1994; Norkko 1998), and by increased food availability (Lauringson and Kotta 2006). In my feeding choice experiment, both \textit{Gammarus} spp. and \textit{I. chelipes} were found to consume considerably more of the epiphytic algae \textit{Cladophora glomerata} than \textit{Chara baltica, M. spicatum} and \textit{P. pectinatus} (Fig. 7). Additionally, the stable isotope analyses (paper II) indicated that epiphytes and periphyton are utilized as food to a larger degree than coarsely structured plants and algae. These results are in accordance with other studies of herbivorous invertebrates in the Baltic Sea (Goecker and Kåll 2003; Orav-Kotta and Kotta 2004; Boström and Mattila 2005).
Fig. 7. Feeding choice of (a) *Gammarus* spp. and (b) *Idotea chelipes* between pairs of the epiphyte *Cladophora glomerata* (C.glo) and the macrophytes *Myriophyllum spicatum* (M.spi), *Potamogeton pectinatus* (P.pec), and *Chara baltica* (C.bal). Bars show mean (±95% CI) change in wet weight of plants in grazed (G) and control (C) treatments for the three pair-wise comparisons. Stars indicate significant differences (*p*<0.01) in biomass difference between grazed and control pairs tested with Wilcoxon matched-pairs signed rank test.

Just as for macroscopic epiphytes, microscopic epiphytes were found in lowest abundance on *P. perfoliatus*, but no other difference in abundance was found between the macrophytes (Fig. 8). In addition, carbon to nitrogen ratio of the microepiphytes was examined as a measure of food quality for the macroinvertebrates, but no difference was found between the macrophytes (ANOVA, *p*>0.75). Similar microepiphyte abundance and quality on *M. spicatum*, *P. pectinatus*, and *C. baltica* may partly explain why the gastropod *T. fluviatilis* did not make any active habitat choice between these macrophytes in the laboratory experiment (*paper IV*). Microepiphytes were not selectively removed from the plants prior to the experiment and *T. fluviatilis* probably choose habitat based on abundance or quality of microepiphytes rather than based on structure of habitats. Complex structured macrophytes may not be of any higher habitat value to molluscs, as they partly rely on their shells for protection against predators. *Bithynia tentaculata* individuals were mainly found burrowed in the sand and hence no active habitat choice between macrophytes was recorded for this species.
In summary, macroinvertebrates were found to be more abundant on macrophytes with higher morphological complexity than on macrophytes with simpler morphology. The observed pattern could in part be related to increased amounts of food in the form of epiphytic algae and detritus on the more complex plants. Small crustaceans were found to actively choose complex structured macrophytes over simpler, supporting that the animal distribution was also partly driven by differences in morphological complexity between macrophyte species and that plant structure alone can attract some invertebrate taxa. The studied gastropods did, however, not make an active choice between the macrophytes. Variation in crustacean abundance not related to structural complexity could to some extent be related to differences in palatability between the plants.
Concluding remarks

Results from the studies summarized in this thesis show that the macroinvertebrate community differ both between bays that differ in isolation from the sea and between macrophyte habitats within bays. Firstly, macroinvertebrate density and number of taxa was found to decrease, and taxon composition to change, with increased bay isolation. Mechanisms for the observed changes in the faunal community were not studied specifically, but are, based on the results, suggested to be due to a combined effect of altered hydrological conditions and a changed macrophyte community. Results from the stable isotope analysis indicated epiphytes and periphyton as the major carbon resources for most of the examined consumers. A feeding choice experiment supported this finding. However, the relative importance of epiphytes and periphyton in relation to angiosperms and charophytes decreased for some consumers with increased bay isolation. Trophic position of the consumers did not change with increased bay isolation, and utilization of energy derived from terrestrial sources was not found to increase with increased bay isolation.

Secondly, macroinvertebrates were found to be more abundant on macrophytes with higher morphological complexity than on macrophytes with simpler morphology. The observed pattern could be due to increased shelter, increased niche separation, and increased amounts of food in the form of epiphytic algae and detritus for the invertebrates on the more complex plants. In an experiment, small crustaceans were found to actively choose complexly structured macrophytes over simpler, supporting that the animal distribution was at least partly driven by differences in morphological complexity between macrophyte species and that plant structure alone can attract some invertebrate taxa. The studied gastropods did, however, not make an active choice between the macrophytes.

My studies suggest that management of coastal habitats must be dynamic and consider the natural change in macroinvertebrate community accompanying the slow land-uplift-induced isolation of bays from the sea. Sheltered bays harbour both a high number of macroinvertebrate and macrophyte taxa, but the community is naturally impoverished as bays become more isolated from the sea. Both the macroinvertebrate and the macrophyte community change along the bay isolation gradient, and species peak in abundance at different stages along this gradient. In this context, areas for management
should be planned to incorporate different morphometric stages of bays, as well as more open archipelago areas, for long-term conservation of the habitat and its communities.

In addition, my results indicates that potential large-scale changes in the aquatic vegetation due to anthropogenic influences, such as nutrient enrichment and boating activities, could induce changes in the macroinvertebrate community as the plant habitat structure is altered. When structurally complex plant species such as *Myriophyllum spicatum* and *Ceratophyllum demersum*, tolerant to eutrophication and boating activities, increase and replace less complex plants, such as the more sensitive taxon *Chara*, increased macroinvertebrate abundance can be expected, potentially affecting higher trophic levels since invertebrates are important food for many fish and waterfowl species. Contrary, a change in vegetation composition from *Chara* spp. to the even less complex, but more tolerant, *Potamogeton perfoliatus* would instead result in lower macroinvertebrate abundance.
Acknowledgements

I am grateful to Pierre Drackner for illustrative artwork, Gustav Johansson, Matias Scheinin, Ove Eriksson and Ellen Schagerström for valuable comments on the text.
References


BACC Author Team (2008) Assessment of climate change for the Baltic Sea basin. Springer, Heidelberg, Germany


Boström C, Mattila J (2005) Effects of isopod grazing: an experimental comparison in temperate (Idotea balthica, Baltic Sea, Finland) and subtropical (Erichsonella attenuata, of Mexico, USA) ecosystems. Crustaceana 78: 185–200
Hull SL (1997) Seasonal changes in diversity and abundance of ostracods on four species of intertidal algae with differing structural complexity. Marine Ecology Progress Series 161: 71–82


Klugh AB (1926) The productivity of lakes. Quarterly review of Biology 1: 572–577


Lenihan HS, Peterson CH, Allen JM (1996) Does flow speed also have a direct effect on growth of active suspension-feeders: an experimental test on oysters. Limnology and Oceanography 41: 1359–1366


Munsterhjelm R (2005) Natural succession and human-induced changes in the soft-bottom macrovegetation of shallow brackish bays on the southern coast of Finland. Ph. D. Thesis. Faculty of Biosciences, University of Helsinki, Finland


Wallentinus I (1979) Environmental influences on benthic macrovegetation in the Trosa - Askö area, northern Baltic proper. II. The ecology of macroalgae and submersed phanerogams. Contributions from the Askö Laboratory 25, University of Stockholm, Sweden


Grunda vågskyddade vikar i Östersjön har en viktig ekologisk funktion. De hyser ett unikt växtsamhälle och är viktiga reproduktionslokaler för flera fisk- och fågelarter. Kunskapen om ryggradslösa djur i dessa miljöer är dock begränsad. Liksom andra kustmiljöer är de grunda havsvikarna utsatta för mänsklig påverkan genom exempelvis övergödning, båttrafik och muddring. För att förvalta dessa värdefulla miljöer är det viktigt att förstå de ekologiska processerna i vikarna, såsom konsekvenser av att vikarna förändras i form och sakta isoleras från havet genom den naturliga landhöjningen. Det är även viktigt att undersöka skillnader i livsmiljöer inom vikarna och förstå hur dessa kan förändras av mänsklig påverkan. I den här avhandlingen studeras samhället av ryggradslösa djur i grunda Östersjövikar relaterat både till vikens isoleringsgrad från havet och till undervattensvegetationen i vikarna.

Resultaten visade att biomassan och artantalet ryggradslösa djur minskar med den naturliga isoleringen av vikar från havet. Artsammansättningen förändrades från ett samhälle med dominans av musslor och snäckor till ett samhälle bestående av en större proportion insektslarver. Förändringen i djursamhället föreslås vara relaterat både till förändrade hydrologiska förhållanden samt ett förändrat växtsamhälle.

I en analys av stabila isotoper av kol och kväve visade det sig att påväxtorganismer, i form av trådformiga alger och mikroskopiska organismer, är de mest betydelsefulla energikällorna för flertalet av de ryggradslösa djuren i vikarna. Ett födovalsexperiment bekräftade detta resultat. Proportionen påväxtorganismer som föda, i relation till kärlväxter och kransalger, minskade dock för några djur med ökad isoleringsgrad hos vikarna. Detta beror troligtvis på att biomassan av påväxtalger minskade med ökad isoleringsgrad hos vikarna. Analysen visade även att djurens nivå i näringskedjan inte förändrades med vikarnas isoleringsgrad. Vidare visade analysen att inflytandet av organiskt material från land till vikens näringsväv inte ökade med ökad isoleringsgrad.

Vid en jämförelse av mängden ryggradslösa djur mellan olika vattenväxter fann jag ett tydligt samband med växternas struktur. Växter med mer komplex, förgrenad struktur hyste större mängd djur än växter med enklare struktur. Större mängd djur i mer komplexa växter kan vara relaterat till ökat skydd från predation, ökad nischseparation samt ökad mängd föda i form av
påväxtalger och dött organiskt material för djuren. Experiment med två kräftdjur (tångmärla *Gammarus oceanicus* och tånggräsugga *Idotea chelipes*) samt två snäckor (båtsnäcka *Theodoxus fluviatilis* och snytessnäcka *Bithynia tentaculata*) visade att kräftdjuren aktivt valde växter med mer komplex struktur över de med enklare struktur, medan snäckorna inte gjorde något val mellan växterna.

Utifrån de erhållna resultaten föreslås att vid förvaltning och övervakning av de grunda Östersjövikarna bör hänsyn tas till en naturlig förändring av djursamhället med den naturliga isoleringen av vikar från havet. För långsiktigt bevarande av dessa miljöer och dess samhällen bör förvaltning inkludera vikar i olika isoleringsstadijer, samt mer öppna kustområden. Vidare föreslås att eventuella storskaliga förändringar i växtsamhället genom mänsklig påverkan, såsom övergödning, båttrafik och muddring kan leda till förändringar i djursamhället. När exempelvis strukturellt komplexa växter, såsom axslinga (*Myriophyllum spicatum*) och hornsärv (*Ceratophyllum demersum*) vilka är mer tåliga mot övergödning och båttrafik, ökar i utbredning och ersätter växter som är mindre komplexa, såsom de mer känsliga kransalgerna (*Chara*), kan man förvänta sig en ökad mängd ryggradslösa djur. Detta kan i sin tur ge effekter högre upp i näringskedjan eftersom de ryggradslösa djuren är föda åt flera fisk- och fågelarter. Omvänt kan en ökning av mindre komplexa växter, som exempelvis den mer tåliga ålnaten (*Potamogeton perfoliatus*), leda till minskad mängd ryggradslösa djur.
Tack


Mina år som doktorand har inneburit en del undervisning. Stort tack Gunnel Skoog för att du gav mig värdefulla råd inför min första undervisning i limnologi.

Tack mamma och pappa för allt stöd!
Tack Shariar Vatanijalal för ditt miljöengagemang och entusiasmerande, Martin Flodin för att du alltid har en alternativ syn att bidra med, samt alla flygkompisar för livseggande äventyr. Tack Fia Andersson, Sofie Larsson och De Gamla Polarna för lång, pålitlig vänskap.

Sist, men såklart inte minst, vill jag tacka Josefin för att du berikar mitt liv, för att du delar min fascination för undervattensvärlden och för att du stöttar mig i tvivlets stunder. ♥