

# Technical Report

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### Effects of shore-level displacement on the ecology of Baltic Sea bays

Joakim P. Hansen, AquaBiota Water Research

December 2012

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# **Effects of shore-level displacement on the ecology of Baltic Sea bays**

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*Keywords:* Surface ecosystem, Biosphere, Forsmark marine.

This report concerns a study which was conducted for SKB. The conclusions and viewpoints presented in the report are those of the author. SKB may draw modified conclusions, based on additional literature sources and/or expert opinions.

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## Summary

This report presents the up to date understanding of changes in ecological structure of small Baltic Sea bays following shore-level displacement and isolation of bays from the sea. It was produced as a part of the biosphere research programme, which has a strong emphasis on the characterization of properties and processes affecting the fate of potentially released radionuclides from the suggested repository of nuclear waste in the bedrock of the Forsmark area. The report has a focus on ecology and gives a description of input data, methodology and results on changes in flora and fauna communities, as well as some abiotic factors, with topographic isolation of bays from the sea. It is intended to describe the properties and conditions at the Forsmark site and to give information essential for demonstrating site specific understanding of processes and properties linked to a sea-to-lake succession.

Long-term landscape development in the Forsmark area is dependent on two main and partly interdependent factors; shore-level displacement and climate variations. These two factors in combination strongly affect a number of processes, which in turn influence the development of ecosystems. Some examples of such processes are erosion and sedimentation, primary production and decomposition of organic matter. In this work focus has been to report changes in the structure and biomass of flora and fauna communities, which affect primary production, and influence the processes of decomposition of organic matter and sedimentation. A section of the study also deals with the biological processes of primary production, autotrophic carbon uptake and influence of allochthonous energy. The study is part of a description of the Forsmark ecosystem succession during a glacial cycle, which is one of the main objectives of the biosphere modelling at the Swedish Nuclear Fuel and Waste Management Company (SKB).

The biomass of macrofauna was found to decrease with increasing isolation of bays. The changes in the macrofauna community also reflected the animals ability to re-colonize an unstable habitat, where slow colonizers with passively dispersed larvae were almost absent from the most isolated bays. Fast colonizers – particularly the ones with flying adults (insects) – were however found in higher proportions in isolated bays. Contrary to the macrofauna and flora, the zooplankton and juvenile fish increased in biomass with increasing bay isolation. This study describes a significant change in ecological properties of Baltic Sea bays with shore-level displacement. This change affects ecosystem processes which may be of importance for the fate of potentially released radionuclides to the biosphere.

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# 1 Introduction

Fennoscandia in northern Europe is subjected to a glacio-isostatic rebound, whereby land is gradually rising, leading to a continuous alteration of the coastline and archipelago morphometry (Påsse and Andersson 2005, Berglund et al. 2009, Argus and Peltier 2010). The shore-level displacement resulting from uplift of shallow sea bottoms is considerably enhanced by deposition of clay and organic sediments (Ingmar 1975, Åse 1994, Berglund et al. 2009). It is also altered by eustatic variation in sea level, driven by climatic change and global geomorphometric changes. The result of the processes has varied over time, from positive to negative shore-level displacement (Påsse and Andersson 2005). Both shore-level displacement and climate variations strongly affect a number of processes, which in turn affect the development of ecosystems. In the present positive shore-level displacement process in the northern Baltic Sea, coastal bays are continuously formed, slowly become shallower, and eventually become land. Often, formation of thresholds in the bay openings results in wave protected lagoon-like bays that gradually become more isolated from the sea over time and form lakes or wetlands. The bay succession has been categorized by Munsterhjelm (1997, Table 1-1). The shallow sheltered lagoon-like bays have been identified as ecologically important biotopes in the Baltic Sea. They harbour rich communities of plants, algae (Munsterhjelm 2005, Rosqvist et al. 2010) and invertebrates (Hansen 2010, Scheinin and Mattila 2010), and constitute important reproduction areas for a number of fish species (Karås 1999, Snickars 2008), as well as for waterfowl.

Until the last two decades, research and monitoring in the Baltic Sea had largely overlooked the shallow lagoon-like bays, focusing on more open coastal biotopes. However, since implementation of the European Union Habitats Directive (Council Directive 92/43/EEC), the shallow Baltic Sea bays have received much more attention. In the initial surveys for the Habitats Directive, hundreds of bays were examined for macrovegetation by local authorities. Additional research has been conducted relating to the ecology of the bays, focusing on macroflora (Eriksson et al. 2004, Appelgren and Mattila 2005, Rosqvist 2010, Hansen 2012), macrofauna (Hansen et al. 2008a, Hansen 2010), zooplankton (Scheinin and Mattila 2010), fish (Sandström et al. 2005, Hansen et al. 2008b, Snickars 2008, Snickars et al. 2009, 2010), and the food web (Hansen et al. 2012, Eriksson et al. 2009). The increased research efforts have resulted in enhanced knowledge of the ecology of shallow Baltic Sea bays. The flora and fauna communities responds clearly to natural environmental gradients, such as climate, level of wave exposure, and the degree to which a bay is topographically separated from the sea. The degree of isolation from the sea has been identified as the most important factor influencing the composition of organisms in the bays (Appelgren and Mattila 2005, Hansen et al. 2008a, Snickars et al. 2009, Scheinin and Mattila 2010). The present study describes how the communities of flora and fauna changes in relation to the bay isolation gradient, taking also a few other environmental variables into consideration. Apart from changes in the biomass and structure of the flora and fauna communities, a comparison is made of primary production between bays at different levels of isolation from the sea.

**Table 1-1. Definitions of four morphometric stages of Baltic Sea land-uplift bays.**

Bay isolation stage	Definition
Juvenile flad	A water body that is clearly distinct from surrounding waters by islands, capes or submerged thresholds (2–4 m deep), but with a significant water-exchange with the sea.
Flad	A clearly delimited water body connected to the sea by one or just a few small shallow (0.5–2 m) threshold openings.
Glo-flad	A transitional stage between a flad and a glo, with a small shallow (0–0.5 m) threshold opening towards the sea, but with an almost continuous contact with the surrounding water.
Glo	A clearly delimited water body with openings that due to positive shore-level displacement have risen above the mean sea water level. This leads to only occasional contact with the sea during high water levels or though wave action.

Another important question that is investigated is to what extent plants and algae change their way of carbon uptake during the bay isolation process, since changes in abiotic and biotic conditions may alter such an uptake (Prins and Elzenga 1989, Madsen and Sand-Jensen 1991). The carbon uptake can in turn influence the fate of potentially released radionuclides from the repository to the biosphere. Yet another process of importance for bio-modelling at the Forsmark investigation site is whether the input of carbon from terrestrial sources increases with increased bay isolation. Since the relative importance of water run-off from land can be expected to increase relative to seawater, inflow of allochthonous carbon from terrestrial sources may increase with increased bay isolation. This process is further examined in the report.

The report is intended to describe the properties and conditions at the Forsmark site and to give information essential for demonstrating site-specific understanding on processes and properties linked to a sea-to-lake succession. The biosphere at the site during the next 1,000 years is assumed to be quite similar to the present situation. The most important changes are the natural glacio-isostatic land uplift and sedimentation on the sea floor, with its effects on the near-shore areas and the shallow coastal basins. This report reflects biotic changes in distinct water bodies that become isolated from the sea due to the land uplift and sedimentation. It does not describe structural changes in more open shallow areas that do not form distinct water bodies. The report presents potential structural changes in ecology with future shore-level displacement by comparing bays which at present differ in level of isolation from the sea. The effect of climate is investigated by a comparison along a latitudinal gradient in the Baltic Sea, but potential effects of a sea-level rise (due to climate change) have been excluded in the report. The study is part of a description of the Forsmark ecosystem succession during a glacial cycle, which is one of the main aims of the biosphere modelling at the Swedish Nuclear Fuel and Waste Management Company (SKB).

The report addresses the following specific questions; (1) How does the abiotic environment of shallow Baltic Sea bays change with increased isolation of bays from the sea; (2) Does the overall biomass, and biomass of important functional groups of flora and fauna, change with increasing bay isolation; (3) Are the changes dependent on scale (i.e., area of the bays) and climate (i.e., latitude); (4) Does the source of carbon for primary producers change with increasing bay isolation (i.e., dissolved carbon dioxide,  $\text{CO}_2$ , versus bicarbonate,  $\text{HCO}_3^-$ ); and (5) Does the influence on the food web by organic matter from terrestrial sources change with level of bay isolation? In addition, mechanisms for the observed changes are further discussed.

## 2 Materials and methods

The data analysed in this report was acquired from a number of studies which are listed in Table 2-1 and shown in Figure 2-1. Bays in the listed studies have been selected according to the aims of the studies, which have been a) to describe the biological communities of small semi-enclosed shallow Baltic Sea bays, or b) to survey juvenile fish and vegetation for conservation of biotopes in local coastal zone management or in the EU Natura 2000 network (EC 2007). Bays have been selected to include a gradient from open bays and sounds to bays that are completely cut-off from the sea at mean sea water level. The selected bays are shallow and have a mean water depth of about 0.5 to 2.5 m. Large water basins (>120 ha) have not been sampled in the compiled studies, and most of the studied bays are <20 ha (median 3 ha). All the bays included in this study have been sampled in late summer to early autumn (late July to September).

Data on macrophyte cover was acquired from Hansen (2012) and included a latitudinal gradient from the southern Baltic Proper (Blekinge Län) to the western Bothnian Sea (Gävleborg Län). Bays with a potential local anthropogenic impact was excluded from the analysis since the aim was to describe natural processes in the bays without interference from marinas, boating activities or local eutrophication. Effects of these anthropogenic activities on the biota are described elsewhere (e.g. Eriksson et al. 2004, Sandström et al. 2005, Hansen 2012). Data on macroflora and macrofauna biomass was acquired from Hansen et al. (2008a, 2012). These data covered a shorter latitudinal gradient, from the northwestern Baltic Proper to the southwestern Bothnian Sea. Data on zooplankton and young-of-the-year fish abundance was acquired from one area in the northwestern Baltic Proper (Hansen et al. 2012, Hansen J P, unpublished data). The local anthropogenic pressure on the bays sampled in Hansen et al. (2008a, 2012) is limited. The investigated areas are sparsely populated with only a few houses, and only three of the studied bays have a house and a jetty along its shore. The studied areas are located outside catchments of municipal and industrial sewage discharges.

Data on nutrients, chlorophyll *a*, turbidity and salinity in the surface water of the bays was acquired from a number of studies in the northern Baltic Proper (Appelgren and Mattila 2005, Hansen 2012, Scheinin and Mattila 2010, Mattila J, unpublished data, Persson J, unpublished data). Data was chosen from this region since measurements in other regions are of poorer quality and often includes only salinity. Data on volatile solids, carbon and nutrients in the sediment of the bays were acquired from three reports from the same area (Wallström and Persson 1997, 1999, Wallström et al. 2000).

A stable isotope ratio of carbon ( $^{13}\text{C}:^{12}\text{C}$ ) was analysed to examine whether the source of carbon for autotrophs change with the bay isolation process, and whether the influence on the food web by organic matter from terrestrial sources change with level of bay isolation. The data was acquired from Hansen et al. (2012) and additional unpublished data sampled and analysed within the same project (Hansen J P, unpublished data).

**Table 2-1. Details of the datasets analysed.**

Dataset	Reference	Region	Replicates	Sampling year	Predictor variables	Statistical test
Macrophyte cover	Hansen 2012	SW Baltic Proper NW Baltic Proper SW Bothnian Sea	113 samples and bays	2001–2010 <sup>a</sup>	Latitude Wave exposure ( <i>Ln</i> ) Area ( <i>Ln</i> ) Isolation index Latitude × isolation index Wave exposure × isolation ind. Area × isolation index	Multiple regression and NP-Manova (composition of functional groups)
Macroflora biomass ( <i>Ln</i> )	Hansen et al. 2008a Hansen et al. 2012	NW Baltic Proper SW Bothnian Sea	162 samples 18 bays	2003, 2005 <sup>b</sup>	Area ( <i>Ln</i> ) Topographic openness ( <i>Ln</i> ) Area × topogr. openness	Mixed-effects model and NP-Manova (composition of functional groups)
Periphyton biomass ( <i>Ln</i> )	Hansen et al. 2012 J. P. Hansen, unpublished	NW Baltic Proper	32 samples 6 bays	2007, 2008	Topographic openness	Mixed-effects model
POM biomass ( <i>Ln</i> )	Hansen et al. 2012 J. P. Hansen, unpublished	NW Baltic Proper	35 samples 6 bays	2007, 2008	Topographic openness	Mixed-effects model
Chlorophyll <i>a</i> ( <i>Ln</i> )	J. Mattila, unpublished	N Baltic Proper	12 samples and bays	2010	Topographic openness	Regression
Zooplankton biomass ( <i>Ln</i> )	Hansen et al. 2012 J. P. Hansen, unpublished	NW Baltic Proper	43 samples 6 bays	2007, 2008	Topographic openness	Mixed-effects model
Macrofauna biomass ( <i>Ln</i> )	Hansen et al. 2008a Hansen et al. 2012	NW Baltic Proper SW Bothnian Sea	162 samples 18 bays	2003, 2005 <sup>b</sup>	Area ( <i>Ln</i> ) Topographic openness ( <i>Ln</i> ) Area × topographic openness	Mixed-effects model and NP-Manova (composition of functional groups)
Yoy-fish abundance and biomass	Hansen et al. 2012 Hansen et al. 2008b J. P. Hansen, unpublished	NW Baltic Proper	7 and 19 samples and bays for biomass and abundance respectively	2007, 2008	Topographic openness	Regression and NP-MANOVA (composition of functional groups)
Salinity	Appelgren and Mattila 2005 Hansen 2012 Scheinin and Mattila 2010 J. Mattila, unpublished J. Persson, unpublished	N Baltic Proper	72 samples and bays	2001–2010 <sup>c</sup>	Longitude Wave exposure ( <i>Ln</i> ) Area ( <i>Ln</i> ) Topographic openness ( <i>Ln</i> ) Long. × topogr. openness Wave exp. × topogr. openness Area × topogr. openness	Multiple regression



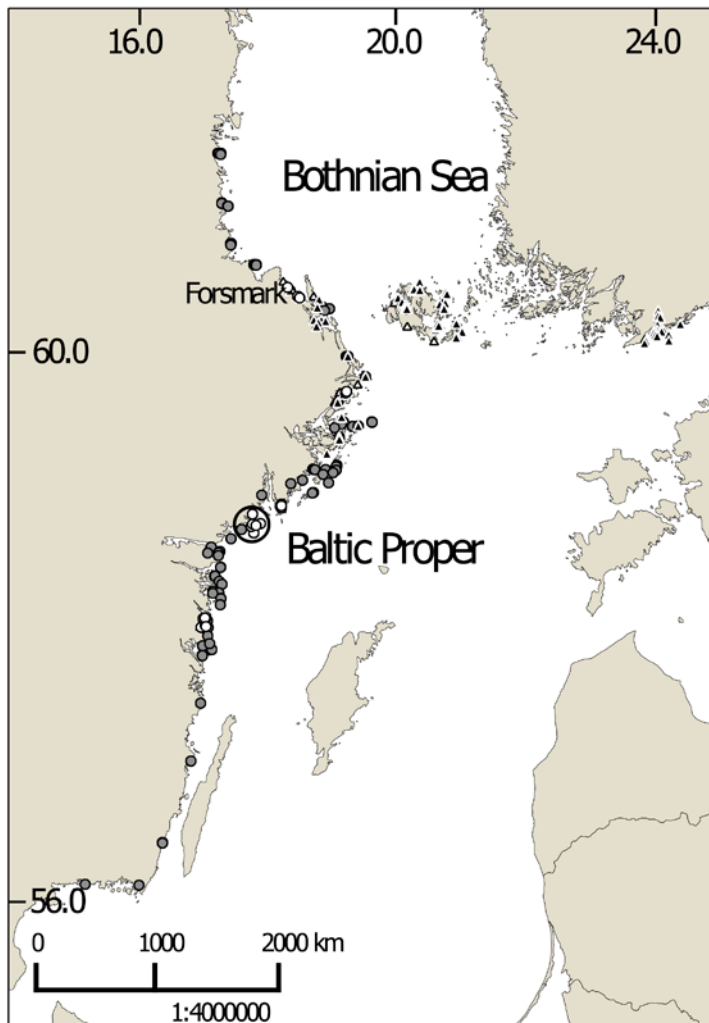
Dataset	Reference	Region	Replicates	Sampling year	Predictor variables	Statistical test
Turbidity ( <i>Ln</i> )	Scheinin and Mattila 2010 J. Mattila, unpublished J. Persson, unpublished	N Baltic Proper	68 samples and bays	2001–2010 <sup>c</sup>	Longitude Wave exposure ( <i>Ln</i> ) Area ( <i>Ln</i> ) Topographic openness ( <i>Ln</i> ) Long. × topogr. openness Wave exp. × topogr. openness Area × topogr. openness	Multiple regression
Total phosphorus ( <i>Ln</i> ) and total nitrogen concentration in the water	Appelgren and Mattila 2005 Hansen 2012 Scheinin and Mattila 2010 J. Mattila, unpublished J. Persson, unpublished	N Baltic Proper	72 samples and bays	2001–2010 <sup>c</sup>	Longitude Wave exposure ( <i>Ln</i> ) Area ( <i>Ln</i> ) Topographic openness ( <i>Ln</i> ) Long. × topogr. openness Wave exp. × topogr. openness Area × topogr. openness	Multiple regression
Volatile solids, total phosphorus ( <i>Ln</i> ), total nitrogen ( <i>Ln</i> ) and total carbon ( <i>Ln</i> ) concentration in the sediment	Wallström and Persson 1997, 1999, Wallström <i>et al.</i> 2000	N Baltic Proper	32 samples and bays	1995–1999 <sup>d</sup>	Area ( <i>Ln</i> ) Topographic openness ( <i>Ln</i> ) Area × topogr. openness	Multiple regression
Isotope ratio of carbon ( <sup>13</sup> C: <sup>12</sup> C) for functional and taxonomic groups of flora and fauna	Hansen <i>et al.</i> 2012 J. P. Hansen, unpublished	N Baltic Proper	6 bays	2007–2008	Topographic openness	No analysis

<sup>a</sup> Forty-one (41) bays were sampled more than one year, while all other bays were sampled only one year.

<sup>b</sup> Each bay was sampled only one year.

<sup>c</sup> Twenty-eight (28) bays were sampled more than one year, while all other bays were sampled only one year.

<sup>d</sup> Fifteen (15) bays were sampled two years, while all other bays were sampled only one year.



*Figure 2-1. Map showing the data included in the report. Filled grey circles show bays with data on macrophyte cover, and white circles show bays sampled for macrofauna and macroflora biomass. Solid circle marks location of bays which were additionally sampled for young-of-the-year fish biomass and stable isotopes for some functional groups. Black triangles depict bays with data on salinity, turbidity and nutrient concentrations in the water, while white triangles depict bays with sediment data.*

## 2.1 Environmental variables

Water samples were taken, and salinity measured, at a depth of 0.5 m in three locations in the central part of each studied bay on each sampling occasion. Salinity was measured in practical salinity units (PSU) and water samples were used for analysis of chlorophyll *a*, turbidity (nephelometric turbidity units; NTU), total phosphorus (TP) and nitrogen concentrations (TN). Chlorophyll *a* was analysed according to the Finnish standard procedure (SFS 1983), and turbidity was measured on a formacin-calibrated turbidimeter (HACH 2100P). Total phosphorus and total nitrogen concentrations were analysed according to methods described in Goedkoop and Sonesten (1995).

The sediment was sampled using a cylindrical acrylic sediment coring device. Samples were taken in a central part of each bay where the sediment could be assumed to be representative for a large part of a bay. In a few cases more than one sample was taken in the bays (see Wallström et al. 2000 for details), and in such cases a mean value was used for the analysis. The top 2 cm of the sediment sample was analysed for volatile solids content, total carbon, total phosphorus and total nitrogen concentration. The percentage of volatile solids were analysed after combustion at 550°C in two hours (Goedkoop and Sonesten 1995), while total carbon and nitrogen concentration was analysed by combustion using a LECO CHNS-932 Elemental Analyser. Total phosphorus was analysed by a digestion-method in an acid solution according to Goedkoop and Sonesten (1995).

In addition to water and sediment samples, two geographical and hydrological features were estimated for each bay included in the present study; bay isolation and wave exposure. Level of bay isolation was estimated by either topographic openness of the bays or by an isolation index. Topographic openness ( $E_a$ ) was calculated as:

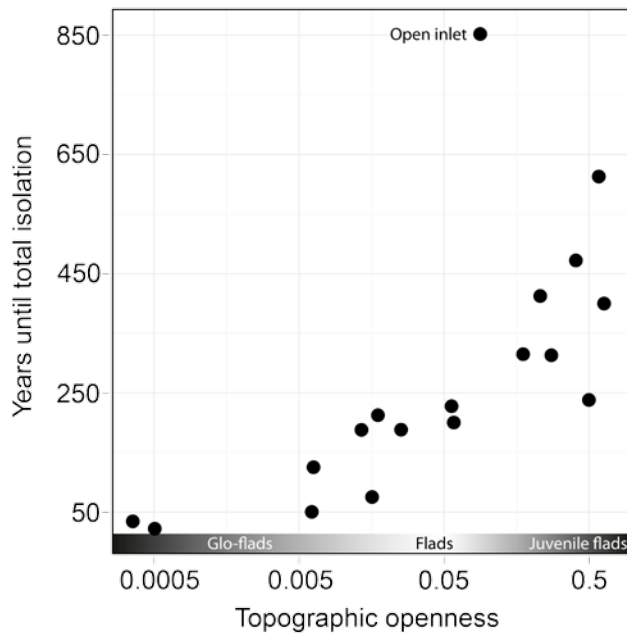
$$E_a = 100 \times \frac{A_t}{a} \quad \text{Equation 1}$$

where  $A_t$  is the smallest cross-section area of a bay connected to the sea, and  $a$  is the water surface area of the bay (Persson et al. 1994, Håkansson 2008). The cross-section area,  $A_t$ , was calculated from depth and distance measurements in the field, while water surface area,  $a$ , was calculated from digital topographic maps using GIS methods. The topographic openness functions as a proxy for surface-water retention time (Håkansson 2008), which affects factors such as water temperature, salinity and particle sedimentation. Topographic openness has been proven to be a useful estimate of the shore-level displacement induced changes in hydrology affecting the bay biota in several studies (e.g. Appelgren and Mattila 2005, Hansen et al. 2008a, Snickars et al. 2009, Scheinin and Mattila 2010).

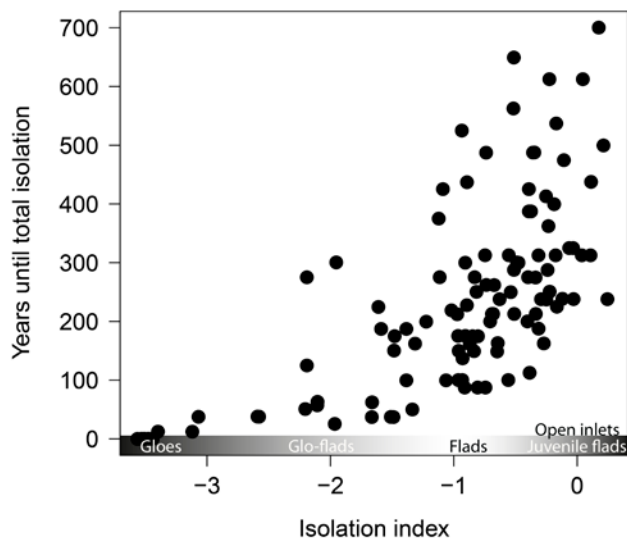
Since bays that have become totally isolated from the sea will have a topographic openness of null, an isolation index was used for the dataset which included such isolated bays (i.e., data on macrophyte cover). The isolation index ( $I$ ) was calculated as:

$$I = \begin{cases} \text{Log}_{10}(E_a) - D, & E_a > 0 \\ -D, & E_a = 0 \end{cases} \quad \text{Equation 2}$$

where  $D$  is the topographically shortest distance to the sea, or to another water body connected to the sea. Distance to the sea was used instead of height over mean sea level of the (former) opening, since no reliable data was available for the latter. To get an approximation of the temporal gradient examined in the present study, the two measures of bay isolation were related to an approximate time until bays will be totally isolated from the sea (Figure 2-2 and Figure 2-3). The time until total isolation was calculated by dividing the maximum depth at the bay opening towards the sea with an approximate land-uplift and sedimentation rate of 8 mm per year (corresponding to the rate at the area of interest – the Forsmark investigation site).



**Figure 2-2.** Relationship between topographic openness of bays and approximate time until bays are completely isolated from the sea (i.e., where the former opening has emerged above the mean sea water level), given the present shore-level-displacement rate in the Forsmark area (SW Bothnian Sea).

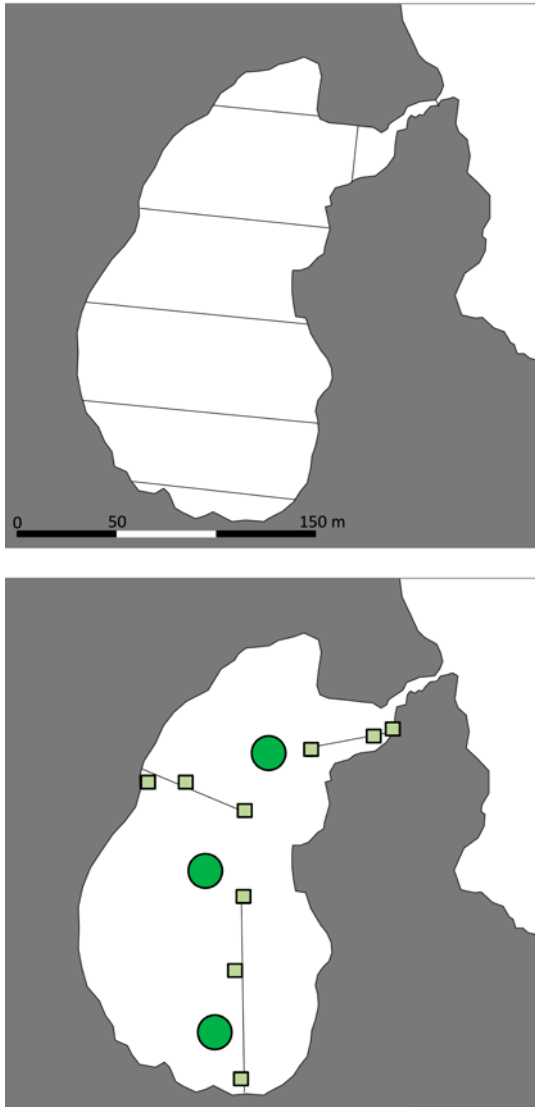


**Figure 2-3.** Relationship between the bay isolation index and approximate time until bays are completely isolated from the sea (i.e., where the former opening has emerged above the mean sea water level), given the present shore-level-displacement rate in the Forsmark area (SW Bothnian Sea).

Wave exposure was used to account for the coastal morphometry outside the bays and level of shelter provided by islands and capes affecting waves reaching the bays. Wave exposure was estimated using a simplified wave model (SWM; Isæus 2004), which calculates the wave impact from fetch and wind data in  $25 \times 25$  m grids using digital nautical charts and GIS methods. The wind speeds used in the model were the mean wind speeds measured at local meteorological stations in the study area. Values representing the wave exposure at the bay openings were calculated as the mean exposure of a  $50 \times 50$  m grid at the openings to avoid large influence of extreme values at the smaller grid size. The SWM functions as a proxy for factors such as water temperature and particle sedimentation, apart from the hydrological movements and forces created by waves.

## 2.2 Macroflora

The macroflora was divided into two functional groups: coarsely structured algae and angiosperms (hereafter, ‘macrophytes’) and ephemeral, mainly epiphytic, algae. The species composition and percentage cover of submersed macrophytes was surveyed using the method of Persson and Johansson (2007), where a free diver estimates macrophyte cover along parallel transect lines that extend perpendicular to the length axis of the bays (Figure 2-4). The number of transect lines was adjusted in relation to the area of the bays, with a higher number of transects in larger bays, but a minimum of three transects. The first transect line was located 10 m from the innermost shore (outside reed belts, if present) and the other transect lines were located 50–200 m apart (depending on inlet area) until the whole bay was surveyed. A final transect line was located across the opening(s) of the bays. The percentage cover of macrophytes was estimated visually every 10 m along the transect lines within a  $0.5 \times 0.5$  m square using a continuous percentage scale individually for each taxon (meaning that the total cover could exceed 100% if the macrophytes overlapped). If a transect was more than 120 m, estimates in survey squares were done every twentieth meter when the distance to the shore was more than 50 m. Ephemeral algae was noted on a 5-point scale, but was not included in the analysis in this report since biomass samples produced a better quantitative estimate for abundance of ephemeral algae (described later). Depth at the position of each survey square was measured with an accuracy of 0.1 m and used for calculations of mean bay depth and maximum depth at the bay opening (after adjustment in relation to mean seawater level).



**Figure 2-4.** Sampling transects for macrophyte cover and young-of-the-year fish (upper panel) and sampling locations for biomass of macroflora and macrofauna (lower panel, filled squares) as well as zooplankton and particulate organic matter (lower panel, filled circles).

Biomass of macroflora was measured by sampling along three transects in each bay (Hansen et al. 2008a). Three samples were taken in the inner part, three in the middle part, and three in the outer part of the bays (Figure 2-4). Transects were located perpendicular to the shoreline, extending from the shore to the deeper central area of the bays. Each transect was divided into three depth intervals relative to the maximum depth of the bays, and each sample was taken from a randomly selected vegetation patch in each interval. The samples were collected by a free diver using a net bag (1 mm mesh size) mounted on a  $0.20 \times 0.20$  m, or a  $0.17 \times 0.17$  m, frame with shears underneath. The sampler was pulled over a stand of vegetation at each sampling site. The macroflora was cut a few centimetres into soft-bottom substrates or at the surface of hard-bottom substrates. Samples were stored in plastic bags under dark, cool conditions until return to the laboratory, where they were deep frozen at  $-20^{\circ}\text{C}$ . The macroflora was identified to species or genus and weighed after drying at  $59^{\circ}\text{C}$  to constant weight. Ash-free dry weight (dryweight expressed as carbon weight) was calculated by multiplying with a carbon weight:dry weight ratio for each taxon presented in Kautsky (1995). In cases when a carbon weight:dry weight ratio was missing for a species, a ratio was obtained from a higher taxonomic or functional group level. Biomass was related to sample area (i.e. biomass per  $\text{m}^2$  was calculated).

### 2.3 Periphyton, particulate organic matter and chlorophyll *a*

Periphyton, particulate organic matter (POM) and chlorophyll *a* were sampled at three locations in each bay (Hansen et al. 2012). One sample was taken in the inner part, one in the middle part, and one in the outer part of the bays (Figure 2-4). Periphyton were sampled on plastic discs (Ø 120 mm) placed at a depth of 0.25 m and left for three weeks to be colonized. The organism community on the upper side of each disc was scraped off, deep frozen at  $-20^{\circ}\text{C}$ , and later dried at  $59^{\circ}\text{C}$  to constant weight. Dry weight was related to disc area and colonization time (i.e., biomass production per  $\text{cm}^2$  and day was calculated). All discs were lost in one bay the first sampling year, and one disc was lost in another bay the next year resulting in an unbalanced dataset. Particulate organic matter was sampled with a phytoplankton net (10  $\mu\text{m}$ ) at each sampling site by vertically hauling the net from the sea bottom to the surface. However, when the depth was less than 0.5 m, water was instead sampled using a bucket and poured through the net. The samples were filtered onto pre-weighed Whatman GF/F filters, deep frozen at  $-20^{\circ}\text{C}$ , and later dried at  $59^{\circ}\text{C}$  to constant weight. Dry weight was related to sample volume (i.e., biomass per litre was calculated). One sample was lost during the process. Chlorophyll *a* was sampled similar as to the POM-samples, but filtered on to Whatman GF/C filters. The pigment was extracted from the filters and analysed using a spectrophotometer. Particulate organic matter and chlorophyll *a* can function as proxies for phytoplankton abundance and biomass, although they do not give exact and exclusive measures of such.

### 2.4 Macrofauna

Samples of phytal macrofauna ( $>1$  mm) were collected concurrent with the macroflora biomass samples (described earlier; Hansen et al. 2008a, 2012). The sampling method collected plant-associated animals and animals living just beneath the plants, but not the deep sediment infauna. The animals were sorted and identified to different taxonomic levels (species, genus, or family). Dry weight was obtained after drying at  $59^{\circ}\text{C}$  to constant weight. For encrusting sessile animals (Bryozoans, Hydrozoans and Poriferans), however, only abundance was noted and biomass was not measured. The carbon weight was calculated using the same procedure as for macroflora. In cases when a carbon weight:dry weight ratio was missing for a taxon, a ratio was obtained from a higher taxonomic level or a morphologically similar taxon. Biomass was related to sample area (i.e. biomass per  $\text{m}^2$  was calculated).

### 2.5 Zooplankton

Zooplankton was sampled with a 100  $\mu\text{m}$  net at the same locations and using the same procedure as used for the POM samples (Figure 2-4; Hansen et al. 2012). In a few cases, duplicate samples were taken at sample locations with a very low density of zooplankton. Samples were stored under dark, cool conditions in bottles until return to the laboratory, where they were deep frozen at  $-20^{\circ}\text{C}$ . The zooplankton were sorted to taxonomic order (Copepoda and Cladocera) and counted under a microscope. Zooplankton biomass was calculated from the abundance measures by first multiplying the abundance with the mean wet weight per individual for the most common taxa of Cladocera and Copepoda in shallow bays of the Baltic Proper (Scheinin M, unpublished data), and thereafter multiplying the wet weight with a dry weight:wet weight ratio, and a carbon weight:dry weight ratio, presented in Ankar and Elmgren (1978). Biomass was related to sample volume (i.e., biomass per litre was calculated).

### 2.6 Young-of-the-year fish

Young-of-the-year (yoy) fish were sampled using small underwater detonations that stun small fish within an area of ca.  $15 \text{ m}^2$ . Only juvenile fish were sampled since they are stationary and largely stay within one bay during the first season. Therefore they represent conditions at a specific bay, while adults are more mobile and can move between bays. The method used allows sampling of fish up to a length of ca. 150 mm, with well-developed swim bladders, in all types of habitats, including dense vegetation. The method has been developed for sampling of warm-water spawning freshwater



species in the brackish Baltic Sea, and records mainly fish of the families Cyprinidae and Percidae, as well as pike (*Esox lucius*) (Sandström et al. 2005, Snickars et al. 2007). As several of the fish species can be associated with particular vegetation types, the sampling locations were randomized along the vegetation line transects in various types of habitats, depending on the vegetation composition and depth measured prior to the fish sampling, similar to the method of Sandström et al. (2005) and Snickars et al. (2009). To elude inference between samples, the sampling locations were located >30 m apart. The sampling effort per bay accounted for differences in area between the bays, ranging from 17 samples in the smallest bay to 23 samples in the largest bay. During sampling, stunned fish in the water were collected using a dip net, identified to species and counted. In addition, length was measured and an average length per species and year was calculated. Fish biomass was calculated by first using a wet weight:length ratio for each species (Sandström A, unpublished data), and thereafter multiplying the wet weight with a dry weight:wet weight ratio, and a carbon weight:dry weight ratio, according to Kautsky (1995). In cases when a wet weight:length ratio was missing for a species (i.e., crusian carp *Carassius carassius*, rudd *Scardinius erythrophthamus* and tench *Tinca tinca*), a ratio was obtained from a mean at a family level (Cyprinidae). The biomass was related to sampling effort (catch per unit effort) and sample size (i.e., biomass per m<sup>2</sup> was calculated).

## 2.7 Stable isotopes

Stable isotopes were analysed to examine whether the source of carbon for autotrophs change with the bay isolation process, and whether the influence on the food web by organic matter from terrestrial sources change with level of bay isolation. For this purpose a stable isotope ratio of C was analysed for the following functional groups; angiosperms (*Potamogeton pectinatus* and *Myriophyllum spicatum*), stoneworts (Charophyceae), bladderwrack (*Fucus vesiculosus*), ephemeral algae, periphyton, POM, zooplankton (Copepoda and Cladocera), filter feeder (*Parvicardium hauniense*, Bivalvia) and yoy-fish (predators; Cyprinidae). For plants and algae, leaves or top thallii were used for the analysis. Epiphytes were manually removed from the plants and algae samples before analysis. For animals, muscle and cuticle tissue were analysed to avoid gut content and tissue with a short turn-over time. In the case of zooplankton, however, whole bodies were used per replicate because of their small individual weights. Animals were freeze-dried and fish muscles were ground to a fine powder for the stable isotope analysis. For each functional group or taxon in each bay, three spatially separated samples were analysed per year. For some taxa with low biomass in the samples, fewer than three samples were analysed. For example, the two outermost zooplankton samples (i.e., middle and outer samples) were always pooled, resulting in duplicate samples per bay and year. The stable isotope ratio of <sup>13</sup>C:<sup>12</sup>C was calculated as a deviation from the international limestone standard Vienna Pee Dee Belemnite (VPDB) (δ<sup>13</sup>C) in parts per thousand (‰) according to:

$$\delta^{13}\text{C} = \left( \frac{(^{13}\text{C} : ^{12}\text{C})_{\text{sample}}}{(^{13}\text{C} : ^{12}\text{C})_{\text{standard}}} - 1 \right) \times 10^3 \quad \text{Equation 3}$$

## 2.8 Data analysis

All statistical tests were performed using the software R, version 2.15.0 (R Development Core Team 2012). Multiple regressions were used to explore the effects of bay isolation on bay mean macrophyte cover (Table 2-1). In addition to the bay isolation index, effects of latitude, wave exposure, area and its interaction with topographic openness was tested. Mixed-effects models ('nlme'-package in R; Pinheiro et al. 2011) were used to test effects of topographic openness on biomass of macroflora, periphyton, POM, macrofauna and zooplankton. Mixed-effects models were applied to handle the spatial hierarchy of samples, with several samples in each bay. Bay was specified as a random blocking factor in the design. The environmental variables latitude and wave exposure were not included in these analyses since the number of investigated bays was low and the sampled latitudinal gradient was short with an unbalanced design. Area and its interaction with topographic openness was included in the analyses on macroflora and macrofauna biomass since the number of bays was higher for these response variables (18) than for zooplankton, periphyton and POM (6). The effect of topographic openness was additionally tested on biomass of yoy fish using a normal regression analysis.

Multiple regressions were applied to test for effects of topographic openness on bay mean chlorophyll *a*, salinity, turbidity, total phosphorus concentration, total nitrogen concentration, and a total nitrogen to phosphorus ratio in the water. Wave exposure and area was included as factors in the analyses on turbidity and nutrients. In addition, longitude was included since the data was sampled in a longitudinal gradient. Effects of topographic openness and area of the bays were additionally tested on percent volatile solids, total carbon, nitrogen and phosphorus concentrations in the sediment, as well as on a carbon to nitrogen, and nitrogen to phosphorus ratio. All of the data was graphically inspected for normality and homogeneity of variances, and response variables were *Ln* transformed when needed to meet assumptions for the parametric tests (Table 2-1). The predictor variables in the models were inspected for non-collinearity (after transformations). The statistical models were simplified by a stepwise removal of dependencies that did not improve the minimal model.

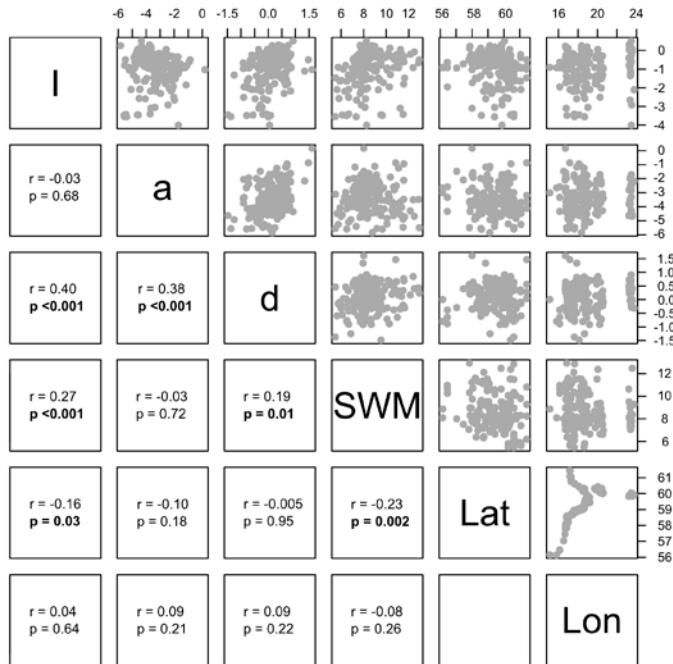
Non-parametric multivariate analysis of variance (NP-Manova) was used to explore the effect of bay isolation on functional groups of macroflora, macrofauna and yoy fish. The multivariate tests were performed using the R-package 'vegan' (Oksanen et al. 2009) and dissimilarity matrices were calculated using the Bray-Curtis equation (e.g. Clarke and Warwick 2001). The macroflora was divided into four functional groups; angiosperms, stoneworts, bladderwrack and other algae (for the response 'cover') or ephemeral algae (for the response 'biomass'). Fish were divided into the taxonomic groups of Cyprinidae, Percidae and *Esox lucius*. The macrofauna was divided into functional groups according to the classification of functional feeding modes of Merritt and Cummins (1984, 2006), which has been developed for aquatic invertebrates in temperate regions with high levels of omnivory. The functional groups used for the macrofauna were filtering collectors (filterers), gathering collectors (gatherers), scrapers, shredders (including also the few piercers and miners found in the samples) and predators. An average biomass per bay was calculated for each functional group and used in the analyses. The statistical models were simplified by a stepwise deletion of non-significant terms.

In addition to analysing the datasets presented in Table 2-1, a comparison of macroflora and macrofauna biomass between bays and areas outside the bays was done with analysis of variance (Anova). Data from outside the bays was acquired from Borgiel (2005) and Kautsky H (unpublished). Anova was also applied to analyse differences in primary production between bays of different degree of isolation from the sea. The data on primary production was acquired from Wijnbladh et al. (2006).



### 3 Results and discussion

A correlation matrix of the predictor variables used in the analyses is presented in Figure 3-1. It also includes data on mean depth of the bays (not included in the regression analyses). The matrix was produced by combining datasets on biological and environmental variables (cp. Table 2-1). There were no strong correlations between the predictor variables used in the models. The mean depth of the bays was, however, positively correlated with the bay isolation index and bay area, and correlated weakly with wave exposure at the bay openings. The bay isolation index was only weakly correlated with wave exposure and latitude. Also wave exposure was weakly correlated with latitude.



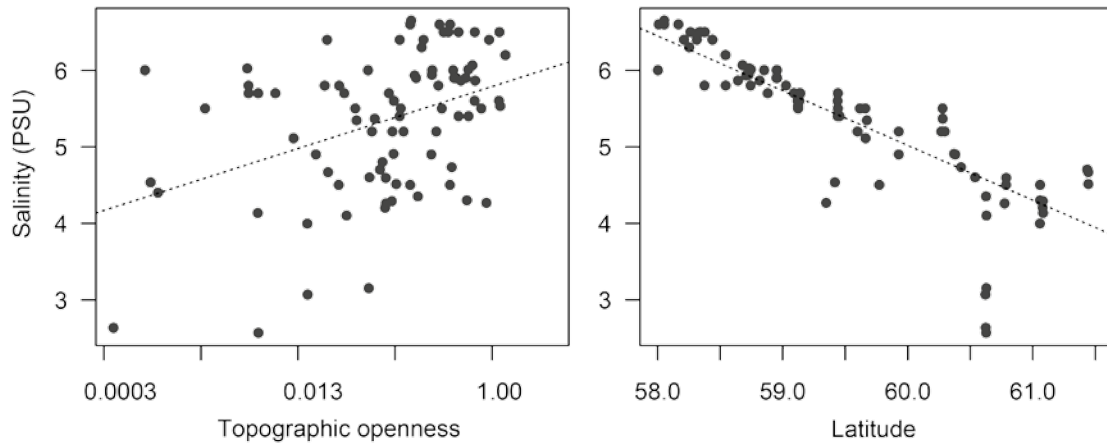
**Figure 3-1.** Correlation matrix of hydrological and geographical features of the bays; the bay isolation index (*I*), bay area (*a*), bay mean depth (*d*), wave exposure at the bay opening (*SWM*), latitude (*Lat*) and longitude (*Lon*). The matrix was produced by combining datasets with data on biological and environmental variables, except sediment characteristics (see Table 2-1). Results show Pearson product-moment correlation coefficients (*r*) and significance is indicated by bold font. Bay area, mean depth and wave exposure were Ln-transformed. The bay isolation index is equal to  $\log_{10}$  of topographic openness (*Ea*) for all datasets, except for data on macrophyte cover, where distance to the sea has been subtracted from  $\log_{10}(Ea)$  (see text for details).

### 3.1 Environmental variables

Surface water salinity was found to increase with increasing bay isolation (i.e., decreasing topographic openness), but only in the eastern area (Table 3-1). This interaction effect was due to influence of a few bays with high topographic openness located in a freshwater influenced fjord in the east, the Pojo bay on the main land of Finland. Removing these bays from the analysis resulted in no relationship between salinity and topographic openness. However, in a study by Hansen (2012) – including a larger number of bays than analysed here – summer salinity was found to decrease with increasing bay isolation along the Swedish Baltic Sea coast (Figure 3-2). All salinity measurements both in the present study and in Hansen (2012) have been made at a few occasions in summer. When salinity has been more frequently measured (Persson J, unpublished data), the observations indicate that the salinity fluctuate more in isolated compared to open bays. A fluctuating salinity is probably also the reason for the large variation in salinity between bays with low topographic openness in Figure 3-2. The larger variation can be explained by a relatively higher influence of precipitation and evaporation in relation to seawater influence in isolated compared to more open bays. For example, during snow melting in spring, salinity become lower in isolated bays compared to more open bays (Scheinin and Mattila 2010, Persson J, unpublished data). In contrast, during shifts between high-precipitation and dry periods in summer, 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.). Salinity in the bays has also been recorded to decrease with latitude following approximately the general pattern of surface water salinity in the Baltic Sea (Figure 3-2; Hansen 2012).

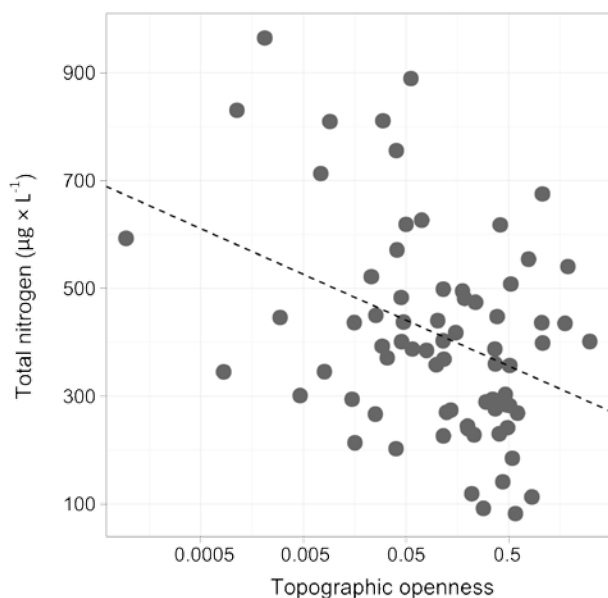
**Table 3-1. Results of regression analyses showing effects of longitude, topographic openness or wave exposure on a) salinity, b) turbidity, c) total nitrogen, d) total phosphorus concentration, or e) a nitrogen to phosphorus ratio. Analyses were based on mean values in 72 bays for salinity and nutrients, and 68 bays for turbidity.**

Factors	Estimate	Std. Error	t-value	P-value
<b>a) Salinity</b>				
Intercept	0.29	1.24	0.24	0.81
Longitude	0.24	0.06	4.18	<0.001
Topographic openness ( <i>Ln</i> )	0.76	0.41	1.85	0.069
Long. × Topo. openness	-0.04	0.02	-2.06	0.044
<b>b) Turbidity (<i>Ln</i>)</b>				
Intercept	0.21	0.96	0.22	0.83
Longitude	0.08	0.04	2.00	0.049
Wave exposure ( <i>Ln</i> )	-0.15	0.07	-2.17	0.034
<b>c) Total phosphorus (<i>Ln</i>)</b>				
Intercept	-0.44	0.60	-0.74	0.47
Longitude	0.17	0.03	5.98	<0.001
<b>d) Total nitrogen</b>				
Intercept	-822	186	-4.41	<0.001
Longitude	55.5	8.90	6.25	<0.001
Topographic openness ( <i>Ln</i> )	-39.5	8.70	-4.55	<0.001
<b>e) Nitrogen:phosphorus</b>				
Intercept	14.20	1.33	10.67	<0.001
Topographic openness ( <i>Ln</i> )	-1.31	0.45	-2.92	0.005



**Figure 3-2.** Relationship between summer water surface salinity and topographic openness of bays (to the left), and latitude of the bays (to the right). The figure is modified from Hansen (2012).

Turbidity was not found to change with topographic openness of the bays. However, it was found to increase with longitude following the similar increase in nutrient concentrations (TP and TN), and also showed a slight increase with decreasing wave exposure (Table 3-1). Apart from a significant effect of longitude, TN increased with decreasing topographic openness of the bays (Figure 3-3), while TP did not. The result is similar to findings of Rosqvist et al. (2010), and can reflect a larger influence of nitrogen-rich run-off from land or higher internal nitrogen loading from the sediments in isolated compared to more open bays. Contrary to the present findings, Scheinin and Mattila (2010) found TP to be higher also in isolated compared to more open bays. However, this difference in nutrient concentration between the bays was evident only early in the season and not at the end of the growing season. The increase in TN with decreasing topographic openness found in the present study was reflected in an increasing nitrogen to phosphorus ratio (N:P) with decreasing topographic openness of the bays. The N:P increased above the Redfield ratio (16:1) at a topographic openness of 0.25, which corresponds approximately to when an open inlet develops into a flad-type bay.



**Figure 3-3.** Relationship between total nitrogen concentration in the water and topographic openness of bays.

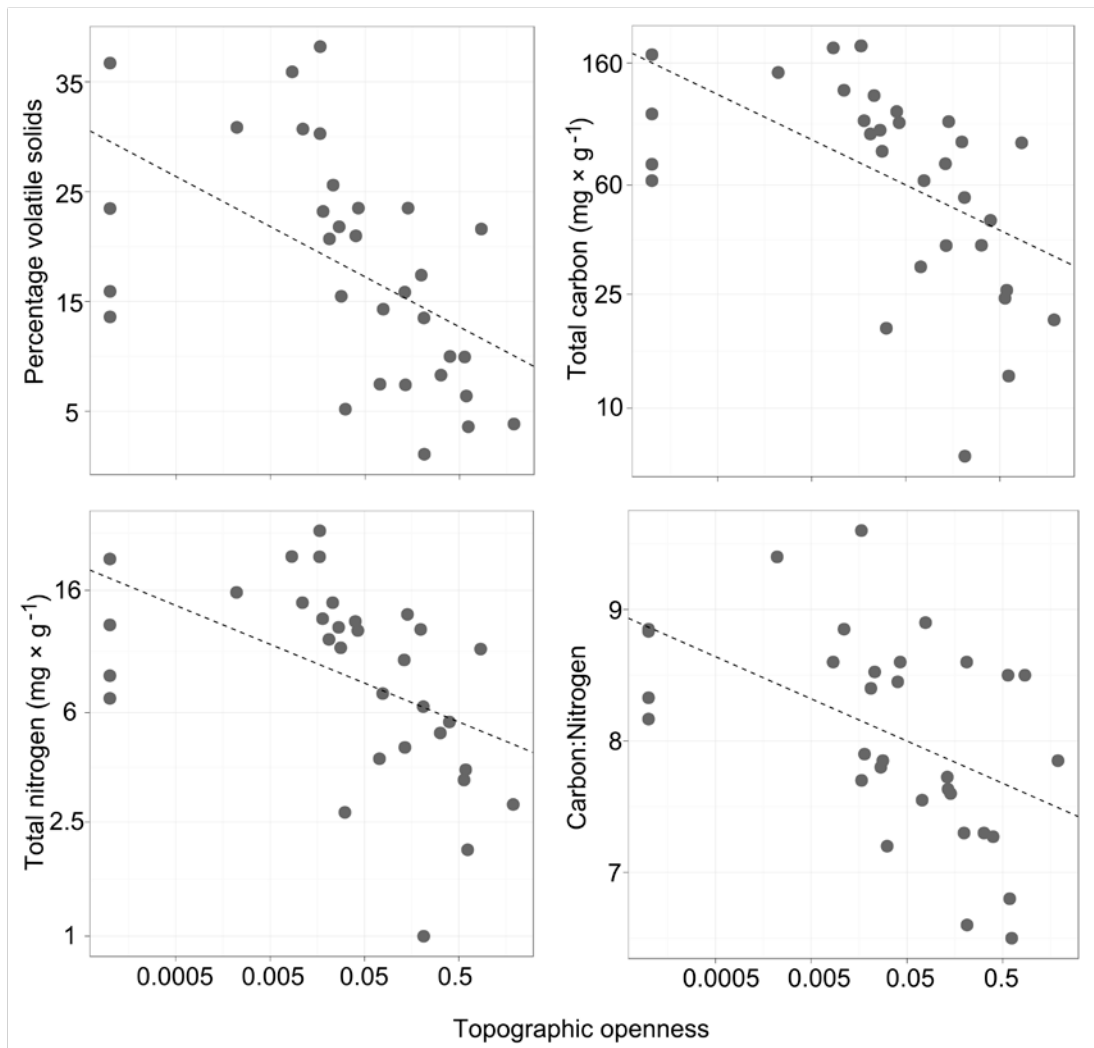
Water temperature was not examined in the present study, but has been examined in several studies previously. The summer water temperature has been recorded to increase with decreasing topographic openness of bays (Munsterhjelm 2005, Hansen et al. 2008b, Snickars et al. 2009, Scheinin and Mattila 2010) and to be about 4–6 °C warmer in the most isolated compare to the most open bays. This difference is most pronounced in early summer, and at the end of the summer the differences are minimal.

The percentage of volatile solids in the sediment, as well as the concentration of total carbon and nitrogen, was found to decrease with decreasing topographic openness of the bays (Table 3-2, Figure 3-4). The carbon to nitrogen ratio also decreased with decreasing topographic openness. Total phosphorus in the sediment did not change with topographic openness ( $p>0.2$ ), resulting in increasing N:P with decreasing topographic openness of the bays. The results reflect the accumulation of organic matter in the semi-enclosed bays (Munsterhjelm 1997), where more organic matter are accumulated in more isolated bays. The higher concentration of nitrogen in the sediment of isolated bays can explain the higher concentration also in the water, due to release from the sediments.

The water and sediment chemistry are not only determined by the geographical and hydrological conditions. Also the biota can influence the water and sediment characteristics. Rooted macrophytes reduce water movements, bind bottom sediments and prevent re-suspension of organic material and diffusion of nutrients from the sediment to the water (e.g. Scheffer 2004). However, they can also enhance phosphorus release from the sediment. Since plants and algae reduce water movements and produce detritus that is mineralized, anoxic conditions can occur, resulting in release of iron-bound phosphorus from the sediment. A reduction of water movements and increased water retention time can increase the sedimentation rate of particles transported to the bays from surrounding waters. Increased pH, as a consequence of high photosynthetic activity, can further stimulate the phosphorus release. Opposite, bioturbation by animals at the sediment surface can oxidize the sediments, preventing release of phosphorus. Processing of organic matter by detritivorous invertebrates and other meio and micro heterotrophs will also affect the sediment composition, and a low rate of processing can result in a high percentage of volatile solids in the sediments.

**Table 3-2. Results of regression analyses showing effects of topographic openness on a) volatile solids, b) total carbon concentration, c) total nitrogen concentration, d) a carbon to nitrogen ratio, and e) a nitrogen to phosphorus ratio in the sediment. Analyses were based on data from 32 bays.**

Factors	Estimate	Std. Error	t-value	P-value
<b>a) Percentage volatile solids</b>				
Intercept	11.3	2.54	4.44	<0.001
Topographic openness ( <i>Ln</i> )	-1.98	0.59	-3.35	0.002
<b>b) Total carbon</b>				
Intercept	3.62	0.20	17.8	<0.001
Topographic openness ( <i>Ln</i> )	-0.16	0.05	-3.34	0.002
<b>c) Total nitrogen</b>				
Intercept	1.62	0.19	8.47	<0.001
Topographic openness ( <i>Ln</i> )	-0.14	0.05	-3.04	0.005
<b>d) Carbon:nitrogen</b>				
Intercept	7.58	0.19	39.0	<0.001
Topographic openness ( <i>Ln</i> )	-0.14	0.05	-3.09	0.004
<b>e) Nitrogen:phosphorus</b>				
Intercept	6.58	0.99	6.65	<0.001
Topographic openness ( <i>Ln</i> )	-0.90	0.23	-3.91	<0.001



**Figure 3-4.** Relationship between sediment characteristics and topographic openness of bays; percentage volatile solids (top left), total carbon concentration (top right) and total nitrogen concentration (bottom left), as well as a carbon to nitrogen ratio (bottom right). Note the difference in scale of the second axis between the panels; concentration of total carbon and nitrogen are expressed on a logarithmic scale, while percentage volatile solids and carbon:nitrogen are expressed on an untransformed scale.

Macrophytes take up nutrients both from the sediment and from the water during the growing season. This uptake can explain why the difference in nutrient concentration between isolated and open bays decreases along the season (Scheinin and Mattila 2010). Early in the season, the difference in nutrient concentration is as largest between open and isolated bays, while later during the season – when the autotrophic productivity is higher – the difference is minor. Furthermore, some plants and algae produce chemicals that hamper phytoplankton growth (allelochemicals). Production and release of such chemicals is quite common among stoneworts (e.g. Wium-Andersen et al. 1982, van Donk and van de Bund 2002). It has been suggested that stonewort-dominated vegetation communities are more capable of both reducing nutrient concentrations in the water and phytoplankton growth and turbidity throughout the season than are angiosperm-dominated vegetation communities (Rosqvist 2010).

In stagnant shallow vegetated waters, dissolved oxygen (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 by consumers can further lower DO, and extensive respiration rates during degradation of organic material can lead to anoxic conditions (Brönmark and Hansson 2005). Such conditions can further result in formation of toxic hydrogen sulphide (H<sub>2</sub>S) (Wetzel 2001) when sulphate-reducing microbes obtain energy from organic compounds in the absence of oxygen. Hypoxic or 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 for its biota. The seasonal and diurnal fluctuations in environmental conditions in the bays need further exploration by empirical data.

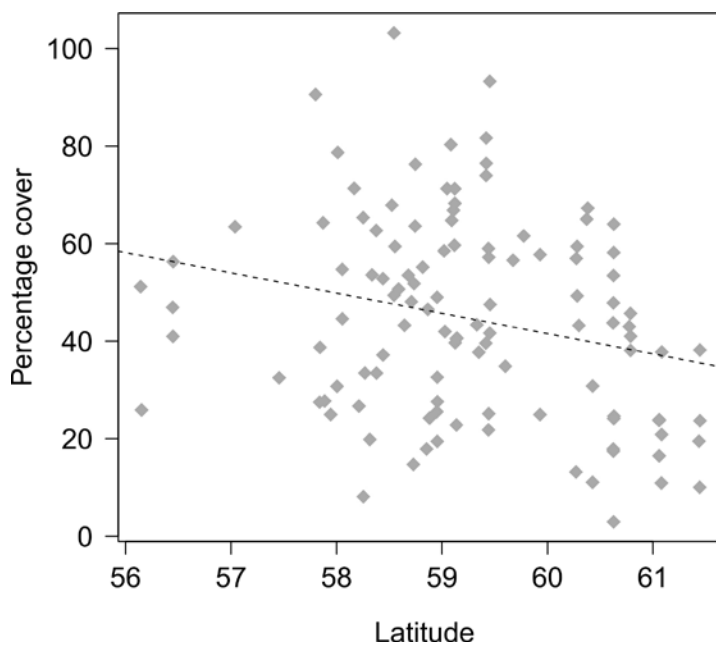
## 3.2 Macroflora

There was no significant effect of the tested environmental variables on cover of macrophytes, except for a small negative effect of latitude on cover (Table 3-3, Figure 3-5). The variation in cover around the estimated slope in response to latitude was very large. The biomass of macroflora, however, changed significantly with topographic openness of the bays. But the change depended on area of the bays. That is, whereas biomass decreased with topographic openness in small bays (<10 ha), no such effect was apparent for large bays (>10 ha) (Table 3-3, Figure 3-6). This scale dependency has not been examined in the previous studies of macroflora biomass in Baltic Sea bays (Hansen et al. 2008a, 2012). The result could be explained by faster recovery of the plant community (here expressed as biomass) after disturbance in large compared to small bays. The flora in the investigated bays can experience severe disturbances due to ice conditions in winter and spring, with anoxia under the ice cover, bottom-freezing, and ice scraping of the bottom. Re-colonization after such disturbance will either occur through drifting shoots or propagules, or via dispersal vectors such as waterfowl. A small opening area and limited water exchange with the open sea of isolated bays may reduce the colonization through passively drifting plants. Re-colonization after a disturbance is hence likely slower in more isolated bays than in more open bays. Furthermore, a large water area will be more frequently visited by waterfowl than a smaller water area (cf. species-area relationship, e.g. Rosenzweig 1995), and therefore the colonization rate may be lower in small compared to large bays, partly explaining the biomass pattern observed here. Slightly deeper water in larger and more open bays can potentially also result in more refuge for the plants to escape destruction from ice scraping. These hypotheses needs, however, to be further examined and empirically tested.

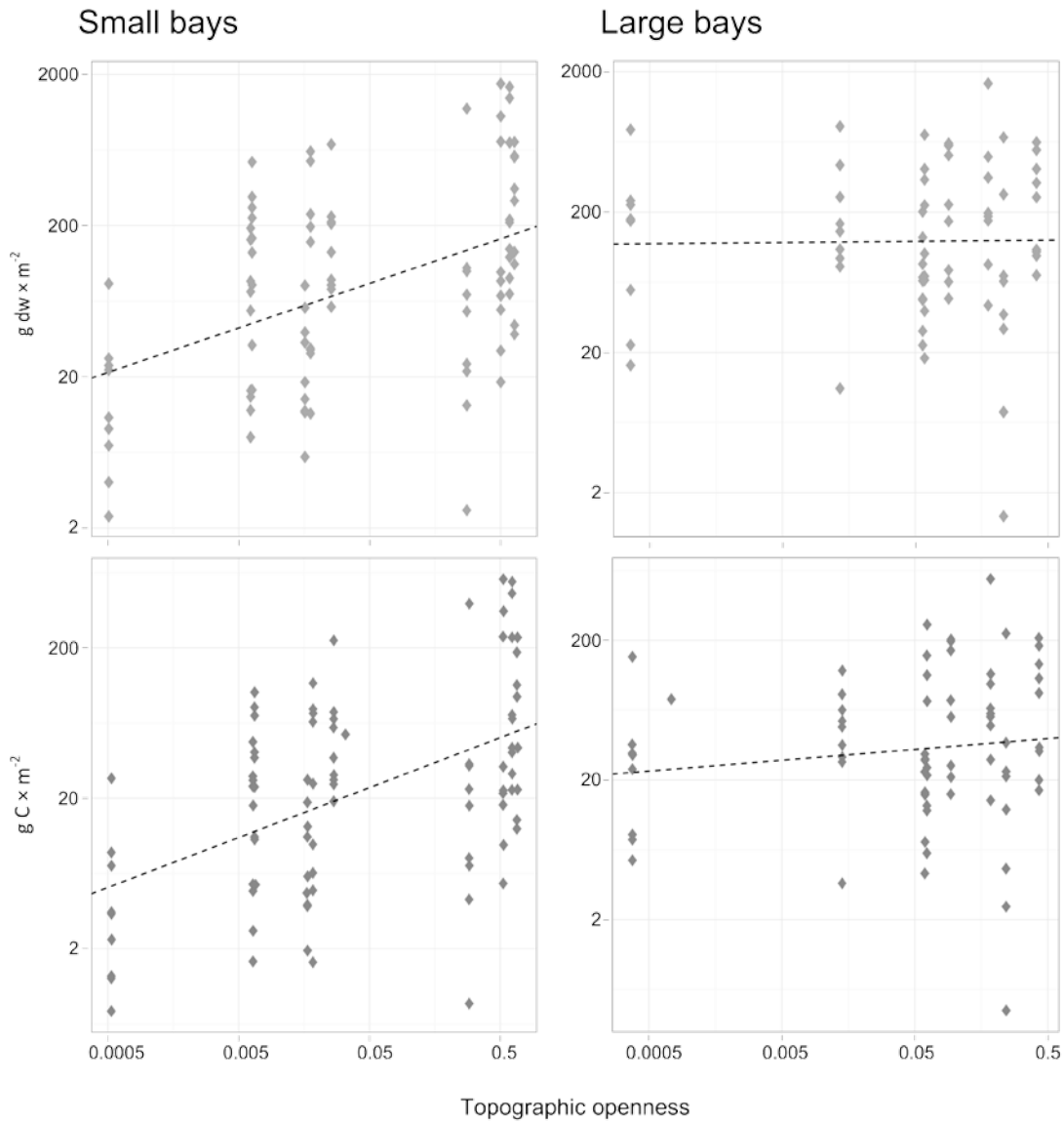
There was a significant change in group composition of macrophytes with increasing bay isolation (Table 3-4, Figure 3-7 and 3-8). The most pronounced change was a decrease in cover and biomass of bladderwrack, as well as a decrease of other, mainly marine, algae with increasing bay isolation. Also the angiosperm cover and biomass showed a tendency to decrease with increasing isolation. The cover and biomass of stoneworts showed a large variation, but with a higher frequency of bays with low cover at low bay-isolation scores. The results are in line with Hansen et al. (2008b), Appelgren and Mattila (2005), and Munsterhjelm (1997), who all recorded changes in species composition with increased bay isolation, with bladderwrack mainly found in open bays. They also recorded changes in angiosperm composition with increased bay isolation, with higher abundance of e.g. some *Potamogeton* and *Ruppia* species in open and intermediately isolated bays, but higher abundance of the species *Najas marina* in more isolated bays. The abundance of several stoneworth species has been recorded to increase with increased bay isolation, e.g. *Chara tomentosa* and *Chara baltica*. Rosqvist (2010) further reported that the difference in species composition is present throughout the growing season, but with a slightly higher increase in cover over the season in isolated bays dominated by stoneworts.

**Table 3-3. Effects of a) latitude on macrophyte cover, and effects of bay area and topographic openness on macroflora biomass expressed as b) dry weight or c) carbon weight. The regression analysis in a) were based on mean cover in 112 bays. Analyses in b) and c) were done using mixed effects models on 168 samples in 18 bays (9 samples per bay), with bay as random blocking factor.**

Factors	Estimate	Std. Error	DF	t-value	P-value
<b>a) Macrophyte cover</b>					
Intercept	291	92.1	111	3.16	0.002
Latitude	-4.15	1.55	111	-2.67	0.009
<b>b) Macroflora dry weight</b>					
Random factor: bay; intercept 0.51, residual 1.22					
Intercept	4.04	0.68	144	5.93	<0.001
Area ( <i>Ln</i> )	-0.35	0.22	14	-1.61	0.13
Topographic openness ( <i>Ln</i> )	-0.32	0.22	14	-1.43	0.17
Area × Topographic openness	-0.18	0.07	14	-2.40	0.031
<b>c) Macroflora carbon weight</b>					
Random factor: bay; intercept 0.48, residual 1.21					
Intercept	2.98	0.66	144	4.55	<0.001
Area ( <i>Ln</i> )	-0.33	0.21	14	-1.55	0.14
Topographic openness ( <i>Ln</i> )	-0.23	0.21	14	-1.07	0.30
Area × Topographic openness	-0.16	0.07	14	-2.30	0.038



**Figure 3-5. Effect of latitude on mean cover of macrophytes in bays along the Swedish Baltic Sea coast from Blekinge to Gävleborg county.**

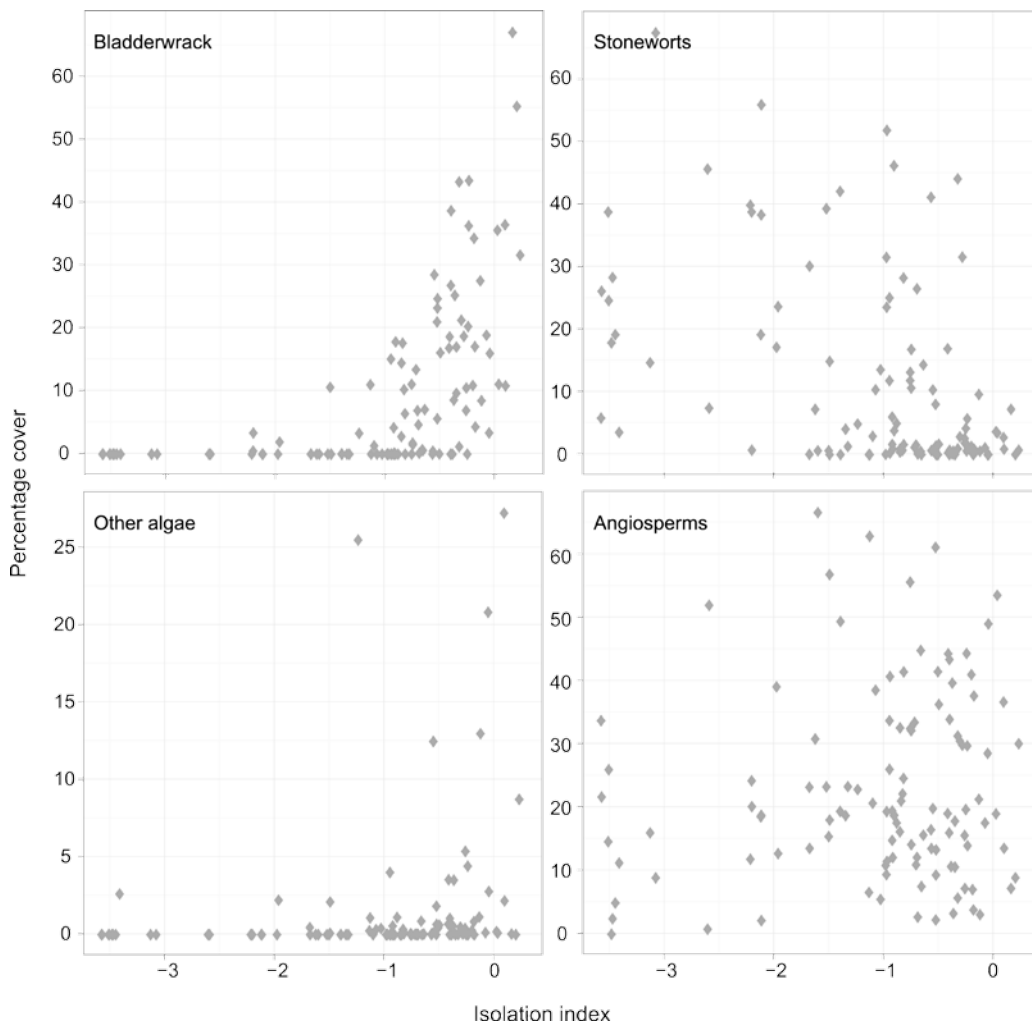


**Figure 3-6.** Effect of topographic openness on biomass of macrophytes in small (<10 ha) and large (>10 ha) bays respectively. The upper two panels show biomass expressed as dry weight per area, while the lower figures show biomass expressed as carbon weight per area. The data consisted of nine samples per bay.

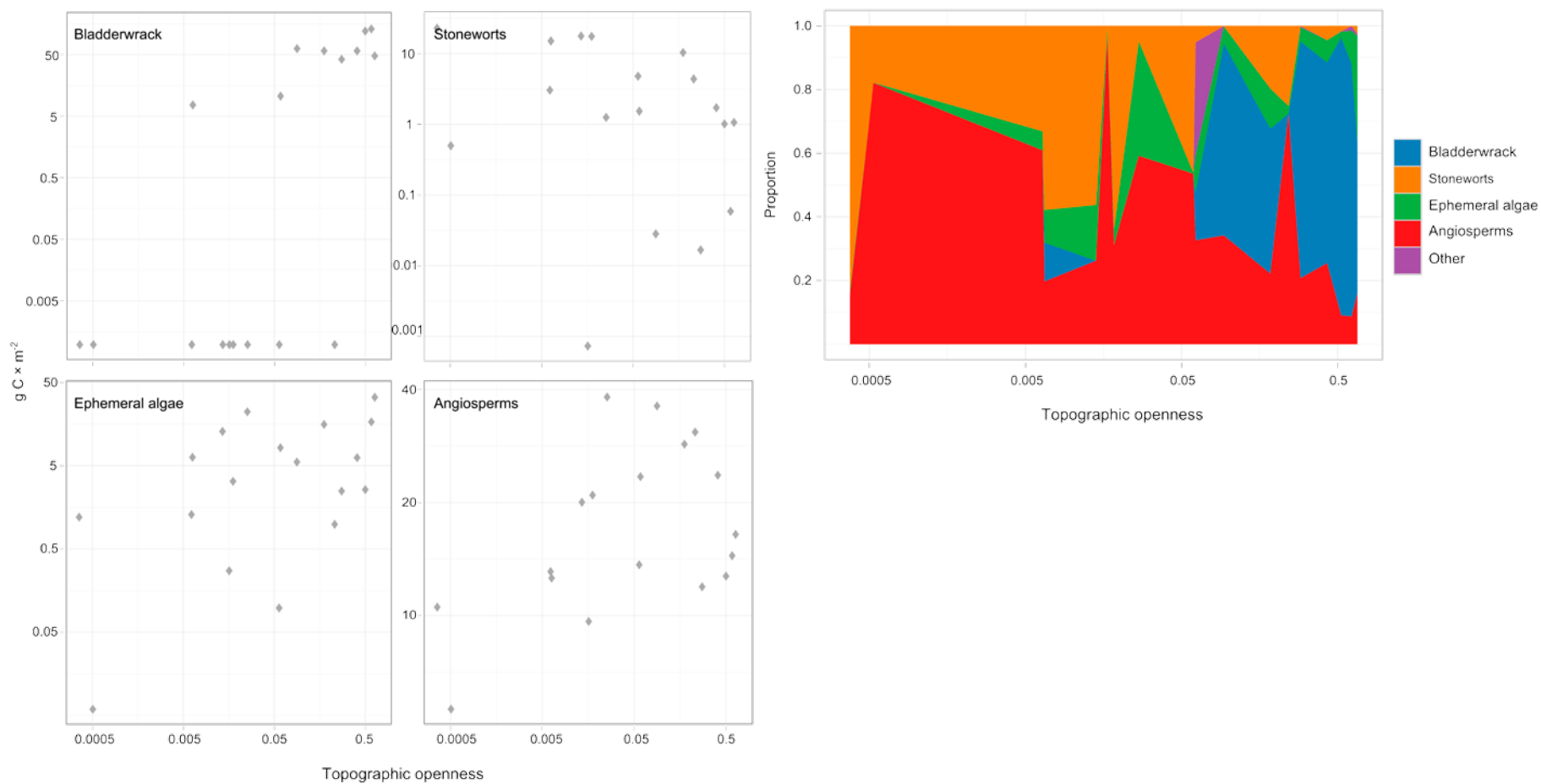


**Table 3-4. Result of NP-Manova showing a) effects of latitude, wave exposure and isolation index on macrophyte group composition based on cover, or b) and c) effects of topographic openness on macroflora biomass expressed as dry weight or carbon weight. Analyses were done on mean values of functional groups of macroflora from 113 bays (cover) or 18 bays (biomass).**

Factors	DF	Sums of squares	Mean squares	Pseudo-F	R <sup>2</sup>	P-value
<b>a) Macrophyte cover</b>						
Latitude	1	0.86	0.86	6.48	0.05	0.001
Wave exposure ( <i>Ln</i> )	1	0.94	0.94	7.07	0.05	0.001
Isolation index	1	2.34	2.34	17.6	0.13	0.001
Residuals	109	14.5	0.13		0.78	
Total	112	18.6			1.00	
<b>b) Macroflora dry weight</b>						
Topographic openness ( <i>Ln</i> )	1	1.05	1.05	7.26	0.31	0.001
Residuals	16	2.31	0.14		0.69	
Total	17	3.36			1.00	
<b>c) Macroflora carbon weight</b>						
Topographic openness ( <i>Ln</i> )	1	1.12	1.12	8.68	0.35	0.001
Residuals	16	2.06	0.13		0.65	
Total	17	3.17			1.00	



**Figure 3-7. Effects of the bay isolation index on mean bay cover of four groups of macrophytes; bladderwrack (*Fucus vesiculosus*), stoneworts (*Charophyceae*), other algae (excluding ephemeral algae) and angiosperms.**



**Figure 3-8.** Effects of topographic openness on biomass of four groups of macroflora; bladderwrack (*Fucus vesiculosus*), stoneworts (*Charophyceae*), ephemeral algae and angiosperms, expressed as carbon weight per area. Proportion of the groups in relation to topographic openness is shown in the upper right panel.

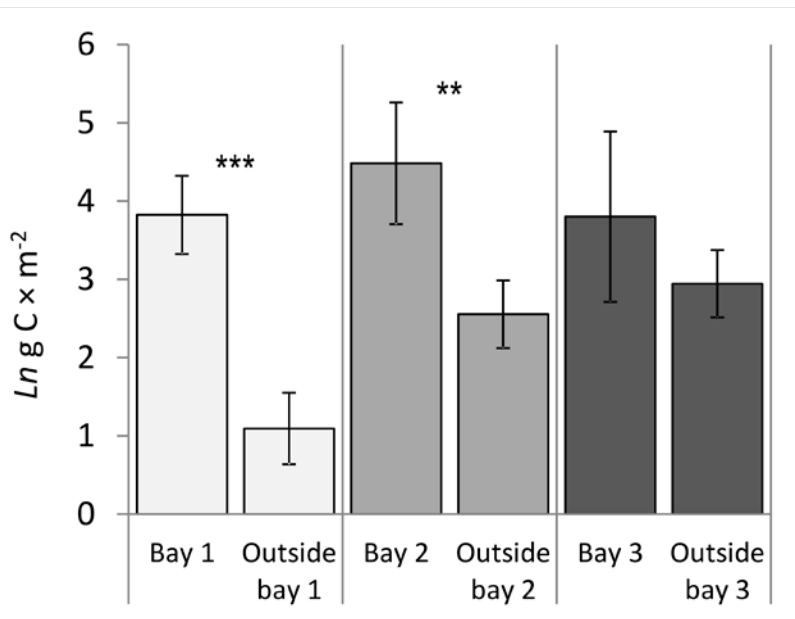
The change in species composition can be a result of several processes; a decrease in water movements, decreased salinity, changed characteristics of the bottom substrate, or an increased variation in water chemistry. The gradual change in abiotic conditions with bay isolation represents a gradient in which the plants and algae have different growth condition limits and optimum. The low salinity of the most isolated bays – at least during spring – may prevent establishment of bladderwrack in these bays (<4.5 PSU). Changed bottoms, from gravel and sand to loose gyttja and a high percentage of volatile solids, can result in increased stress on plant roots due to low oxygen levels. Some angiosperms cannot grow in stagnant water with oxygen depletion near the bottom, while others, such as *Najas marina*, and many stoneworts are capable of growing under such conditions (Munsterhjelm 1997). Seeds of *N. marina* are even stimulated by anaerobic conditions (Van Vierssen 1982, Agami and Waisel 1984). Differences in temperature optima will further affect the plant community. For example, *N. marina* requires a temperature above 16°C and has an optimum germination as high as at 20–25°C (Forsberg 1966, Agami and Waisel 1984, Van Vierssen 1982).

When comparing the pattern observed in species composition along the bay isolation gradient with a classification of the species according to life strategies (Kautsky 1988), one finds that the community changes from a dominance by competitive species at low bay isolation to dominance of ruderal or stunted species at high bay isolation. The first group has developed life strategies for habitats with low stress and disturbance, while the latter two groups have developed strategies for habitats with high level of disturbance (Kautsky 1988). Only a few species have a life strategy for coping with both high disturbance and stress. One of these, *Chara aspera*, is frequently found in very isolated glo-type bays. These findings support the hypothesis of increased stress and disturbance on the macroflora with increased bay isolation.

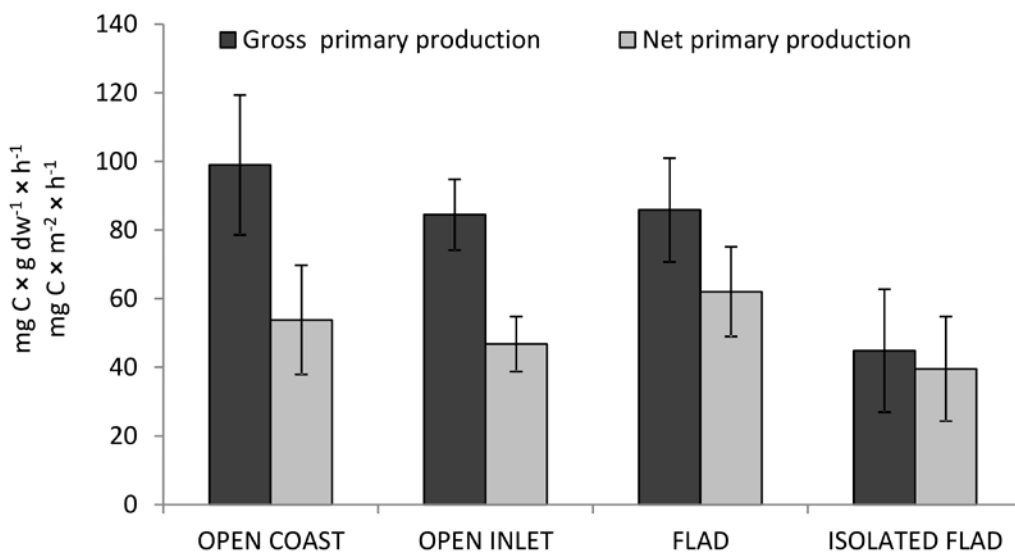
Apart from influence of abiotic factors, the distribution of plants and algae along the bay-isolation gradient will be affected by interactions between the species. This topic is, however, poorly studied in the Baltic Sea bays (Kautsky 1991, Hansen et al. 2008b).

In addition to effects of bay isolation, the macrophyte group composition changed in relation to latitude and wave exposure. The result was mainly due to a decrease in cover of bladderwrack with increasing latitude and decreasing wave exposure. The result is similar to findings of Hansen et al. (2008b), and likely reflects a negative response of bladderwrack to decreasing salinity with increasing latitude, as well as the positive response to increased wave activity and water circulation in the examined gradient. Analysis of macrophyte composition at a species level, rather than at a higher taxonomic group level, shows a change also in angiosperm composition with latitude (Hansen et al. 2008b). The seagrass *Ruppia* spp. has been found mainly in the south, while some freshwater species have only been found at higher latitudes (Hansen et al. 2008b), most likely as a response to changed salinity with latitude. Analysis at a species level also shows that some stoneworts increase in cover with increasing wave exposure of bays (e.g. *Tolypella nidifica*), while most other show the opposite pattern (Hansen et al. 2008b).

In comparison with areas outside the sheltered bays, biomass of macrophytes was found to be higher (Figure 3-9). This can be related both to higher nutrient concentrations and warmer water inside as compared to outside the bays, facilitating growth – although the biomass does not increase with a further increase in bay isolation. In a study by Wijnbladh et al. (2006), benthic primary production was examined in an archipelago area in the southwestern Baltic Proper. A comparison of the mean summer primary production between bays and an open coastal site indicated no significant difference (Figure 3-10) despite the difference found in biomass in Figure 3-9. Neither was there a significant difference in primary production between bays of different degree of isolation from the sea (Figure 3-10). However, there was a trend towards lower gross primary production in the most isolated bay as compared to the other investigated sites. This means that the difference in biomass recorded in late summer only is reflected in a slightly lower primary production in the most isolated bay. The primary production in the bays needs however a further examination, since there are temporal differences in temperature peak and nutrient inflow depending on the bays degree of isolation from the sea, and the production may vary considerably over the season.



**Figure 3-9.** Comparison of macroflora biomass between bays and areas just outside bays. Bars show mean ( $\pm$  95% CI) biomass expressed as carbon weight per area. The data consisted of 9 samples per bay or areas outside bays, sampled at a depth of  $>0<6$  m using similar sized sampling frames. Samples in bays and outside bays were taken the same year and time of year in area 2 and 3, but not in area 1. Area 1 is situated near Forsmark in the southern Bothnian Sea, while area 2 and 3 are situated near Askö in the northern Baltic Proper. Data on biomass outside bays was achieved from Borgiel (2005; area 1), and H. Kautsky (unpublished marine monitoring data, area 2 and 3).



**Figure 3-10.** Comparison of benthic primary production during summer between bays at different degrees of isolation from the sea, as well as one open coast site. Bars show mean ( $\pm$  95% CI) gross or net primary production. The number of samples differed between the bays. There was no significant difference in either gross or net primary production between the bays or the open coastal site (Anova,  $p=0.17$  and  $p=0.18$  for gross and net production respectively). The data was achieved from Wijnbladh et al. (2006).

### 3.3 Periphyton, particulate organic matter and chlorophyll *a*

There was no relationship between topographic openness of the bays and biomass of periphyton, POM, nor with chlorophyll *a* concentration. The periphyton biomass was related to colonization time and hence can be viewed as a measure of biomass productivity, or rather potential productivity since the discs constituted artificial substrates in the bays. The result supports the previously presented findings of no large difference in benthic primary production between bays of different degree of isolation from the sea (Figure 3-10). It should be noted, however, that all these data were sampled in late summer. Scheinin and Mattila (2010) concluded that the difference in productivity potential (nutrients and temperature) between four bays in the northern Baltic Proper (Åland) was the least in late summer and at largest in spring to early summer. They recorded higher chlorophyll *a* concentration in two isolated bays compared to two more open bays in spring, but not later during the summer. To get a better understanding of the processes in the bays a more throughout sampling over the season should be conducted.

### 3.4 Macrofauna

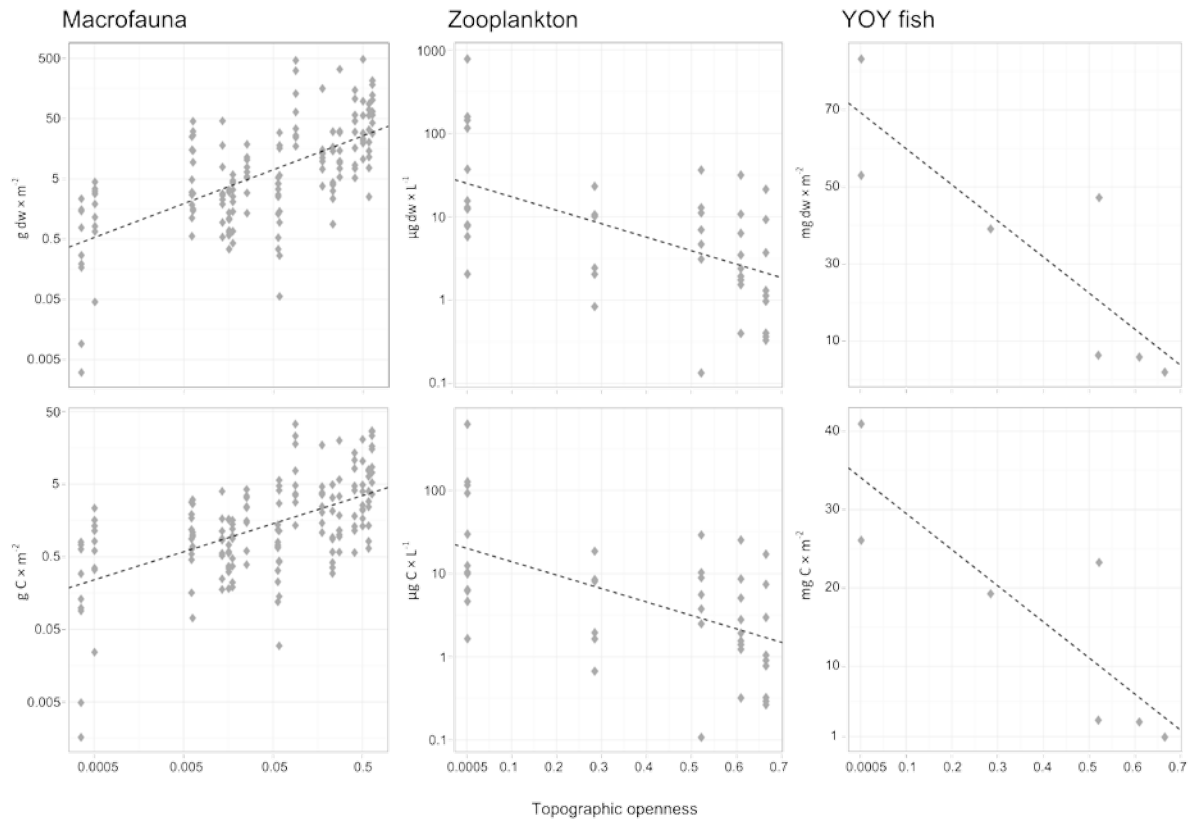
The topographic openness had a significant positive effect on the biomass of macrofauna, while bay area and its interaction with topographic openness had no effect (Table 3-5, Figure 3-11). The result was similar for biomass expressed as dry weight and carbon weight. This means that the biomass decreases with increasing isolation of bays following the shore-level displacement process. Results showed a reduction in biomass to about half at a topographic openness of approximately 0.2. This corresponds to when an open inlet changes to a flad-type bay forming a distinct water body with a small opening. It takes place approximately at 300–350 years before the bay is totally isolated from the sea. The change in biomass can to a large part be explained by a changed composition of the macrofauna (Table 3-6, Figure 3-12). The decrease in biomass with decreasing topographic openness was most pronounced for filterers and scrapers, mainly bivalves and gastropods. These taxa dominate the macrofauna community in open bays, but were replaced by gatherers and predators, which dominated in the most isolated bays. The group of gatherers mainly consisted of crustaceans and insect larvae, where insects dominated in more isolated bays, as did insect predators (Hansen et al. 2008a, 2012). The group of shredders also consisted of crustaceans and insects, with a change in composition from crustaceans (e.g. *Idotea* and *Gammarus*) to insects of the families Coleoptera and Trichoptera with increasing bay isolation (Hansen et al. 2008a, 2012).

In comparison to areas outside bays, the macrofauna biomass was lower in the two investigated areas in the south (bay 2 and 3), but not in the northern area (bay 1, Figure 3-13). The result can mainly be attributed to higher biomass of bivalves outside the bays in the southern area. Here, water movements and readily availability of hard substrates for colonization provide a favourable habitat for bivalves. In the northern area, the bivalve abundance in the sea is lower due to lower salinity. No freshwater bivalves have been found in these samples.

Several factors related to the bay isolation process could cause the observed changes in macrofauna community composition with level of bay isolation. For example, a small opening area and limited water exchange with the open sea in isolated bays may reduce colonization rate, as is probably the case also for the macroflora. 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 macrofauna from the sea. This will be most clear in the case of gloes where the former opening has completely emerged above the sea level. Although aquatic macrofauna can be dispersed via waterfowl (Figuerola and Green 2002, Bohonak and Jenkins 2003, Green and Figuerola 2005) a small threshold openings towards the sea may constitute a significant barrier for colonizers from surrounding waters. This will be more prominent for macrofauna with passive dispersal. The supply of planktophytic macrofauna larvae with long-distance dispersal (i.e., bivalves) to sheltered bays may decrease with increased bay isolation due to a 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.

**Table 3-5. Effects of topographic openness on; a and b) macrofauna, c and d) zooplankton, and e and f) yoy-fish biomass, expressed as dry weight and carbon weight. Analyses on macrofauna and zooplankton biomass were done with mixed effects models on 168 or 43 samples in 18 or 6 bays respectively, with bay as random blocking factor. The analysis on yoy-fish was done with a regression on mean values in 7 bays.**

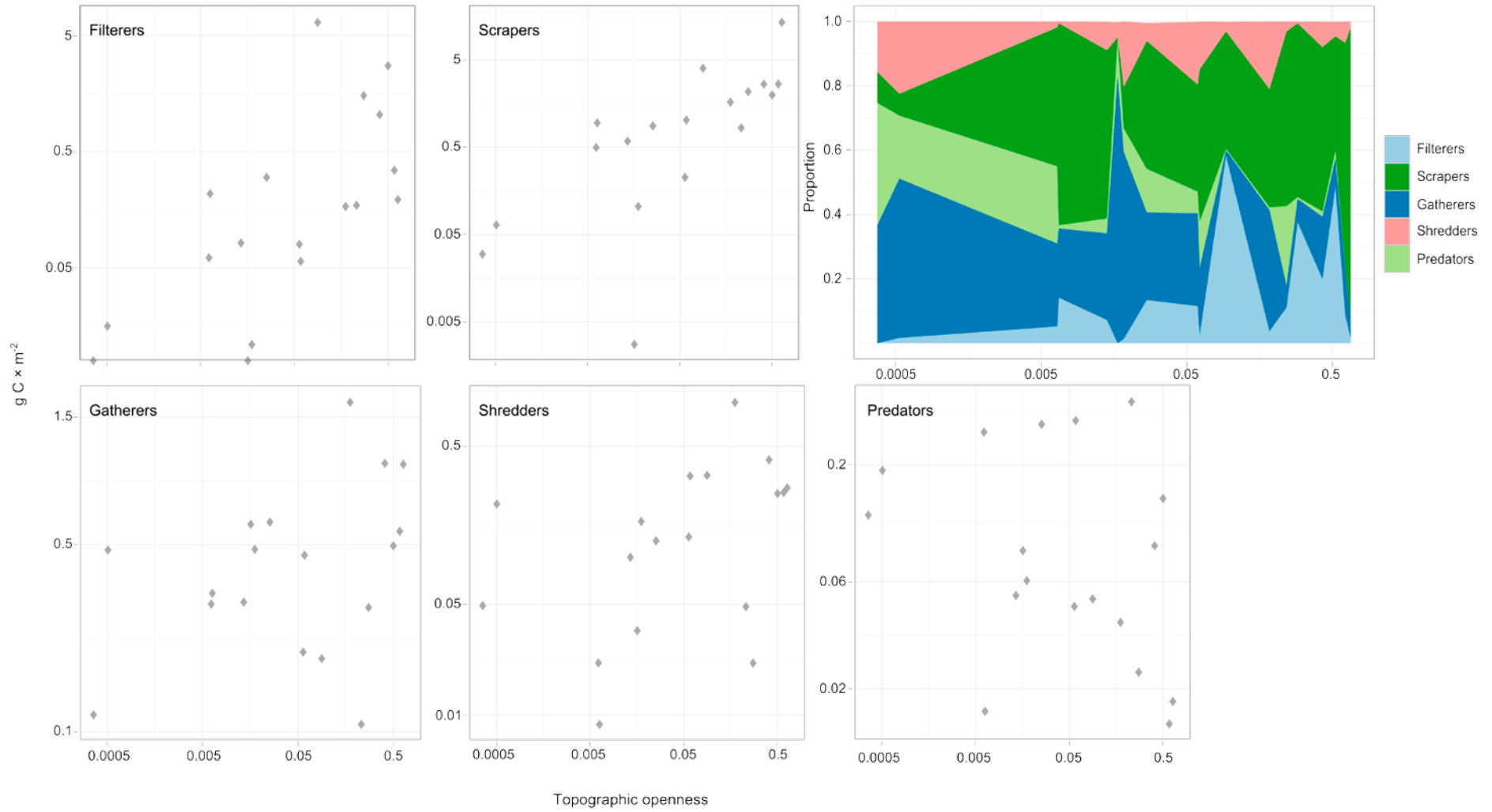
Factors	Estimate	Std. Error	DF	t-value	P-value
<b>a) Macrofauna dry weight</b>					
Random factor: bay; intercept 0.78, residual 1.29					
Intercept	3.64	0.37	144	9.93	<0.001
Topographic openness ( <i>Ln</i> )	0.56	0.10	16	5.90	<0.001
<b>b) Macrofauna carbon weight</b>					
Random factor: bay; intercept 0.55, residual 1.13					
Intercept	1.51	0.28	144	5.54	<0.001
Topographic openness ( <i>Ln</i> )	0.39	0.07	16	5.41	<0.001
<b>c) Zooplankton dry weight</b>					
Random factor: bay; intercept $5.70 \times 10^{-5}$ , residual 1.48					
Intercept	3.23	0.41	37	7.83	<0.001
Topographic openness ( <i>Ln</i> )	-3.72	0.86	4	-4.33	0.012
<b>d) Zooplankton carbon weight</b>					
Random factor: bay; intercept $5.70 \times 10^{-5}$ , residual 1.48					
Intercept	3.00	0.41	37	7.29	<0.001
Topographic openness ( <i>Ln</i> )	-3.72	0.86	4	-4.33	0.012
<b>e) YOY-fish dry weight</b>					
Intercept	69.4	11.4	5	6.08	0.002
Topographic openness ( <i>Ln</i> )	-93.8	25.0	5	-3.76	0.013
<b>f) YOY-fish carbon weight</b>					
Intercept	34.1	5.61	5	6.08	0.002
Topographic openness ( <i>Ln</i> )	-46.1	12.3	5	-3.76	0.013



**Figure 3-11.** Effects of topographic openness on macrofauna, zooplankton and young-of-the-year fish biomass, expressed as dry weight (upper panels) or carbon weight (lower panels). Note the logarithmic scale on both axis for macrofauna, the second axis for zooplankton, but none of the axis for yoy fish. Data on macrofauna and zooplankton consisted of several samples per bay, while yoy fish is expressed as catch per area and bay (see text for more details).

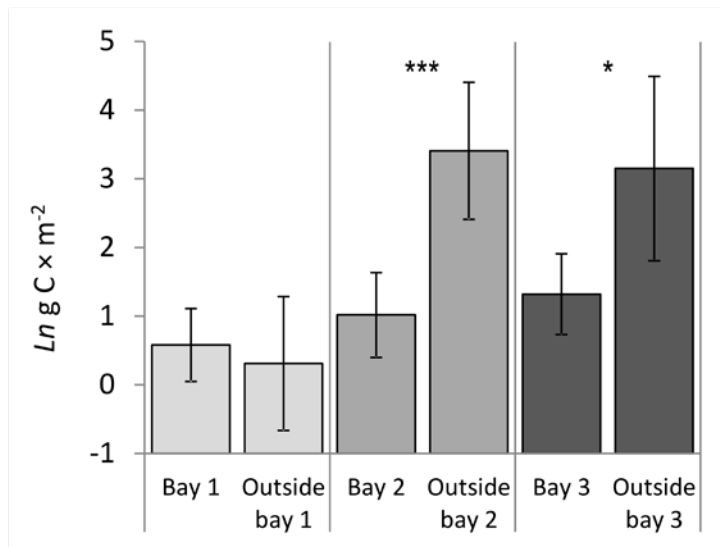
**Table 3-6.** Result of NP-Manova showing effects of topographic openness on; a) and b) macrofauna group composition and c) yoy-fish composition, expressed as dry weight or carbon weight. Analyses were done on mean biomass of functional or taxonomic groups per 18 bays for macrofauna and 7 bays for yoy-fish.

Factors	DF	Sums of squares	Mean squares	Pseudo-F	R <sup>2</sup>	P-value
<b>a) Macroinvertebrate dry weight</b>						
Topographic openness ( <i>Ln</i> )	1	1.23	1.23	6.24	0.28	0.001
Residuals	16	3.16	0.20		0.72	
Total	17	4.39			1.00	
<b>b) Macroinvertebrate carbon weight</b>						
Topographic openness ( <i>Ln</i> )	1	1.02	1.02	7.05	0.31	0.002
Residuals	16	2.31	0.14		0.69	
Total	17	3.32			1.00	
<b>c) YOY-fish dryweight (and carbon weight)</b>						
Topographic openness ( <i>Ln</i> )	1	0.75	0.75	4.70	0.48	0.043
Residuals	5	0.80	0.16		0.52	
Total	6	1.55			1.00	



**Figure 3-12.** Relationship between topographic openness and biomass of five functional groups of macrofauna, expressed as carbon weight per area and bay. Proportion of the functional groups in relation to topographic openness is shown in the upper right panel.





**Figure 3-13.** Comparison of macrofauna biomass between bays and areas just outside bays. Bars show mean ( $\pm$  95% CI) biomass expressed as carbon weight per area. The data consisted of 9 samples per bay or areas outside bays, sampled at a depth of  $>0<6$  m using similar sized sampling frames. Samples in bays and outside bays were taken the same year and time of year in area 2 and 3, but not in area 1. Area 1 is situated near Forsmark in the southern Bothnian Sea, while area 2 and 3 are situated near Askö in the northern Baltic Proper. Data on biomass outside bays was achieved from Borgiel (2005; area 1), and H. Kautsky (unpublished marine monitoring data, area 2 and 3).

Decreased water movements in isolated bays can further restrict 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). These species benefit from a constant flow of food particles to filter out from the water column. For rivers, a ratio of filtering collectors to gathering collectors have been suggested as an indication of whether an aquatic ecosystem is dominated by influence of suspended particulate organic matter or by deposited organic matter (Merritt et al. 2002). The change in macrofauna composition of the Baltic Sea bays examined here points towards a system that is increasingly influenced by benthic particulate organic matter with increasing bay isolation, which also correlates to the increase in volatile solids with increasing bay isolation.

Low salinity in the most isolated bays may hinder permanent establishment of some Baltic Sea macrofauna of marine origin in isolated bays. For example, the crustaceans *Palaemon adspersus* and *Idotea balthica* have an approximate lower salinity tolerance of about 5 PSU (Barnes 1994, BACC author team 2008). Similarly, high salinity may prevent permanent establishment of some freshwater macrofauna in the most open bays. The effect of salinity is reflected in a decrease in the mean proportion of macrofauna of marine origin with increasing bay isolation (Hansen 2010). However, mean salinity may not be the most important factor here, but rather the peaks of a seasonally fluctuation salinity, which can be higher in more isolated bays compared to open bays. Similarly, fluctuations in DO (as explained earlier) will affect the macrofauna. Only animals capable of coping with these fluctuating abiotic conditions will be able to establish in the more isolated bays. The combination of potentially more frequent disturbance in isolated bays, and increased dispersal barrier for colonizers from the sea (through decreased openness), may contribute to explain the decrease of relatively slow colonisers (bivalves and gastropods) and increased proportion of faster colonisers (arthropods) with increased bay isolation, especially those with high dispersal rates due to airborne life stages (insects).

The macrofauna community can also respond to changes in the macrophyte composition that accompany the bay isolation process. The macrophyte community can affect the faunal community in a variety of ways. Macrophytes provide habitat structure for macrofauna, facilitating shelter against predation and niche separation. They also constitute an energy source for consumers. As macroflora differ in habitat and food quality (Hansen et al. 2010, Hansen 2012), changes in taxon composition of macroflora with bay isolation can directly affect the faunal community as habitat structure and food resources are altered. A higher biomass of macroflora in open bays also means that the

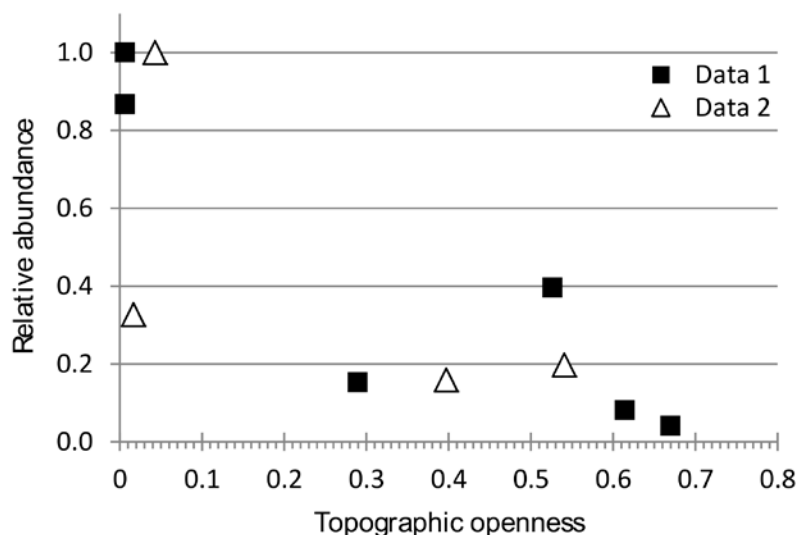
colonisable area for plant-associated invertebrates is larger here, which partly can explain the higher macrofauna biomass in more open compared to isolated bays. The ratio of scrapers and grazing shredders in relation to detritivorous shredders and collectors have been suggested as an indication of changes in a system from autotrophic to heterotrophic (Merritt et al. 2002). The results of the present study points towards a decreasingly autotrophic-fed system with increased bay isolation (i.e. decreasing ratio of primary consumers), although it is difficult to categorize the fauna of the shallow Baltic Sea bays into strict trophic levels (Hansen et al. 2012).

Top-down control of shallow Baltic Sea areas has been suggested by Eriksson et al. (2009, 2011; in conjunction with bottom-up processes). As the density of macrofauna-feeding cyprinid fishes is higher in more isolated than open bays, predation pressure on the macrofauna may be higher in such bays. This is another possibility explaining the decrease in macrofauna biomass along the bay isolation gradient and should be further explored.

Since mechanisms for the changed macrofauna community composition was not specifically tested, the relative importance of the mentioned factors (and possibly others) needs to be further explored. Both seasonal variation and dispersal of animals needs to be examined. In addition, infauna of these bays must be more thoroughly examined. Today, only a few bays have been examined for infauna (Wallström et al. 2000). The effect of latitude on the macrofauna community was not examined in the present study because of a short gradient sampled with an unbalanced design. The sampled data suggest a small difference in macrofauna composition between regions, but the effect of latitude on the macrofauna in the bays needs to be further explored.

### 3.5 Zooplankton

The zooplankton biomass decreased significantly with increasing topographic openness of the bays (Table 3-5, Figure 3-11). This means that the biomass of zooplankton increases as bays becomes more isolated in the shore-level displacement process and is doubled about the time when an open inlet changes to a flad-type bay (topographic openness of ca. 0.2 and ca. 300–350 years before a bay is totally isolated from the sea). The method applied here (Hansen et al. 2012) did not sample small zooplankton. Hence, data was compared with Scheinin and Mattila (2010), where also small zooplankton were sampled (50 µm-net; including also rotifers) and the results were similar. The two most isolated bays in Scheinin and Mattila's (2010) study had significantly higher biomass than had the two more open bays studied. The two datasets of Scheinin and Mattila (2010) and Hansen et al. (2012) were combined in Figure 3-14, where the relative abundance in relation to the maximum is expressed as a function of topographic openness. Relative abundance was used since methods of the two studies differed and data could not be straightly compared. The study of Scheinin and Mattila (2010) also sampled zooplankton throughout the season and it is important to note that the difference in abundance between bays was smaller in late summer (as in Figure 3-14) compared to earlier in the season (Scheinin and Mattila 2010), as well as later during the autumn (M. Scheinin pers. comm.). In turn of the months May–June, the zooplankton abundance was more than 25-times higher in the isolated bays as compared to the more open bays (Scheinin and Mattila 2010). In agreement, Kallasvuo et al. (2010) recorded more than 10 times higher densities of zooplankton during spring in reed-covered shores in the inner archipelago compared more exposed shores in the northeastern Baltic Proper. The increased zooplankton biomass with more sheltered conditions and increased bay isolation has been suggested to be related the combination of both high temperature and nutrients (Scheinin and Mattila 2010). These factors affect productivity with a resulting higher food availability in the form of phytoplankton and higher growth rate of the zooplankton. However, a higher chlorophyll *a* concentration was not found in the present study. Input of organic matter via run-off from land is another potential factor that can promote zooplankton growth. Isolated bays may potentially be more influenced by allochthonous carbon from terrestrial sources as the inflow from land run-off can be expected to increase relative to seawater inflow. In addition, zooplankton are fast colonizers since they have high population growth rates and are readily dispersed at distances up to 10 km directly via air or via vectors such as waterfowl (Havel and Shurin 2004). They may hence be early colonizers in an unexploited habitat after disturbance, possibly adding to explain their high abundance in the more variable habitats of the isolated bays.

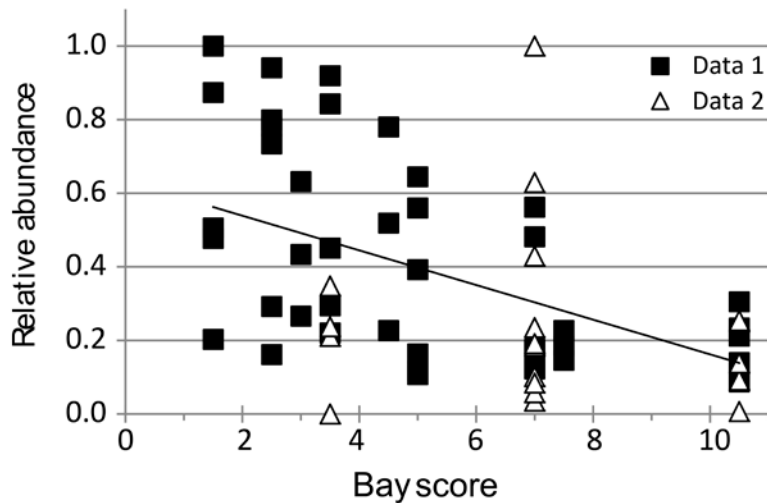


**Figure 3-14.** Abundance of zooplankton in relation to topographic openness, combining data from two studies in the northern Baltic Proper (Data 1: Hansen et al. 2012, Data 2: Scheinin and Mattila 2010). Abundance is expressed as relative to the maximum observed in the studies, since sampling methods of the two studies differed.

Effects of latitude and area, and its interaction with topographic openness, were not examined because of a low number of bays sampled for zooplankton. These effects should be investigated in the future together with a more thorough examination of mechanisms regulating the zooplankton biomass and taxon composition, complementing the studies of Scheinin and Mattila (2010) and Hansen et al. (2012).

### 3.6 Young-of-the-year fish

The yoy-fish biomass decreased significantly with increasing topographic openness of the bays (Table 3-5, Figure 3-11). This means that as bays become more isolated from the sea they also become more important as spawning sites for warm-water spawning fish in the coastal area. The fish biomass was doubled in the step when an open inlet changes to a flad-type bay (at a topographic openness of about 0.3, corresponding to ca. 350–400 years before a bay is totally isolated from the sea). The reason for this can largely be attributed higher temperature in more isolated bays in late spring and early summer. Several of these fish species have a growth rate that is clearly positively related to water temperature (e.g. Karås 1996, 1999). However, high biomass of zooplankton in isolated bays is also an important factor that can explain the pattern. In addition, low salinity – especially during spring – will affect the fish spawning since these fish species are of freshwater origin and some require salinities below 4 PSU for their early embryonic development (e.g. roach, Schoefer 1979, Lappalainen and Urho 2006, Härmä et al. 2008). Location in the archipelago area has been shown to be important for the yoy-fish abundance. Sheltered inner archipelago areas produce better reproduction habitats than outer more wave exposed archipelago areas. The combined effect of topographic openness and wave exposure on yoy-fish abundance has been shown by Snickars et al. (2009) and Hansen et al. (2012). In Figure 3-15 data from the two studies and from Hansen et al. (2008b) have been combined, showing the relative abundance in relation to the maximum, since the methods differed between the studies. In addition to abiotic conditions and zooplankton densities, vegetation in the bays have been suggested to affect the yoy-fish abundance (Snickars 2008, Snickars et al. 2009, 2010, Rosqvist 2010). For example, reed and large perennial submerged species are important spawning substrates for perch (Snickars et al. 2010). Tall stands of vegetation have also been suggested to have positive effects on yoy-fish diversity in the bays (Snickars 2008, Rosqvist 2010).

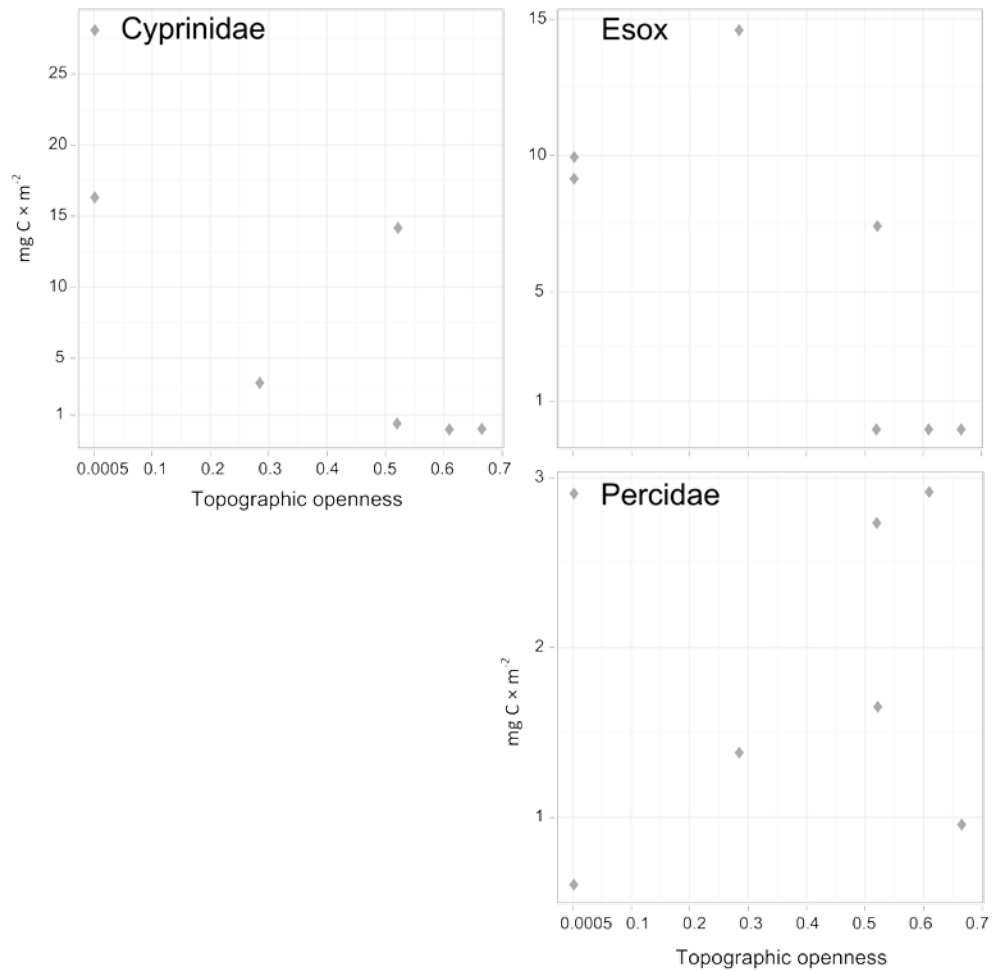


**Figure 3-15.** Relationship between abundance of young-of-the-year fish and a gradient combining topographic openness and wave exposure (bay score; Snickars et al. 2009). Low bay scores corresponds to bays with low topographic openness situated in archipelago areas with low wave exposure (inner coast), while high bays scores corresponds to open bays in archipelago areas with high wave exposure (outer coast). Data are combined from studies in the northern Baltic Proper and the southern Bothnian Sea (Data 1: Snickars et al. 2009, Data 2: Hansen et al. 2008, 2012, unpublished). Abundance is expressed as relative to the maximum observed in the studies, since sampling methods of the studies differed.

The composition of yoy fish changed with increasing topographic openness of the bays (Table 3-5, Figure 3-16). An increase in biomass with increasing bay isolation was pronounced for cyprinid-fish, while no clear relationship was evident for perch (*Perca fluviatilis*). Among cyprinids, crucian carp (*Carassius carassius*), tench (*Tinca Tinca*) and rudd (*Scardinius erythrophthalmus*) was most abundant in the most isolated bays, while bleak (*Alburnus alburnus*) was abundant in more open bays, and minnow (*Phoxinus phoxinus*) in the most open bays (Hansen et al. 2008b, 2012, Snickars et al. 2009). Pike showed a tendency of a unimodal response to bay isolation, with highest abundance in moderately isolated bays.

In autumn the water temperature decreases in the bays, often more rapidly than in the sea. When the temperature drops the yoy fish migrate out from the bays. This migration represents an export of energy from the bays and the fish are potential vectors for transport of radionuclides out of the bays to other archipelago areas. Today there is a shortage in knowledge about the magnitude and spatial extent of the transport and this needs to be further investigated.

To the best of my knowledge, no peer-reviewed studies have been published regarding the relationship between topographic openness of bays and abundance of adult fish. The patterns observed for juvenile fish abundance is probably similar in the adult fish community. This applies specifically to the spring period, when fish migrate to warm water areas that provide suitable temperature conditions for recruitment (e.g. Snickars et al. 2010). Several studies suggest strong homing behaviour towards spawning sites for pike, perch and pike-perch (*Stizostedium lucioperca*) (Karàs and Lehtonen 1993, Saulamo and Neuman 2002, Bergek et al. 2010, Olsson et al. 2011). Bergek et al. (2010) showed a genetic differentiation in perch between bays as close as 3 km from each other. After spawning the adult fish migrate to feeding areas often close to the spawning area. Later, towards winter, the fish move to deeper areas. Pike is the most stationary of the three mentioned species due to its territorial and ambush-hunting behaviour, and it seldom migrates longer than 5 km



**Figure 3-16.** Relationship between topographic openness and biomass of three taxa of young-of-the-year fish, expressed as carbon weight per area and bay.

(90% recapture  $\leq 5$  km from tagging site; Saulamo and Neuman 2002). The corresponding figures for perch and pike-perch are 80% within 10 km, and 75% within 9 km, respectively. These fish species can however migrate longer distances, and migrations over 100 km are not unusual (Lehtonen 1979, cited in Saulamo and Neuman 2002). The fish migrate longer distances in sheltered archipelago areas (with abundant suitable habitats) as compared to more open coastal areas (with less suitable habitats) (Saulamo and Neuman 2002). Studies in freshwater systems have reported several cyprinids to also show quite strong site fidelity (Popova et al. 1998, Winter and Fredrich 2003, Skov et al. 2008). However, the migration behaviour of cyprinids can differ at an individual level due to both environmental cues and migration history (Skov et al. 2010).

### 3.7 Stable isotopes

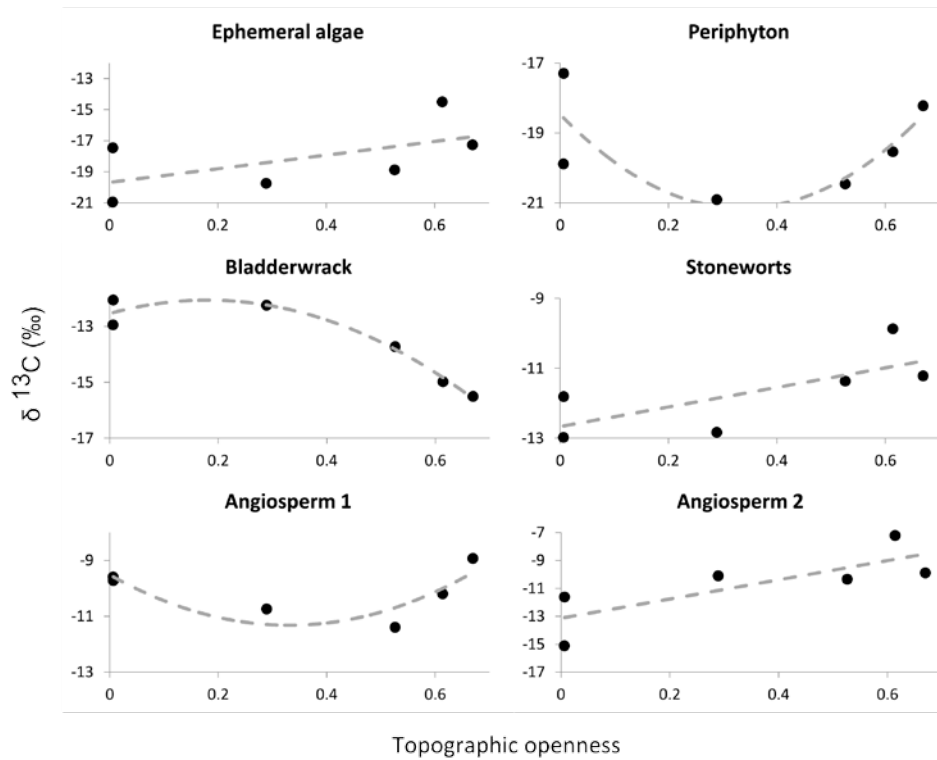
The ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  ( $\delta^{13}\text{C}$ ) in relation to topographic openness of the bays was studied graphically (Figure 3-17 and 3-18), and no regression tests were performed because of the low number of bays studied and no clear linear relationships. Instead the results are briefly discussed from an ecological point of view. More details, and statistical test of effects of bay isolation on both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , can be found in Hansen et al. (2012). The variation in  $\delta^{13}\text{C}$  around the mean for each bay is found in Table 3-7.

One question of interest for the biosphere modelling is whether plants and algae change their way of uptake of carbon. Submerged aquatic plants and algae are generally good at exploiting bicarbonate ( $\text{HCO}_3^-$ ) as a carbon source when dissolved  $\text{CO}_2$  in the water decreases. Such a situation can emerge in stagnant water during high photosynthetic activity. Then carbon can become a growth-limiting element (Vadstrup and Madsen 1995). Such conditions are probably more frequent in isolated than open bays. The resulting pattern in  $\delta^{13}\text{C}$  would be an increase with increasing bay isolation (i.e. decreasing topographic openness). Interpreting from the results presented in Figure 3-17 this does not seem to be the general case for the primary producers. Only bladderwrack showed a tendency to increase in  $\delta^{13}\text{C}$  with decreasing topographic openness. Ephemeral algae, stoneworts and one angiosperm (*Myriophyllum spicatum*) showed instead a tendency towards the opposite, i.e. decreased  $\delta^{13}\text{C}$  with increasing bay isolation. Not only uptake of  $\text{HCO}_3^-$  affects the  $\delta^{13}\text{C}$  signal of the primary producers (Keely and Sandqvist 1992). A decrease in  $\delta^{13}\text{C}$  with decreasing bay isolation can be the result of decreased growth rate (Carvalho et al. 2009) because of increased competition for carbon, but could also arise from an increased uptake of carbon of respiratory origin (Keeley and Sandqvist 1992). In stagnant shallow waters, carbon of respiratory origin may constitute a significant proportion of the available pool, due to high decomposition rate in organic-rich sediments and to plant respiration at night. The observed pattern in  $\delta^{13}\text{C}$  is a result of several simultaneously on-going processes and should be exclusively examined in the future using manipulative studies.

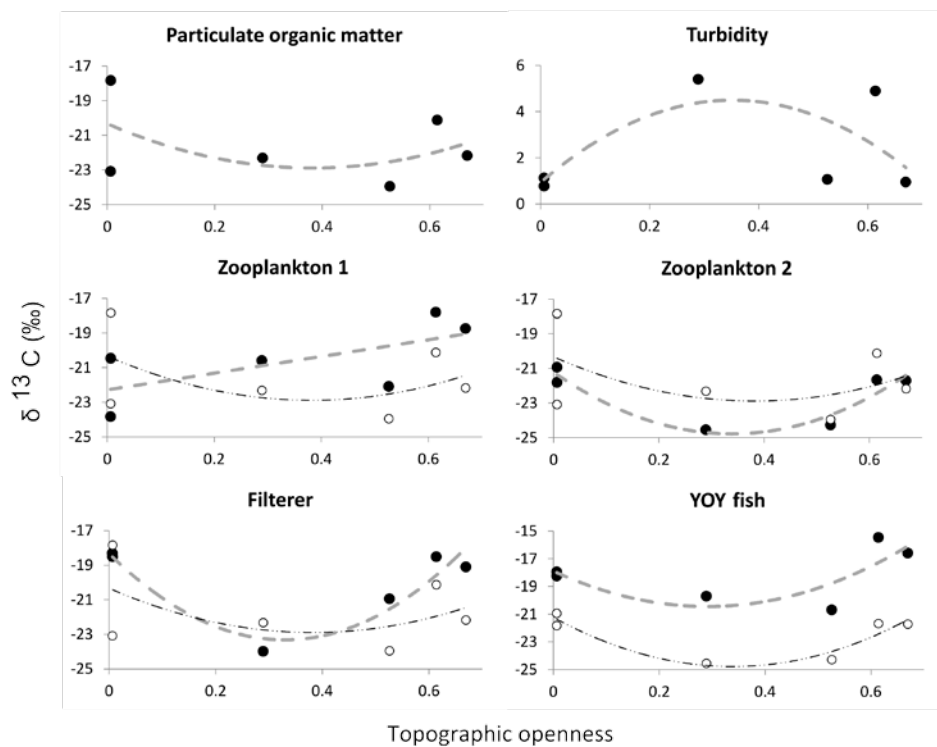
Another question of concern for understanding ecology of the shallow bays is whether the input of carbon from terrestrial sources increases with increasing bay isolation. Since the relative importance of water run-off from land can be expected to increase relative to seawater inflow, allochthonous carbon from terrestrial sources may increase with increasing bay isolation. Organic carbon from terrestrial sources has lower  $\delta^{13}\text{C}$  than carbon produced in aquatic and marine environments. Shore vegetation along the investigated bays has been recorded to have a  $\delta^{13}\text{C}$  of about  $-27$  (reed) to  $-29$  (deciduous tree) (Hansen et al. 2012), in comparison to the higher  $\delta^{13}\text{C}$  of submerged primary producers (Figure 3-17, Table 3-7). If the ratio of terrestrial to marine organic carbon would increase with increased bay isolation, so would potentially the  $\delta^{13}\text{C}$ -signal of particulate organic matter in the water (POM). This signal would further be reflected in pelagic primary consumers or benthic filter feeders acquiring food from particles in the water, but with a fractionation of about  $-1$  to  $+2$  ‰ (Van der Zanden and Rasmussen 2001, Caut et al. 2009). This is not the case in the investigated bays (Figure 3-18). The POM signal did not change much along the studied gradient in topographic openness. It showed a tendency of a unimodal response, in contradiction to what would be expected if allochthonous terrestrial carbon increased in proportion with increasing bay isolation. Another interesting result is that the potential consumers of POM, zooplankton and a filtering bivalve, did not seem to consume POM. In comparison, the  $\delta^{13}\text{C}$  of the sampled yoy fish followed the signal of one of the zooplankton (Copepoda) with an approximate expected fractionation of just over  $+2$ ‰ (Van der Zanden and Rasmussen 2001, Caut et al. 2009), and hence reflects this predator-prey relationship.

The tendencies in the data point towards a possible relationship between turbidity, and the  $\delta^{13}\text{C}$  value for one of the zooplankton and the filtering bivalve. It is possible that these consumers selectively use food sources that are more depleted in  $^{13}\text{C}$  than is the bulk POM. They may utilize smaller-sized carbon sources than obtained in the POM samples of  $10\ \mu\text{m}$ . In comparison, Jones et al. (1999) observed depletion of zooplankton  $\delta^{13}\text{C}$  with increased water colour in forest lakes in Finland. The stable isotope signatures of Copepods (zooplankton 2) and the filter feeding bivalve may thus be derived from the utilization of dissolved or small-sized particulate carbon of terrestrial origin, possibly altered through microbial processes (Jones et al. 1999, Karlsson et al. 2004). The results suggest that the importance of terrestrial carbon as a food source is not related to bay isolation, but should be studied more in relation to other characteristics of the bays, such as turbidity, which in turn is affected by for example features of the catchment area. However, a more rigid sampling of a higher number of bays during several occasions throughout the season would generate a better understanding of the influence of terrestrial energy on the aquatic food web in the bays. It is possible that the spring flood (which was not sampled here) produces the most important inflow of energy to the bays (Berggren et al. 2010), and that this energy stays for a long period of time in the food web.





**Figure 3-17.** Isotope ratio of  $^{13}\text{C}:^{12}\text{C}$  ( $\delta^{13}\text{C}$ ) in relation to topographic openness of bays for six groups of primary producers (angiosperm 1 is *Potamogeton pectinatus* and angiosperm 2 is *Myriophyllum spicatum*). Points show mean values per bay and year (bays were sampled in two years). Regression lines were fitted manually. See text and Table 3-7 for more details.



**Figure 3-18.** Isotope ratio of  $^{13}\text{C}:^{12}\text{C}$  ( $\delta^{13}\text{C}$ ) in relation to topographic openness of bays for particulate organic matter and four groups of consumers (zooplankton 1 is Cladocera and zooplankton 2 is Copepoda). Upper right panel shows turbidity in relation to topographic openness of the bays. Points show mean values per bay and year (bays were sampled for stable isotopes in two years). Black points and broken grey line show stable isotope values of the consumer groups, while open circles and dash-dotted lines represent the isotope values of expected prey for the consumers. Regression lines were fitted manually. See text and Table 3-7 for more details.

**Table 3-7. Mean  $\pm$  SE isotope ratio of  $^{13}\text{C}:^{12}\text{C}$  ( $\delta^{13}\text{C}$  in parts per thousand) of eleven functional or taxonomic groups in six bays in the northwestern Baltic Sea Proper. The functional groups are ephemeral algae (filamentous rhodophyta, phaeophyta and chlorophyta), periphyton, bladderwrack (*Fucus vesiculosus*), stoneworts (*Chara* spp.), angiosperm 1 (*Potamogeton pectinatus*), angiosperm 2 (*Myriophyllum spicatum*), particulate organic matter, zooplankton 1 (Cladocera), zooplankton 2 (Copepoda), filterer (*Parvicardium hauniense*) and yoy fish (Cyprinidae). First column lists topographic openness of the bays (Ea).**

Bay name	Ea	Ephemeral algae		Periphyton		Bladderwrack		Stoneworts		Angiosperm 1		Angiosperm 2		Particulate org. matter		Zooplankton 1		Zooplankton 2		Filterer		YOY fish	
Gråshålet	0.670	-17.3	0.7	-18.2	0.3	-15.5	1.1	-11.2	1.0	-8.9	0.8	-9.9	1.0	-22.2	1.4	-18.8		-21.7	1.0	-19.1	0.4	-16.6	0.4
Hamnhamn	0.614	-14.5	0.9	-19.5	0.3	-15.0	3.7	-9.9	0.6	-10.2	1.6	-7.2	0.2	-20.1	0.7	-17.8	1.7	-21.7	1.1	-18.6	0.9	-15.5	0.3
Svarthålet	0.526	-18.8	0.5	-20.5	0.6	-13.7	1.1	-11.4	0.5	-11.4	0.9	-10.3	0.5	-24.0	0.3	-22.1		-24.3	0.8	-22.1	0.4	-20.7	0.4
Kuggviken	0.289	-19.8	0.6	-20.9	0.4	-12.3	0.2	-12.8	0.7	-10.7	1.3	-10.1	0.7	-22.3	0.8			-24.6	0.5	-23.6	1.4	-19.7	0.5
Lermaren	0.007	-17.5	1.1	-17.3	0.8	-12.1	0.9	-11.8	0.7	-9.7	0.6	-11.6	0.6	-17.8	1.8	-20.5	1.0	-20.9	1.0	-17.9	1.6	-18.2	0.4
Stenmars-fladen	0.006	-21.0	0.4	-19.9	0.5	-12.9	4.3	-13.0	0.4	-9.6	0.4	-15.1	1.1	-23.1	0.5	-23.8	0.8	-21.8	1.4	-20.0	1.0	-18.0	0.5



## 4 Conclusion

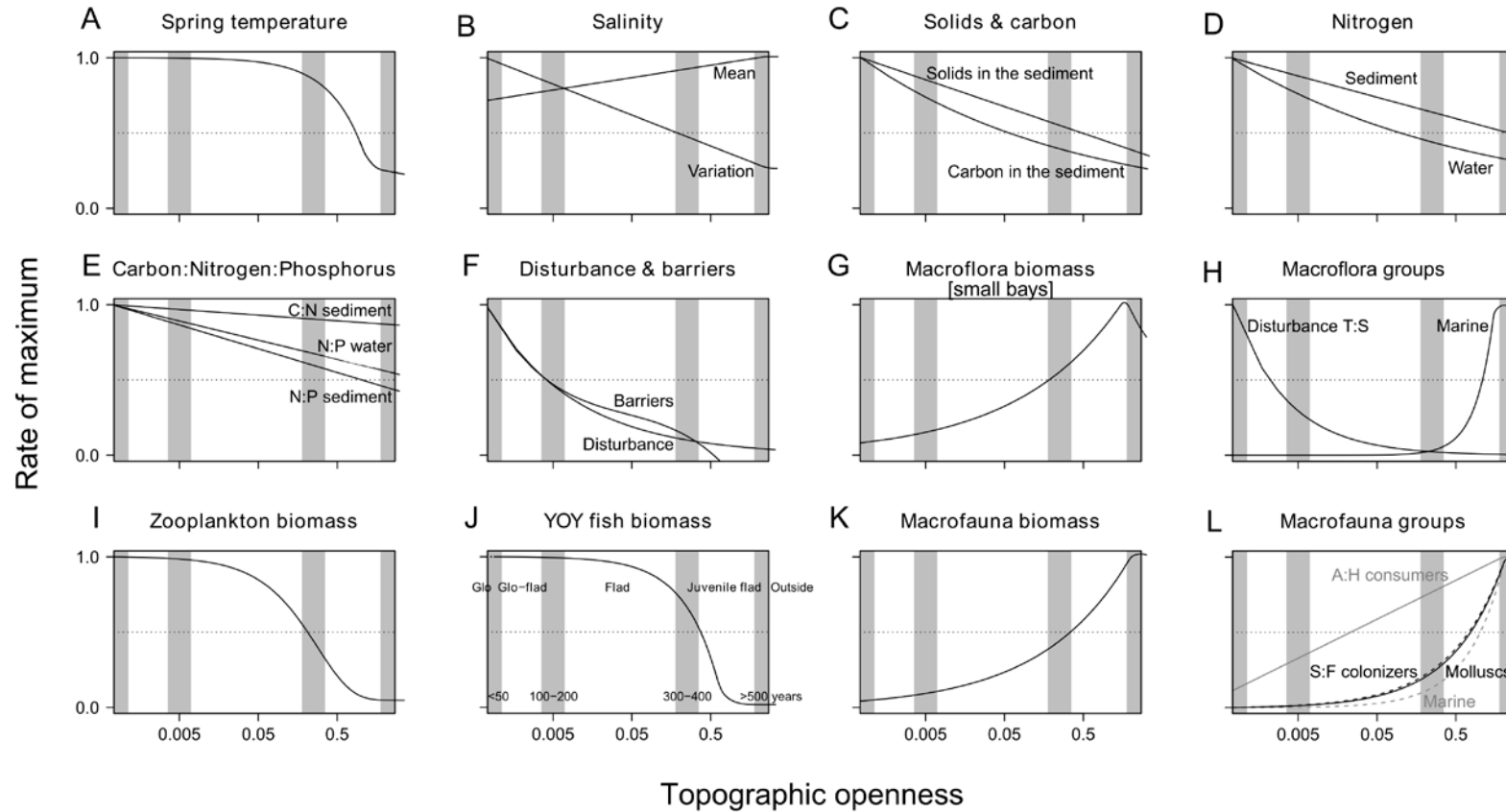
The aim of this report was to describe changes in ecological properties of Baltic Sea bays following shore-level displacement and isolation of bays from the sea. The investigated bays represented a temporal gradient of about 700 years of shore-level displacement at the Forsmark investigation site. During the process of positive shore-level displacement, the bays topographic openness towards the sea decreases, affecting the bays water exchange with the sea and water retention time in the bays. These changes result in altered water properties and bottom-substrate characteristics, which has a clear effect on the ecological structure of the bays.

The biomass of macrofauna was found to decrease with increasing isolation of bays. This could primarily be ascribed to a decline in mollusc biomass. A similar pattern was observed for the macroflora biomass in small bays, partly due to a decrease of algae of marine origin. The decrease in macroflora biomass was only weakly reflected in a trend of reduced gross primary production with increasing bay isolation. The form of carbon uptake by plants and algae was also examined, as this could potentially change along the bay isolation gradient. But no general relationship was detected.

The decrease in biomass of macroflora and macrofauna was suggested to partly be related to a transition from comparably stable abiotic conditions in the open bays to more variable conditions and a harsher environment in enclosed bays. For instance, low salinity during high precipitation events may prevent establishment of species of marine origin in isolated bays. Furthermore, re-colonization after disturbance, such as bottom-freezing and anoxia, can potentially be hampered by the small threshold openings of isolated bays. The changes in the macrofauna community also reflected the animals ability to re-colonize an unstable habitat, where slow colonizers with passively dispersed larvae were almost absent from the most isolated bays. Fast colonizers – particularly the ones with flying adults (insects) – were however found in higher proportions in isolated bays. The changed macrofauna composition also indicated that the consumer web changes from an autotrophic-fed web of mainly primary consumers to a more heterotrophic system, which is more dependent on benthic particulate organic matter as an energy source.

Contrary to the macrofauna and flora, the zooplankton and juvenile fish increased in biomass with increasing bay isolation. The increase in zooplankton biomass is probably related to higher spring and summer temperatures in isolated bays. High zooplankton abundance can potentially also be related to higher phytoplankton biomass and input of organic matter via run-off from land. However, in the present study no support was found for higher phytoplankton biomass or inflow of carbon from terrestrial sources in isolated bays. The observed increase in biomass of juvenile warm water-spawning fish with increasing bay isolation is likely related to higher temperature in combination with higher zooplankton abundance in the isolated bays. The high productivity of these fish species represents an energy export from the bays since the young fish migrate out from the bays after their first growth season.

To conclude, this study describes a significant change in ecological properties of Baltic Sea bays with shore-level displacement. This change affects ecosystem processes which may be of importance for the fate of potentially released radionuclides to the biosphere. The changes in ecology along the bay isolation gradient are summarized in Figure 3-19, and complementing information is given in Table 3-7.



**Figure 4-1.** Schematic summary of the main findings in the present study. The panels present response to topographic openness for the variables (from the upper left): **A)** spring temperature (in May), **B)** mean salinity and variation in salinity (maximum-minimum), **C)** volatile solids and total carbon in the sediment, **D)** total nitrogen in the sediment and in the water, **E)** total carbon to total nitrogen, and total nitrogen to total phosphorus ratios, **F)** frequency of disturbance (e.g. by ice scraping and/or anoxia) and potential rate of barriers for aquatic dispersal to the bays (topographic and biotic [emergent vegetation]), **G)** macroflora biomass (only valid for small [ $<10$  ha] bays), **H)** biomass of marine macrophytes (mainly bladderwrack) and ratio of disturbance tolerant to sensitive soft bottom macrophytes (sensu Kautsky 1988), **I)** zooplankton biomass, **J)** young-of-the-year fish biomass (warm-water spawning species), **K)** macrofauna biomass, and **L)** biomass of marine macrofauna and molluscs, as well as ratio of slow to fast colonizers and autotrophic to heterotrophic fed consumers (sensu Merritt et al. 2002). The response variables are expressed as the relative rate of the maximum found in the studied gradient on an untransformed scale (vertical dotted line depicts 0.5). Topographic openness (first axis) is expressed on a logarithmic scale, with bay categories shown in the lower middle panel (separated by grey areas). The numbers in the lower middle panel refer to the approximate years until bays are totally isolated from the sea, given the present shore-level-displacement rate in the Forsmark area. The lines in the panels express functions found in the present study, except for spring temperature, salinity, frequency of disturbance and rate of dispersal barriers. The spring temperature is based on the result of Snickars et al. (2009), the mean salinity is based on the result of Hansen (2012), and the variation in salinity is an assumption based on pers. obs. The disturbance frequency and rate of barriers for aquatic dispersal are hypothetical (see text for details). The lines have been extended to conditions outside bays by drawing by hand.

**Table 4-1. Mathematical functions expressing response of the variables (Y) in Figure 3-19 to topographic openness (X) of shallow Baltic Sea bays. See Figure 3-19 and the text for more details.**

Variable	Function
Spring temperature (°C)	$Y = -8.78 \times X + 15.3$
Salinity (mean PSU)	$Y = 0.21 \times \ln(X) + 5.79$
Salinity (max-min PSU)	$Y = -0.42 \times \ln(X) + 1.65$
Total carbon in the sediment (mg × g <sup>-1</sup> )	$\ln(Y) = -0.16 \times \ln(X) + 3.62$
Volatile solids in the sediment (%)	$Y = -1.98 \times \ln(X) + 11.3$
Total nitrogen in the sediment (mg × g <sup>-1</sup> )	$\ln(Y) = -0.14 \times \ln(X) + 1.62$
Total nitrogen in the water (µg × L <sup>-1</sup> )	$Y = -36.9 \times \ln(X) + 330.6$
C:N in the sediment	$Y = -0.14 \times \ln(X) + 7.58$
N:P in the water	$Y = -1.31 \times \ln(X) + 14.2$
N:P in the sediment	$Y = -0.90 \times \ln(X) + 6.58$
Rate of dispersal barriers	$Y = -0.0058 \times \ln(X)^3 - 0.055 \times \ln(X)^2 - 0.23 \times \ln(X) - 0.12$
Frequency of disturbance (10 <sup>-y</sup> )	$\ln(Y) = -0.39 \times \ln(X) - 0.056$
Macroflora biomass [small bays] (g C × m <sup>-2</sup> )	$\ln(Y) = 0.33 \times \ln(X) + 4.15$
Marine macrophyte biomass (g C × m <sup>-2</sup> )	$\ln(Y) = 1.88 \times \ln(X) + 3.60$
Disturbance tolerant:sensitive macrophytes	$\ln(Y) = -0.64 \times \ln(X) + 2.37$
Zooplankton biomass (µg C × L <sup>-1</sup> )	$\ln(Y) = -3.72 \times X + 3.00$
Yoy fish biomass (mg C × m <sup>-2</sup> )	$Y = -46.1 \times X + 34.1$
Macrofauna biomass (g C × m <sup>-2</sup> )	$\ln(Y) = 0.39 \times \ln(X) + 1.51$
Marine macrofauna biomass (g C × m <sup>-2</sup> )	$\ln(Y) = 0.94 \times \ln(X) + 1.73$
Mollusc biomass (g C × m <sup>-2</sup> )	$\ln(Y) = 0.67 \times \ln(X) + 1.82$
Slow:fast colonizers	$\ln(Y) = 0.64 \times \ln(X) + 2.40$
Autotrophic:heterotrophic fed consumers	$Y = 0.65 \times \ln(X) + 5.33$

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