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Taxon composition and food-web structure in a morphometric gradient of Baltic Sea land-uplift bays

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Shallow Baltic Sea bays undergo a process of morphometric isolation from the sea due to post-glacial land uplift. Recent studies have documented that both flora and fauna communities change along this gradient. Changes in taxon composition may in turn alter feeding ecology and trophic relationships. In addition, the relative importance of energy from terrestrial sources may increase with bay isolation. In accordance with previous studies, we found a change in the community composition of both flora and fauna with bay isolation. Results of a stable-isotope analysis ($\delta^{13}C$, $\delta^{15}N$) suggested that epiphytes and periphyton are the major carbon sources for most benthic primary consumers, but that their importance in relation to angiosperms and charophytes decreased with bay isolation. The results also indicated that filter feeders utilize terrestrially-derived carbon, but its importance could not be critically related to bay isolation. Trophic positions of the consumers were similar across the bay isolation gradient.

Introduction

Northern Scandinavia is subjected to a post-glacial land uplift, whereby land is continuously rising (maximum 10 mm year^{-1}), resulting in a constant change in coastline and archipelago morphometry (Påsse and Andersson 2005, Berglund *et al*. 2009, Argus and Peltier 2010). The land uplift is considerably enhanced by sedimentation (maximum 5 mm year^{-1}, Ingmar 1975; *see* also Åse 1994, Berglund *et al*. 2009). In the land-uplift process, 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. These shallow sheltered lagoon-like bays have been identified as ecologically important habitats in the Baltic Sea. They harbour a high species diversity of both macrophytes (Munsterhjelm 1997, Rosqvist *et al*. 2010) and invertebrates (Hansen *et al*. 2008), and constitute important reproduction areas for a number of fish species (Karås 1999, Snickars *et al*. 2009). Like many other coastal habitats, the sheltered Baltic Sea bays are strongly influenced by anthropogenic pressures, such as increased nutrient inflow from land, boating activities, and dredging (Eriksson *et al*. 2004, Munsterhjelm 2005, Sandström *et al*. 2005). To manage these anthropogenic threats, it is crucial to understand consequences of the

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gradual isolation of the bays from the sea, with resulting changes in abiotic conditions, for the ecological processes in the bays.

Several recent studies have documented that macrovegetation (Munsterhjelm 1997, Appelgren and Mattila 2005, Rosqvist *et al*. 2010) as well as communities of zooplankton (Scheinin and Mattila 2010), macroinvertebrates (Hansen *et al*. 2008), and fish (Snickars *et al*. 2009) change as bays are more isolated from the sea. Both taxon composition and population densities differ significantly between open and enclosed bays. Such changes in abundance and taxon composition may in turn alter feeding ecology and trophic relationships. For example, the decrease in plant biomass, taxon number, and amount of ephemeral algae with increased topographic isolation of bays from the sea (Hansen *et al*. 2008) represents a changed resource base for primary consumers. Littoral herbivorous consumers in the Baltic Sea, such as *Gammarus oceanicus* and *Idotea balthica*, are known to consume both ephemeral algae and coarse algae or angiosperms (Goecker and Kåll 2003, Kotta *et al*. 2004, Orav-Kotta and Kotta 2004, Boström and Mattila 2005). Although ephemeral algae are often the preferred food (Goecker and Kåll 2003, Kotta *et al*. 2004, Orav-Kotta and Kotta 2004, Boström and Mattila 2005), these consumers may change diet when the composition of primary producers changes. Apart from changes in internal primary production, the relative importance of allochthonous terrestrial organic matter as energy source may increase with increased bay isolation as the inflow from land run-off can be expected to increase relative to seawater inflow. Terrestrial input can add considerable organic material to coastal food webs (Chanton and Lewis 2002, Attrill *et al*. 2009), but its role in lagoon-like land-uplift bays in the Baltic Sea has not been investigated.

Stable isotopes have frequently been used to study the often complex food webs in coastal lagoons and estuaries, with a large diversity of potential food sources (Chanton and Lewis 2002, Fry 2006 and references therein, Attrill *et al*. 2009, Fox *et al*. 2009). The stable isotope ratios of carbon (C) and nitrogen (N) of primary producers are affected by their habitat, their C and N sources, their biochemical structure, and the photosynthetic process and typically differ clearly between terrestrial and aquatic primary producers and between different aquatic primary producers (reviewed in Peterson 1999, Fry 2006). The stable isotope ratios of consumers reflect the stable isotope composition of their food sources, though with some predictable change due to isotopic fractionation (Fry 2006). A stable-isotope analysis can, therefore, be used to estimate the relative importance of primary producers, with different isotopic signals (e.g., seagrass/ephemeral algae, phytoplanktic/benthic algae, and aquatic/terrestrial producers) for consumers (Moncreiff and Sullivan 2001, Chanton and Lewis 2002, Fry 2006 and references therein), and to test for spatial and temporal variability in resource utilization and trophic position of the consumers (Fox *et al*. 2009, Nordström *et al*. 2009).

To the best of our knowledge, no study has previously investigated effects of the land-uplift-induced bay isolation gradient on macrovegetation, macroinvertebrates, plankton, and fish simultaneously, or investigated stable isotope ratios to examine the food-web structure in shallow sheltered Baltic Sea bays. In the present study, we first examine whether the biomass or abundance and taxon composition of flora and fauna change in relation to the bay isolation gradient. Second, we explore whether there is also a change in the food-web structure of the bays along the isolation gradient, using stable isotope ratios of C and N.

Material and methods

We analysed data from a four-year monitoring program (2004–2007) of macrovegetation and young-of-the-year fish in six bays (Fig. 1) in a newly established marine protected area (2007) in the western Baltic Sea. Each bay was surveyed in each of the four years except one bay, which was not visited in 2005 (Bay A, Fig. 1). In addition, in 2007, we conducted biomass sampling of macrovegetation and macroinvertebrates, and sampled zooplankton. These bays represent a gradient in bay isolation, ranging from open, moderately wave-exposed bays to enclosed, very wave-protected bays. All samples

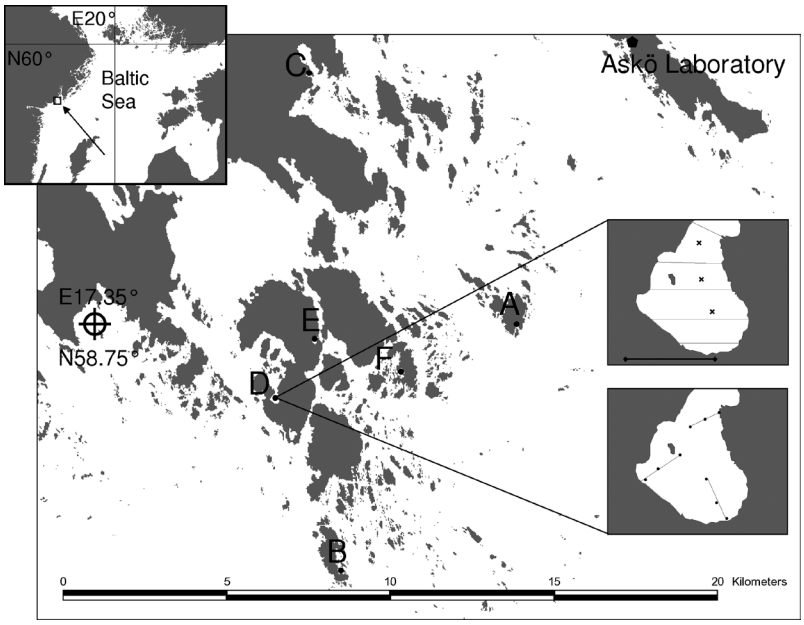

Fig. 1. Map of study area in the Baltic Sea. Sampled bays are indicated by letters A–F. Right-hand-side inset figures show survey line transects for bay D. The upper right-hand-side inset figure shows transects for survey of macrophyte cover and sampling of young-of-the-year fish. Crosses indicate sampling locations for zooplankton, periphyton, and particulate and sedimentary organic matter (POM and SOM). The lower right-hand-side inset figure shows transects for macrophyte, epiphyte, and macroinvertebrate biomass sampling, with small solid circles indicating sampling locations. The scale line in the upper right-hand-side inset figure indicates 200 m.

were collected in August. For the stable-isotope analysis, we used the numerically most dominant taxa of functional groups that were present in all bays along the bay isolation gradient. The local anthropogenic pressure in the study area is limited. The area is sparsely populated with only a few houses, and only one of the studied bays has a house and a jetty along its shore (bay C, Fig. 1). The study area is located outside the catchment area of municipal sewage discharged from southern Stockholm (Savage and Elmgren 2004) and the post-glacial land-uplift rate is approximately 3–4 mm year^{-1} (Påsse and Andersson 2005).

Environmental variables

The level of bay isolation was identified using the site scores of the first axis of a principal component analysis (PCA; 'Vegan' package in R 2.10.1, R Development Core Team 2009, Oksanen *et al*. 2009) of the two factors topographic openness and wave exposure. The total inertia of the PCA was 2, and the eigenvalue of the first axis was 1.7. Topographic openness (E_a) of the bays was calculated as:

$$E_a = 100A_t/a \quad (1)$$

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. Water surface area, a, was calculated from aerial photographs using GIS methods in ArcView 3.2 (ESRI, Redlands, CA). The topographic openness function as a predictor of surface-water retention time (Håkansson 2008), which affects factors such as water temperature, particle sedimentation, and internal and external nutrient loading. Wave exposure was used to account for the coastal morphometry just outside the bay and level of shelter provided by islands and capes affecting waves reaching

the bays. Level of wave exposure at the bay opening will in turn, in addition to topographic openness, affect the water exchange rate of 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 × 25-m grids using digital nautical charts and GIS methods. Fetch is an estimate of the distance over which waves can potentially collect wind energy before reaching a site. The wind speeds used in the model were the mean wind speeds in 16 directions over a five-year period (1998–2003) measured at a meteorological station located approximately 20 km east of the study area. Values representing the wave exposure at the bay openings were calculated as the mean exposure of a 50 × 50-m grid at the openings. The SWM has been proven to provide useful wave-exposure estimates in several studies (e.g., Eriksson *et al*. 2004, Sandström *et al*. 2005, Snickars *et al*. 2009), and apart from the hydrological movements and forces created by waves, it functions as a proxy for factors such as water temperature and particle sedimentation.

In addition, salinity and turbidity were measured at a depth of 0.5 m in three locations in the central part of each studied bay on each monitoring occasion. Salinity was measured in practical salinity units (PSU) and turbidity in nephelometric turbidity units (NTU). The environmental data are listed in Table 1.

Macrovegetation

Macrovegetation was divided into two functional groups: coarsely structured algae and angiosperms (hereafter, 'macrophytes') and ephemeral, mainly epiphytic, algae (hereafter, 'epiphytes'). The percentage cover of macrophytes was surveyed using the method for vegetation surveys in the European Union Natura 2000 habitats 'lagoons' and 'large shallow inlets and bays' in Sweden (habitat codes 1150 and 1160; Persson and Johansson 2007), a method similar to that of Snickars *et al*. (2009) and Rosqvist *et al*. (2010). Macrophyte composition was surveyed by a free diver along parallel transect lines that extended perpendicular to the length axis of the bays (Fig. 1). The first transect line was located 10 m from the innermost shore (outside reed belts, if present); the second transect line was located approximately 50 m from the first one, and the rest of the transect lines approximately 50 m from the previous ones until the entire bay was surveyed. A final line was located across the bay opening towards the sea. The percentage cover of macrophytes was estimated every 10 m along the transect lines within a 0.5 × 0.5-m square, using a continuous percentage scale individually for each taxon (i.e., total cover could exceed 100% if the macrophytes overlapped). Average cover over the years was calculated for each macrophyte species and for all species combined in each bay. Percentage cover of epiphytes was not examined in the survey. Depth at the position of each square was measured to the nearest 0.1 m and used for calculations of the mean and maximum bay depths (Table 1).

Biomass of macrophytes and epiphytes was measured by sampling according to the method

Table 1. Morphometric characteristics, salinity and turbidity for the bays included in the study. Bays are ranked according to isolation scores (index A–F). Topographic openness and bay isolation score are dimensionless.

Bay index	Bay name	Topographic openness	Ln(wave exposure) (m^2 s^{-1})	Mean depth (m)	Max depth (m)	Area (ha)	Isolation score	Salinity (PSU)	Turbidity (NTU)
A	Hamnhamn	0.615	12.4	1.1	2.5	1.4	–0.99	6.0	1.1
B	Gräshålet	0.673	10.8	1.1	1.9	1.8	–0.73	6.1	0.8
C	Svarthålet	0.505	7.7	0.9	3.2	2.2	–0.15	5.9	4.9
D	Kuggviken	0.288	7.2	1.1	2.0	5.0	0.06	6.0	5.4
E	Lermaren	0.007	6.6	1.0	4.9	2.5	0.88	5.8	1.0
F	Stenmarsfladen	0.006	6.3	0.7	1.3	3.7	0.93	6.1	1.1

of Hansen *et al*. (2008). Samples were taken along three transects in each bay: one in the inner part, one in the middle part, and one in the outer part of the bay (Fig. 1). Transects were located perpendicular to the shoreline, extending from the shore to the deeper central area of the bay. Each transect was divided into three depth intervals relative to the maximum depth of the bays; a sample was taken from a randomly selected vegetation patch in each interval. Only vegetated areas were sampled. The samples were collected by a free diver using a net bag (1-mm mesh size) mounted on a 0.17 × 0.17-m frame with shears underneath. The sampler was pulled over a stand of macrophytes at each sampling site. The macrophytes were cut a few centimetres into soft-bottom substrates or at the surface of hard-bottom substrates. Samples were immediately transferred to plastic bags and stored under dark, cool conditions until return to the laboratory, where they were deep frozen at –20 °C. Macrophytes and epiphytes were identified to species or genus and weighed after drying at 59 °C to constant weight.

Macroinvertebrates

Samples of phytal macroinvertebrates were collected at the same time as the macrophyte biomass samples (described earlier). The sampling method collected plant-associated animals and animals living just beneath the plants, but not the deep sediment infauna. The macroinvertebrates were sorted, counted, and identified to different taxonomic levels (species, genus or family). The two bivalve species *Parvicardium hauniense* and *Cerastoderma glaucum* were pooled (hereafter, '*Parvicardium hauniense*'), as large proportions were juveniles, which are difficult to identify to the species level. The biomass of the animals was determined by multiplying the abundance of a certain taxon by a standard dry weight for that taxon in a specific size class (three size classes were used for all common taxa). These standard weights were taken from a previous study conducted in similar habitats (Hansen *et al*. 2008) or from pooled samples of several individuals from all bays in the current study (dried at 59 °C to constant weight). The weights included the shells of the molluscs.

Zooplankton

Zooplankton were sampled at three locations in each bay: one in the inner part, one in the middle part, and one in the outer part of the bay (Fig. 1). During sampling, a 100-μm net was hauled vertically from the sea bottom to the surface. The procedure was repeated several times, depending on depth, to acquire large enough quantities for the stable-isotope analysis. When the depth was less than 0.5 m, water was sampled using a bucket and poured through the nets. Samples were stored under dark, cool conditions in bottles until return to the laboratory, where they were deep frozen at –20 °C until analysis. The zooplankton were sorted to taxonomic order (Copepoda and Cladocera) and counted under a microscope. Abundance was related to sample volume (i.e., density per litre was calculated).

Young-of-the-year fish

Young-of-the-year (YOY) fish were sampled using small underwater detonations that stunned all small fish within an area of approximately 15 m^2 (Sandström *et al*. 2005, Snickars *et al*. 2007). The method allows sampling of fish up to a length of approximately 150 mm, with well-developed swim bladders, in all types of habitats, including dense vegetation. Fish with a poorly developed swim bladder, or lacking one, were excluded from the study (i.e., flounders, Pleuronectidae, and gobies, *Gobius* spp.). As several fish species sampled are 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 bathymetry data collected before the fish sampling (Fig. 1), similar to the method of Sandström *et al*. (2005) and Snickars *et al*. (2009). The sampling locations were located > 30 m apart to ensure that they did not interfere with each other. The number of samples was chosen to account for differences in water surface area of the bays, ranging from 17 in the smallest bays to 23 in the bay with largest surface area. During sampling, all stunned fish in the water were collected using a dip net, identified to species, and counted. Breams (*Abramis*

brama and *Abramis bjoerkna*) were pooled (hereafter, *Abramis* spp.), as these juveniles are difficult to identify to species level. An average catch per unit effort (CPUE) per bay and year was calculated for each taxon and for all taxa combined. Fish sampled in 2007 were used for the stable-isotope analysis and were deep frozen at –20 °C until preparations for the analysis.

Stable isotopes

Samples of macrophytes, epiphytes, macroinvertebrates, zooplankton, and YOY fish were selected for the analysis of stable isotopes of C and N. The numerically most dominant taxa of each functional group occurring in all bays were selected for analysis (Appendix). This means that only part of the food web was sampled. As the YOY-fish abundance differed considerably between bays in 2007, we could include only one family, Cyprinidae, that occurred in all bays. We included several taxonomically distinct taxa of each functional group when possible. Functional groups of invertebrates were determined according to the classification of functional feeding modes of Merritt and Cummins (1984, 2006), which was developed for aquatic invertebrates in temperate regions with high levels of omnivory. We included three taxa of filtering collectors (Copepoda, Cladocera, and *Parvicardium hauniense*), two of scrapers (*Theodoxus fluviatilis* and *Radix balthica*), one of shredders (*Gammarus* spp.), two of gathering collectors (Chironomidae and Ostracoda), and two of predators (Odonata and Cyprinidae). In addition to these samples, periphyton, particulate and sedimentary organic matter (POM and SOM), terrestrial plants growing near the shore (*Alnus glutinosa* and the herbs *Tanacetum vulgare* and *Glaux maritima*), and the emergent reed *Phragmites australis* were sampled.

Periphyton, POM, and SOM were sampled at approximately the same locations where the zooplankton were sampled (Fig. 1). Periphyton were sampled on plastic discs (∅ 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 °C, and later dried at 59 °C for the stable-isotope analysis. All discs in bay E were lost. Particulate organic matter was sampled with a 10-μm net using the same procedure as used for the zooplankton samples. The POM samples were filtered through Whatman GF/F filters (Whatman, Maidston, UK), deep frozen at –20 °C, and later dried at 59 °C for the stable-isotope analysis. Sedimentary organic matter was sampled using a cylindrical acrylic sediment coring device (inner ∅ 64 mm). The top 5 mm of this sediment sample (excluding sand and visible living benthic organisms) was dried at 59 °C, ground to a fine powder, and used for the stable-isotope analysis.

Macrophytes were cleaned from epiphytes, and only leaves or top thallii were used in the stable-isotope analysis. Similarly, only leaves were used in the stable-isotope analysis of the terrestrial plants and *P. australis*. Epiphytes were pooled in taxonomic groups of Chlorophyta, Phaeophyta, and Rhodophyta for analysis. Animals were freeze-dried and fish muscles were ground to a fine powder for the stable-isotope analysis. If possible, individuals were analysed as replicates, and muscle and cuticle tissue were used to avoid gut content in the analysis (Appendix). In the case of small animals, however, whole bodies and pooled individuals were used per replicate because of their small individual weights (< 0.7 mg). For each functional group or taxon in each bay, three spatially separated samples were analysed. For some taxa with low biomass in the samples, fewer than three samples were analysed; for example, the two outermost samples of zooplankton (i.e., middle and outer samples) were always pooled. In addition, analyses were conducted on two geographically separated samples of terrestrial plants and *P. australis*.

The stable isotope ratios of C and N were measured at the UC Davis Stable Isotope Facility (University of California, Davis, CA) using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Crewe, UK). Isotope ratios were calculated as deviations from the international limestone standard Vienna Pee Dee Belemnite (VPDB) (δ^{13}C) and from atmospheric N (δ^{15}N) in parts per thousand (‰) as follows:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \quad (2)$$

where R is $^{13}C:^{12}C$ or $^{15}N:^{14}N$. The isotope samples were not pre-treated with acid.

Statistics

All statistical tests were performed using the software R 2.10.1 (R Development Core Team 2009). Multivariate tests were performed using the 'Vegan' package in R (Oksanen *et al*. 2009). Linear regression was used to explore the effects of bay isolation on bay mean biomass of macrophytes, macroinvertebrates, proportion of epiphyte biomass to total macrophyte biomass, and bay mean abundance of zooplankton and YOY fish. The data were tested for normality by the Shapiro-Wilk test and inspected for homogeneity of variances using residual plots. The ratio of epiphytic algal biomass to macrophyte biomass and the zooplankton abundance were ln-transformed to meet assumptions for a parametric test. The criteria for a parametric test could not be fulfilled for all tested responses. However, in cases were assumptions could not be fulfilled (for vegetation cover and macroinvertebrate biomass), tests on these response variables indicated no significant relation with bay isolation. Hence, there was no risk of committing a type I error.

A canonical correspondence analysis (CCA) was conducted to explore the effect of bay isolation on taxon composition of macrophytes, macroinvertebrates, and YOY fish. Before analysis, the mean macrophyte cover and YOY-fish abundance were $^{2}\sqrt{}$-transformed, and the macroinvertebrate biomass was $^{4}\sqrt{}$-transformed, to reduce the influence of taxa with very high cover, abundance, or biomass. Zooplankton (abundance) was not included in the analysis of macroinvertebrate composition. To explore whether the composition of the different taxonomic groups showed the same pattern in relation to the bay isolation gradient, we tested if there was a correlation between the dissimilarity matrices of macrophytes and macroinvertebrates or YOY fish using the Mantel test (Legendre and Legendre 1998).

A redundancy analysis (RDA) was conducted on $\delta^{13}C$ and $\delta^{15}N$ to investigate the effect of bay isolation on the stable isotope ratios of aquatic flora and fauna in the ecosystem. Mean $\delta^{13}C$ and $\delta^{15}N$ for each taxon or functional group per bay was used in the analysis. To achieve a balanced dataset including all sampled taxa and functional groups, a mean was calculated for a taxa or functional group from all bays and used in the cases in which data were missing for one bay (Appendix).

A diet-mixing model (IsoError 1.04; Phillips and Gregg 2001) was used to estimate possible diet shifts along the bay isolation gradient for the consumers *Theodoxus fluviatilis*, *Radix balthica*, *Gammarus* spp., and Chironomidae. In diet-mixing models, fractionation in stable isotope ratios between trophic levels must be considered. Fractionation can vary considerably for consumers, depending partly on the food source (Vander Zanden and Rasmussen 2001, Vanderklift and Ponsard 2003, Caut *et al*. 2009). As the fractionation factors were unknown to us, we used only $\delta^{13}C$ in the model, since the stable isotope ratio of C generally displays smaller changes and variability between trophic levels than does that of N (Vander Zanden and Rasmussen 2001, McCutchan *et al*. 2003, Vanderklift and Ponsard 2003). We used the mean fractionation of C for invertebrates (0.1), from a meta study by Vander Zanden and Rasmussen (2001), to calculate the proportions of epiphytes and periphyton in relation to three macrophytes as carbon sources in the diet of the consumers.

Results

Biomass and abundance

The mean macrophyte biomass decreased significantly with increased bay isolation ($r^2 = 0.7$, $p < 0.05$; Fig. 2a), while the mean macrophyte cover did not (Fig. 2b). The ratio of epiphytic algal biomass to total macrophyte biomass was highest in the two most open bays and tended to decrease with increased bay isolation (ln-transformed, $r^2 = 0.6$, $p = 0.08$; Fig. 2c). In contrast, both mean zooplankton abundance (ln-transformed, $r^2 = 0.7$, $p < 0.05$; Fig. 2d) and mean YOY-fish abundance increased ($r^2 = 0.7$, $p < 0.05$; Fig. 2f) with increased bay isolation. The macroinvertebrate biomass was lowest in the most isolated bays, but there was no significant relationship with the bay isolation gradient (Fig. 2e) as the bay with highest isolation score

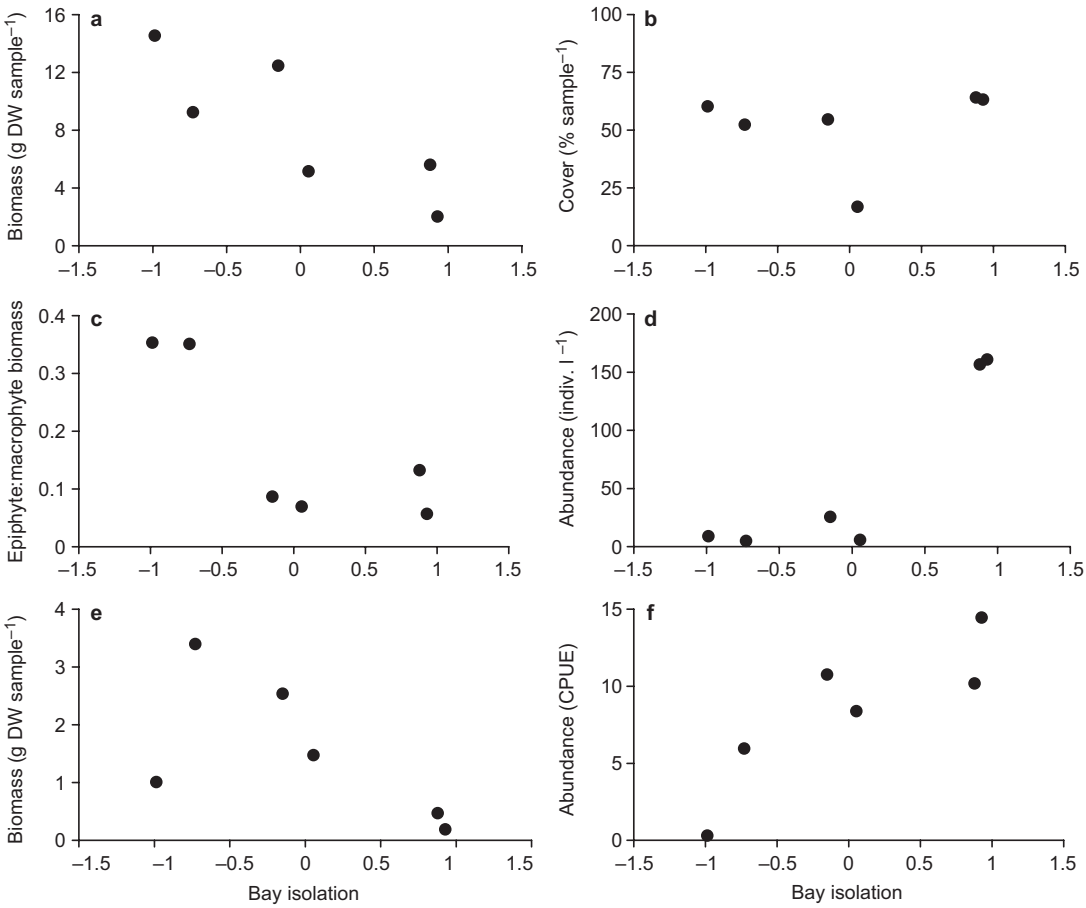

Fig. 2. Relationship between bay isolation and bay mean (**a**) macrophyte biomass, (**b**) macrophyte cover, (**c**) ratio of epiphyte to macrophyte biomass, (**d**) zooplankton abundance, (**e**) macroinvertebrate biomass, and (**f**) YOY-fish abundance. With increasing bay isolation scores, bays are more isolated from the sea.

had a low macroinvertebrate biomass. The plots indicate different relations between bay isolation and the various response variables. It should be noted that other functions than linear relations could apply, but because of the low number of bays sampled such functions were not tested.

Taxon composition

The taxon composition of macrophytes, macroinvertebrates, and YOY fish changed significantly along the bay isolation gradient (Table 2). Between 34% and 43% of the variation in taxon composition was explained by the constrained ordination axis. The difference in taxon composition of macrophytes between bays correlated with the difference in taxon composition of macroinvertebrates (Mantel: $r = 0.51$, $p < 0.05$) and YOY fish (Mantel: $r = 0.54$, $p < 0.05$).

Macrophyte species that had their highest cover in open bays were the marine algae *Furcellaria lumbricalis*, *Chorda filum*, and *Fucus vesiculosus*, as well as *Tolypella nidifica*, *Ranunculus peltatus* ssp. *baudotii*, and *Ruppia cirrhosa* (Fig. 3a). With increased bay isolation, cover of *Myriophyllum spicatum*, and especially of *Chara baltica*, *Chara horrida*, *Chara tomentosa*, and *Najas marina* increased. The decreased cover of *F. vesiculosus* can explain the decrease in macrophyte biomass with increased bay isolation, as the biomass of this species was considerably higher (mean 30.6 g DW sample^{-1}) than that of other species more common in isolated

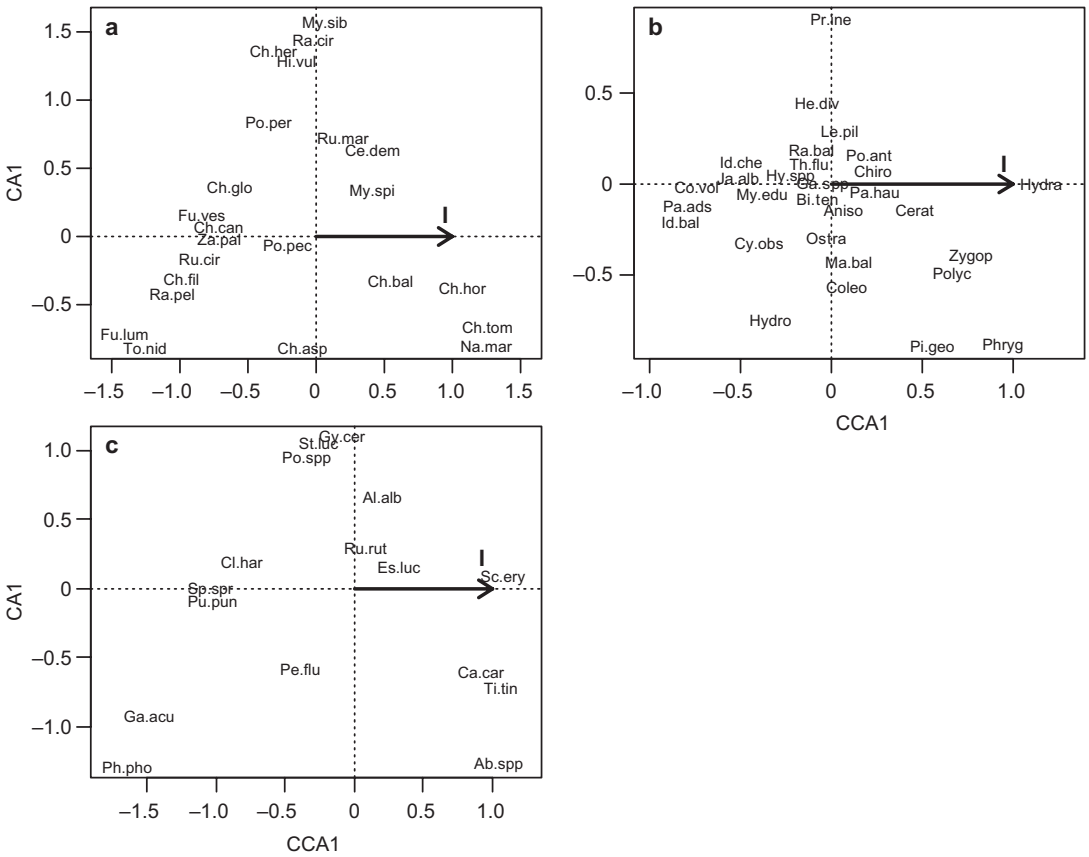

Fig. 3. Ordination graphs of first constrained ordination axis (CCA1) with bay isolation (I) and residuals on the second axis (CA1) for (**a**) macrophytes, (**b**) macroinvertebrates, and (**c**) YOY fish. Abbreviations of taxonomic names are underlined: (**a**) macrophytes *Callitriche hermaphroditica*, *Ceratophyllum demersum*, *Chara aspera*, *Chara baltica*, *Chara canescens*, *Chara globularis*, *Chara horrida*, *Chara tomentosa*, *Chorda filum*, *Fucus vesiculosus*, *Furcellaria lumbricalis*, *Hippuris vulgaris*, *Myriophyllum sibiricum*, *Myriophyllum spicatum*, *Najas marina*, *Potamogeton pectinatus*, *Potamogeton perfoliatus*, *Ranunculus peltatus* ssp. *baudotii*, *Ranunculus circinatus*, *Ruppia cirrhosa*, *Ruppia maritima*, and *Tolypella nidifica*; (**b**) macroinvertebrates Anisoptera, *Bithynia tentaculata*, Chironomidae, Ceratopogonidae, Coleoptera, *Corophium volutator*, *Cyanophthalma obscura*, *Gammarus* spp., *Hediste diversicolor*, Hydrachnidae, *Hydrobia* spp., Hydroptilidae, *Idotea balthica*, *Idotea chelipes*, *Jaera albifrons*, *Macoma balthica*, *Mytilus edulis*, *Leptocheirus pilosus*, Ostracoda, *Palaemon adspersus*, *Parvicardium hauniense*, Phryganeidae, *Piscicola geometra*, Polycentropodidae, *Potamopyrgus antipodarum*, *Praunus inermis*, *Radix balthica*, *Theodoxus fluviatilis*, and Zygoptera; (**c**) YOY fish *Abramis* spp., *Alburnus alburnus*, *Carassius carassius*, *Clupea harengus*, *Esox lucius*, *Gasterosteus aculeatus*, *Gymnocephalus cernuus*, *Perca fluviatilis*, *Phoxinus phoxinus*, *Pomatoschistus* spp., *Pungitius pungitius*, *Rutilus rutilus*, *Scardinius erythrophthalmus*, *Stizostedion lucioperca*, *Sprattus sprattus*, and *Tinca Tinca.*

Table 2. Canonical correspondence analysis (CCA) testing the effect of bay isolation on taxon composition of macrophytes, macroinvertebrates, and YOY fish. Significance was tested using 9999 permutations; *p* values at which effects are considered significant are set in boldface.

Factor	Total inertia	Constrained inertia (axis 1)	Explained variation (%)	Pseudo-*F*	*p*
Macrophytes	1.29	0.56	43	3.06	< **0.05**
Macroinvertebrates	0.35	0.12	34	2.03	< **0.01**
YOY fish	1.55	0.65	42	2.89	< **0.05**

bays, such as *C. tomentosa* (5.8 g DW sample^{-1}) and *Najas marina* (0.38 g DW sample^{-1}) (calculations from biomass samples with > 75% dominance of one species). Species with a large residual variance in relation to CCA axis 1 and to the bay isolation gradient were *Myriophyllum sibiricum*, *Ranunculus circinatus*, *Callitriche hermaphroditica*, and *Hippuris vulgaris*.

Macroinvertebrate species that had their highest biomass in the open bays were the marine crustaceans *Palaemon adspersus*, *Idotea balthica*, *Corophium volutator*, *Idotea chelipes*, *Jaera albifrons*, and the bivalve *Mytilus edulis* (Fig. 3b). Macroinvertebrates that had their highest biomass in the isolated bays were the insect larvae of Ceratopogonidae, Zygoptera, Polycentropodidae, and Phryganeidae, as well as the water mite Hydracarina and the fish leach *Piscicola geometra*.

The YOY fish found in higher abundance in the open bays were the freshwater species common minnow *Phoxinus phoxinus*, sticklebacks *Gasterosteus aculeatus/Pungitius pungitius*, and the marine species sprat *Sprattus sprattus* and herring *Clupea harengus*. Warm-water-spawning cyprinids such as rudd *Scardinius erythrophthalmus*, crucian carp *Carassius carassius*, tench *Tinca tinca*, breams *Abramis* spp., and roach *Rutilus rutilus*, as well as pike *Esox lucius* were mainly found in more isolated bays (Fig. 3c).

Stable isotopes

Both the floral and faunal δ^{13}C composition changed significantly along the bay isolation gradient, while the δ^{15}N composition did not change significantly (Table 3). The explained variation in floral δ^{13}C was 53% (Table 3). The δ^{13}C decreased with increased bay isolation for epiphytic algae, *Myriophyllum spicatum*, periphyton, and *Chara* spp. (Fig. 4a), while the opposite was the case for *Fucus vesiculosus* and *Potamogeton pectinatus*. The explained variation in faunal δ^{13}C was 42%. The δ^{13}C decreased with increased bay isolation for Cladocera, Odonata, Cyprinidae, *Gammarus* spp., *Radix balthica*, *Theodoxus fluviatilis*, and Chironomidae (Fig. 4b).

The combined change in δ^{13}C and δ^{15}N along the bay isolation gradient of both flora and fauna is presented in Fig. 5. Mean stable isotope ratios of taxa or functional groups were calculated for the two most open bays, the two intermediately isolated bays, and the two most isolated bays. In all three graphs, organisms living in the more pelagic zone or feeding on small particles from this zone, i.e., phytoplankton (included in POM) and filtering collectors, were separated from benthic organisms on the δ^{13}C axis. POM and the filtering collector Copepoda had low δ^{13}C, while benthic algae, angiosperms, and benthic consumers (*T. fluviatilis*, *R. balthica*, *Gammarus* spp., Chironomidae, Ostracoda, and Odonata) were more enriched in ^{13}C. The filtering collectors Cladocera and *Parvicardium hauniense* also had low δ^{13}C, though they varied more in ^{13}C enrichment. Angiosperms and *Chara* spp. were clearly more enriched in ^{13}C than were epiphytic algae. *Fucus vesiculosus* was about as enriched as were the epiphytic algae in the open bays, but increased in ^{13}C enrichment with increased bay isolation. The taxonomic groups of epiphytic algae had very similar, but still distinguishable, stable isotope values. The benthic consumers had δ^{13}C between that of the epiphytes and that of the angiosperms and *Chara* spp., except for Ostracoda, which was considerably enriched in

Table 3. Redundancy analysis (RDA) testing for effects of bay isolation on stable isotope composition of flora and fauna. Significance was tested using 9999 permutations; *p* values at which effects are considered significant are set in boldface.

Factor	Total inertia	Constrained inertia (axis 1)	Percentage explained variation	Pseudo-*F*	*p*
Flora δ^{13}C	30.4	16.1	53%	4.53	< **0.05**
Flora δ^{15}N	30.2	11.3	38%	2.41	0.11
Fauna δ^{13}C	35.3	14.9	42%	2.93	< **0.05**
Fauna δ^{15}N	19.5	2.85	15%	0.68	0.70

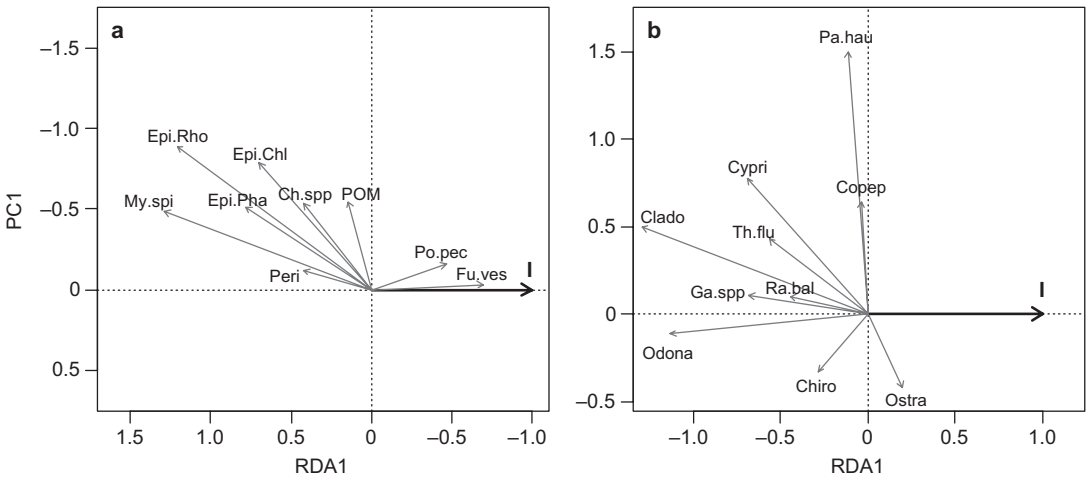

Fig. 4. Ordination graphs of first constrained ordination axis (RDA1) with bay isolation (I) and residuals on the second axis (PC1) for (**a**) δ^{13}C of flora, and (**b**) δ^{13}C of fauna. Abbreviations of functional groups and taxonomic names are underlined: (**a**) *Chara* spp., epiphytic Chlorophyta, epiphytic Phaeophyta, epiphytic Rhodophyta, *Fucus vesiculosus*, *Myriophyllum spicatum*, particulate organic matter (POM), periphyton, and *Potamogeton pectinatus*; (**b**) Chironomidae, Cladocera, Copepoda, Cyprinidae, *Gammarus* spp., Odonata, Ostracoda, *Parvicardium hauniense*, *Radix balthica*, and *Theodoxus fluviatilis*.

^{13}C. Although the δ^{15}N composition of flora did not change significantly along the bay isolation gradient (Table 3), there was a tendency toward lower δ^{15}N of *P. pectinatus*, *Chara* spp., and *M. spicatum* in the most isolated bays (Fig. 5). The small difference in δ^{15}N between producers and consumers suggests that the fractionation between trophic levels was low.

The results of the diet-mixing model indicated that epiphytes and periphyton are more important food sources for the benthic consumers *T. fluviatilis*, *R. balthica*, *Gammarus* spp., and Chironomidae than are the macrophytes *Chara* spp., *M. spicatum*, and *P. pectinatus* throughout the bay isolation gradient (Fig. 6). In the most open bays, macrophyte carbon did not contribute to the diet of *T. fluviatilis* and Chironomidae; however, the proportion of macrophyte carbon increased in the more isolated bays for these taxa. Macrophytes may account for up to approximately 40% of the carbon consumed by the benthic consumers in these bays, according to the specified model.

Discussion

We found a change in the community composition of both flora and fauna with increased shelter and isolation from the sea of Baltic Sea land-uplift bays. Both the macrophyte and macroinvertebrate communities changed from a diverse mixture of marine and freshwater taxa with high overall biomass in open bays to communities with larger proportions of a few freshwater taxa with lower overall biomass in isolated bays. In contrast, the zooplankton and YOY-fish abundance increased with increased bay isolation. The taxon composition of fish changed from a mixture of marine and freshwater taxa to an increased proportion of warm-water-spawning freshwater taxa. The results are consistent with the general changes in taxon composition and population densities found previously with increased bay isolation (measured as decreased topographic openness) for macrophytes (Munsterhjelm 1997, Appelgren and Mattila 2005, Rosqvist *et al*. 2010), macroinvertebrates (Hansen *et al*. 2008), zooplankton (Scheinin and Mattila 2010), and YOY fish (Snickars *et al*. 2009).

The concordant changes in the composition of macrophytes, invertebrates, and YOY fish could result from the similar responses of the communities to the significant changes in abiotic conditions along the bay isolation gradient. Decreased water circulation due to decreased topographic openness is known to affect the

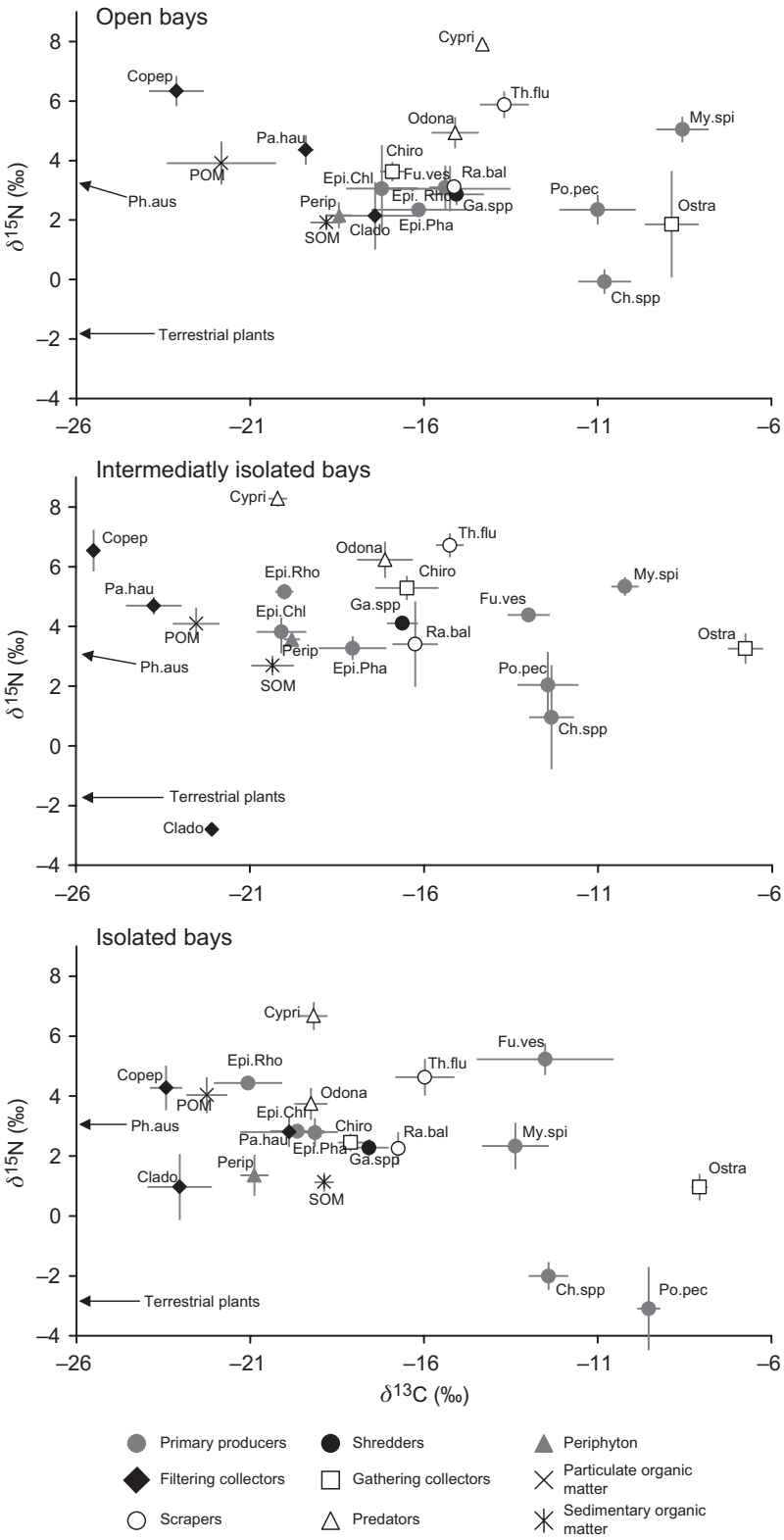

Fig. 5. Stable isotope signatures of functional groups or taxa along the bay isolation gradient. Mean (± SE) $\delta^{13}C$ and $\delta^{15}N$ were calculated from samples in two bays for each bay category. Abbreviations of functional group and taxonomic names are underlined: **primary producers** *Chara* spp., epiphytic Chlorophyta, epiphytic Phaeophyta, epiphytic Rhodophyta, *Fucus vesiculosus*, *Myriophyllum spicatum*, *Phragmites australis*, *Potamogeton pectinatus*, and terrestrial plants; **filtering collectors** Cladocera, Copepoda, and *Parvicardium hauniense*; **scrapers** *Radix balthica* and *Theodoxus fluviatilis*; **shredders** Gammarus spp.; **gathering collectors** Chironomidae and Ostracoda; **predators** Cyprinidae and Odonata; **periphyton**; **particulate organic matter** (POM); and **sedimentary organic matter** (SOM).

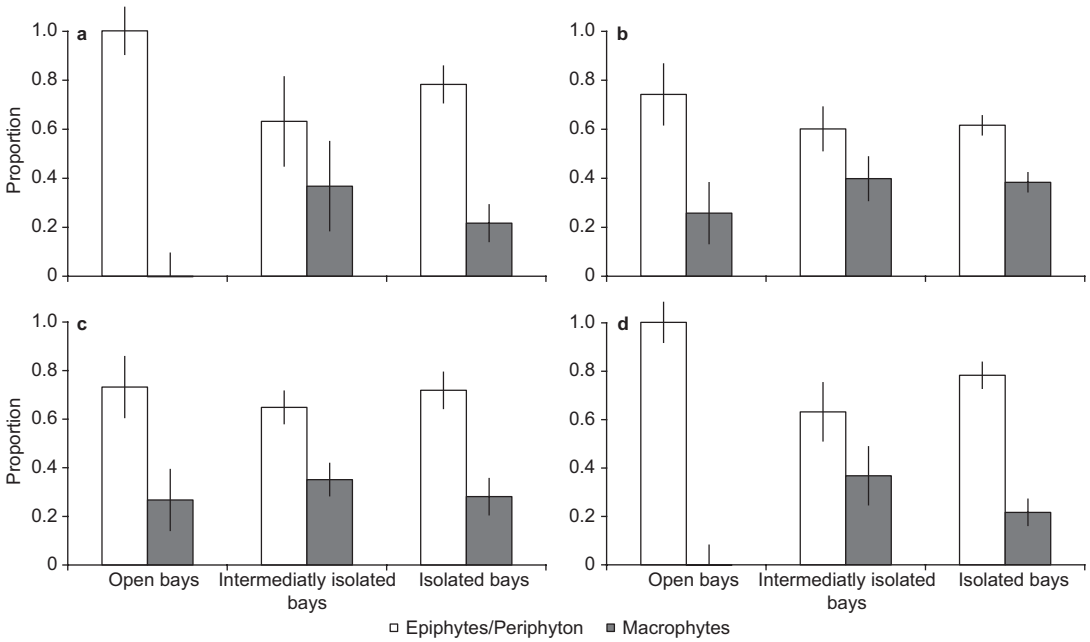

Fig. 6. Mean proportion (± SE) of epiphyte/periphyte and macrophyte (*Chara* spp., *Myriophyllum spicatum*, and *Potamogeton pectinatus*) carbon in the diets of the benthic consumers (**a**) *Theodoxus fluviatilis*, (**b**) *Radix balthica*, (**c**) *Gammarus* spp., and (**d**) Chironomidae along the bay isolation gradient. Proportions were calculated from samples in two bays for each bay category using $\delta^{13}C$ in IsoError 1.04.

macrophyte composition in these bays (Munsterhjelm 1997), and has also been suggested to affect the taxon composition of macroinvertebrates (Hansen *et al*. 2008). Decreased water circulation can explain the decrease in the cover of macrophytes such as *Ranunculus peltatus* ssp. *baudotii* and *Ruppia cirrhosa* (Munsterhjelm 1997) and the decrease in the biomass of filter-feeding bivalves such as *Mytilus edulis* (Hansen *et al*. 2008). In addition, early-season water temperature increases with increased bay isolation (Snickars *et al*. 2009), affecting the taxon composition of both flora and fauna (Munsterhjelm 1997, Snickars *et al*. 2009, Scheinin and Mattila 2010). High spring temperature is for example crucial for the reproductive success of warm-water-spawning freshwater fish species such as rudd *Scardinius erythrophthalmus*, roach *Rutilus rutilus*, pike *Esox lucius*, and perch *Perca fluviatilis* (Karås 1999, Sandström *et al*. 2005). Salinity is another strong structuring factor for both flora and fauna in the Baltic Sea (Kautsky 1988, Snoeijs 1999, Lappalainen and Urho 2006, Aleksandrov *et al*. 2009). We did not record any large differences in salinity between the bays, nor any change in salinity with increased bay isolation. However, salinity changes temporarily and salinity in enclosed bays can fluctuate more than in open bays, as the isolated bays are proportionally more affected by precipitation, land runoff, and evaporation than are the open bays, which have a higher water exchange with the sea. In spring, salinity can become lower in isolated than more open bays (Scheinin and Mattila 2010), which may prevent the permanent establishment of some species of marine origin, such as the macroinvertebrates *Palaemon adspersus* and *Idotea balthica*, which have an approximate lower salinity tolerance of 5 PSU (Barnes 1994, BACC Author Team 2008). Temporarily decreased salinity may, in contrast, benefit species of freshwater origin. For example, salinities below 4 PSU are crucial for the reproductive success of some freshwater fish species, since they are sensitive to higher salinities during their embryonic development (e.g.,

roach; Schoefer 1979, Lappalainen and Urho 2006, Härmä *et al*. 2008).

In more isolated bays, water can become stagnant due to a combination of low wave action, low water exchange with the sea, and dense vegetation. Larger fluctuations in dissolved oxygen concentration and pH in isolated bays are likely due to their stagnant conditions, high primary productivity, and accumulated organic-rich sediments. Oxygen concentration and pH will follow the photosynthetic and respiration cycle of the primary producers (Wetzel 2001, Brönmark and Hansson 2005). High respiration rates of consumers can further lower the dissolved oxygen concentration, and extensive respiration rates during the degradation of organic material can lead to anoxic conditions and the formation of toxic hydrogen sulphide (H_2S). Organisms established in isolated bays must therefore be able to cope with these fluctuations in abiotic conditions.

Macrovegetation is an important habitat modifier in littoral systems, as it provides habitat structure for other organisms (Orth *et al*. 1984, Diehl and Kornijów 1998, Hemminga and Duarte 2000), facilitating shelter from predation and niche separation. Macroinvertebrate biomass or abundance is often found to be positively related to macrophyte biomass or surface area (Diehl and Kornijów 1998, Attrill *et al*. 2000, Taniguchi 2003). The decrease in macrophyte biomass with increased bay isolation we recorded can therefore partly explain the low macroinvertebrate biomass found in the most isolated bays. Inter-specific differences in the habitat quality of Baltic Sea macrophytes have been shown for invertebrates (Hansen *et al*. 2010) and fish (Snickars *et al*. 2010), so the changed composition of macrophytes can affect the faunal community through altered habitat structure. In addition, plants differ in their quality as food, so a change in the composition of primary producers, such as a decreased proportion of epiphytes, could explain the changed composition of consumers along the bay isolation gradient. Such an effect will be significant only if consumers do not display plasticity in feeding ecology and cannot adapt to the changed composition of food sources.

The most prominent effect of increased bay isolation reflected in the stable isotope ratios was ^{13}C depletion of most primary producers. It was therefore not possible to interpret changes in $\delta^{13}C$ of consumers as a direct sign of change in resource utilization. However, most of the benthic primary consumers (the herbivorous/omnivorous *Theodoxus fluviatilis*, *Radix balthica*, *Gammarus* spp., and Chironomidae) had $\delta^{13}C$ signatures close to those of epiphytes and periphyton, and changed in $\delta^{13}C$ in a way similar to the epiphytes and periphyton along the bay isolation gradient. This result suggests that these primary producers are important food sources for the animals, either directly or indirectly through a microbial food chain. This corresponds to previous knowledge of the feeding ecology of herbivorous littoral macroinvertebrates in the Baltic Sea, which feed predominantly on periphyton and epiphytes rather than on coarsely structured algae and angiosperms (e.g. Skoog 1978 [*T. fluviatilis* and *R. balthica*], Goecker and Kåll 2003 [*Gammarus* and *Idotea*], Orav-Kotta and Kotta 2004 [*Idotea*], Boström and Mattila 2005 [*Idotea*], and Råberg and Kautsky 2008 [*T. fluviatilis* and *Idotea*]). However, these primary consumers were less depleted in ^{13}C than were epiphytes and periphyton, which implies that angiosperms and *Chara* spp. may also be important carbon sources for these animals, either fresh or as phytodetritus. The diet-mixing model revealed that angiosperms and charophytes can constitute up to approximately 40% of the carbon source for the consumers *T. fluviatilis*, *R. balthica*, *Gammarus* spp., and Chironomidae. For two of these consumers, *T. fluviatilis* and Chironomidae, a shift in diet was indicated along the bay isolation gradient. In open bays, the utilization of angiosperm and charophyte carbon was negligible, but their importance as food sources increased with increased bay isolation, probably due to decreased amounts of epiphytes. These results are in line with findings regarding seagrass ecosystems: epiphytes are the most important food source for most invertebrate primary consumers in these ecosystems, but the relative importance of epiphyte or seagrass food sources varies spatially, and seagrass detritus can be a significant food source in some areas (Fry 2006).

We could not distinguish any difference in the utilization of periphyton and epiphytes or between different epiphytic algae as these had very similar stable isotope signatures. In addi-

tion, it should be noted that the $\delta^{13}C$ of *Fucus vesiculosus* was similar to that of epiphytes in the most open bays, and similar to that of angiosperms and *Chara* spp. in the intermediately isolated and most isolated bays; indicating that *Fucus vesiculosus* is as likely to be a food source as are epiphytes or the other examined macrophytes. However, the cover of *F. vesiculosus* was very low in the most isolated bays (< 1% cover), and, together with the higher $\delta^{15}N$ of *F. vesiculosus* in relation to the consumers in these bays, makes it a less likely food source here.

Ostracoda had a very different stable isotope signature as compared with that of the other benthic primary consumers. The high $\delta^{13}C$ we recorded suggests that they rely on a completely different diet as compared with the other faunal taxa. The high $\delta^{13}C$ may also be a result of a different morphology or chemistry of the taxon, such as a different lipid content and C to N ratio (Post *et al*. 2007, Logan *et al*. 2008). Ostracoda was indeed found to have a considerably higher ratio of C to N in comparison with the other faunal taxa, making interpretation of differences in stable isotope values in comparison with the other animals difficult. The secondary consumers Cyprinidae and Odonata had the highest $\delta^{15}N$, reflecting their known carnivorous feeding (Corbet 1980, Johnson *et al*. 1987, Peterka and Matěna 2009). Both these predators had lower $\delta^{13}C$ in the intermediately and most isolated bays, possibly linked to the change in $\delta^{13}C$ of their potential prey organisms, i.e., small crustaceans and insect larvae.

The two zooplankton orders, Cladocera and Copepoda, had clearly separate stable isotope signatures, indicating differences in their diet. This result is in line with previous findings regarding lakes (Meili *et al*. 1996, Karlsson *et al*. 2004). The similar stable isotope values of Cladocera and periphyton in the most open bays imply that periphyton may be an important diet for Cladocera in these bays. Cladocera were more depleted in both ^{13}C and ^{15}N in the intermediately isolated and isolated bays, possibly due to utilization of organic matter of terrestrial origin, which is depleted in ^{13}C and ^{15}N. In comparison, Copepoda were depleted in ^{13}C in all bays. The depletion in zooplankton ^{13}C in relation to POM suggests that they must selectively use food sources that are more depleted in ^{13}C than is the bulk POM. The zooplankton may utilize smaller-sized carbon sources than we obtained in our POM samples (10 μm). In support of this possibility, the lowest $\delta^{13}C$ of Copepoda and $\delta^{15}N$ of Cladocera was observed in the intermediately isolated bays with the highest turbidity. In comparison, Jones *et al*. (1999) documented ^{13}C depletion of zooplankton with increased water colour in forest lakes in southern Finland. The stable isotopic signatures of the zooplankton we recorded may thus be derived from the utilization of dissolved or small-sized particulate carbon of terrestrial origin, possibly altered though microbial processes (Jones *et al*. 1999, Karlsson *et al*. 2004). Such utilization of terrestrial carbon may also occur in the case of the filter-feeding bivalve *Parvicardium hauniense* in the intermediately isolated and turbid bays, as this bivalve was depleted in ^{13}C here. Our results suggest that the importance of terrestrial carbon as a food source is not critically 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. Examination of differences in stable isotope values between different size fractions of organic particles would further contribute to a better understanding of the influence of terrestrial energy on the aquatic food web in the bays.

The substantial ^{15}N enrichment of the gastropod *T. fluviatilis* in relation to the other consumers suggests that it feeds on heterotrophic organisms rather than strictly on primary producers. Similarly, Jephson *et al*. (2008) also found ^{15}N enrichment of *T. fluviatilis* in relation to other consumers in habitats of the seagrass *Zostera marina* on the Swedish southeast coast. In contrast to *T. fluviatilis*, we found that *R. balthica* had lower $\delta^{15}N$, suggesting a larger proportion of fresh primary producers in the diet of this species. Jephson *et al*. (2008) also documented lower $\delta^{15}N$ in *R. balthica* than in *T. fluviatilis*, indicating that this may be a general pattern. Differences in fractionation level between organisms could, however, also explain the higher ^{15}N enrichment of *T. fluviatilis* than of the other consumers. Fractionation between trophic levels can vary considerably, depending on metabolic processes and on the $\delta^{15}N$ and C:N of the food

source (Vander Zanden and Rasmussen 2001, Vanderklift and Ponsard 2003, Caut *et al*. 2009) and must be tested for consumers in the shallow sheltered Baltic Sea bays before further examination of the food web in this ecosystem. The close $\delta^{15}N$ of primary producers and consumers we found imply lower fractionation in the studied bays than what is commonly assumed (3.4‰; Vander Zanden and Rasmussen 2001, Post 2002), and recently have been recorded in sandy exposed bays in the northern Baltic Sea (Nordström *et al*. 2009). The potentially low fractionation level we found, however, is similar to the results of Syväranta and Jones (2009) for littoral organisms in a Finnish lake. Gastropods have previously been used as primary consumer baselines for calculating higher trophic positions (Post 2002). But in agreement with Syväranta and Jones (2009), our findings of high $\delta^{15}N$ of *T. fluviatilis* suggest that some gastropods, generally regarded as primary consumers, may be inappropriate as indicators of trophic baselines in littoral systems. We did not find any change in faunal $\delta^{15}N$ with bay isolation. This suggests that the investigated faunal taxa occupy stable trophic positions along the bay isolation gradient, despite altered composition of food sources and omnivorous feeding capabilities of the investigated consumers.

The recorded changes in the stable isotope signatures of the primary producers could represent a response to changed hydrological and chemical conditions in the bays with increased bay isolation. In stagnant water during high photosynthetic activity, carbon can become a growth-limiting element (Vadstrup and Madsen 1995), and such conditions are probably more frequent in isolated than open bays. Uptake of carbon in the form of bicarbonate (HCO_3^-) is common among aquatic plants, and increased such uptake could explain the increased $\delta^{13}C$ of *F. vesiculosus* and *P. pectinatus* with increased bay isolation (Keeley and Sandquist 1992). The decrease in $\delta^{13}C$ of the other benthic primary producers with increased bay isolation could be due to 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 Sandquist 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 lower $\delta^{15}N$ found for angiosperms and *Chara* spp. in the most isolated bays may arise from a generally higher availability of nitrogen in the organic-rich sediments here (Jones *et al*. 2004). The differences in the stable isotopic signatures of the primary producers reflect differences in the ecology of species and how they are affected by changed environmental conditions, and should be further examined to achieve a better understanding of the processes in the shallow sheltered Baltic Sea bays.

Conclusions

Shallow sheltered Baltic Sea bays are complex littoral systems that change in floral and faunal taxon composition as they become more sheltered and isolated from the sea due to post-glacial land uplift and sedimentation. The use of stable isotopes to study changes in food-web structure with bay isolation was found to be difficult, as changes in $\delta^{13}C$ of consumers could not be unambiguously interpreted as a sign of change in resource utilization, since the $\delta^{13}C$ in primary producers also changed along the bay isolation gradient. In addition, fractionation among consumers appeared to differ from that commonly reported and must be further examined. However, epiphytes and periphyton seem to be the most important food sources for most benthic primary consumers, though the relative importance of epiphyte/periphyte versus macrophyte carbon varies spatially. Some investigated benthic consumers varied little in resource utilization along the bay isolation gradient, while other taxa shifted diet, accompanying the changes in floral composition. Stable isotope ratios for filter feeders indicated a possible utilization of food sources of terrestrial origin. The importance of terrestrial carbon as a food source could, however, not critically be related to bay isolation, but seems related to other characteristics of the bays, such as turbidity. The faunal $\delta^{15}N$ values indicated that the investigated taxa occupied stable trophic positions along the bay isolation gradient.

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Appendix. Mean values of stable isotopes of carbon (C) and nitrogen (N) in samples of functional groups and taxa from the six surveyed bays. Bays are ranked according to increasing isolation from the sea (A–F). Full names of the bays are given in Table 1 and locations are shown in Fig. 1. n.d. = no data.

		δ^{13}C Bay index						δ^{15}N Bay index					
Functional group/Taxa	Tissue	A	B	C	D	E	F	A	B	C	D	E	F
Primary producer													
Epiphytic algae													
Epiphytic Chlorophyta	Thallus	–16.3	–17.8	–19.2	–21.0	–18.1	–21.2	1.0	4.4	4.6	3.1	2.7	3.0
Epiphytic Phaeophyta	Thallus	–14.2	–18.1	–17.8	–18.3	–18.5	–19.3	2.2	2.5	3.1	3.5	4.2	2.3
Epiphytic Rhodophyta	Thallus	–14.8	–16.0	–19.8	–20.4	–18.2	–22.0	2.6	3.6	5.5	4.6	4.8	4.3
Primary producer													
Coarse algae													
Fucus vesiculosus	Top thallus	–15.0	–15.5	–13.7	–12.3	–12.1	–12.9	3.1	3.0	4.7	4.1	4.6	5.9
Chara spp.	Top thallus	–9.4	–12.7	–11.8	–12.9	–11.9	–13.0	0.4	–0.8	4.8	–2.9	–0.5	–3.5
Primary producer													
Submerged angiosperm													
Myriophyllum spicatum	Leaf	–7.2	–9.9	–10.3	–10.1	–11.6	–15.1	5.9	4.2	5.4	5.2	3.8	0.9
Potamogeton pectinatus	Leaf	–12.2	–9.8	–12.9	–12.0	–9.5	–9.6	2.9	1.8	3.7	0.4	–0.2	–6.0
Emerged angiosperm													
Phragmites australis	Leaf	–29.0	–27.5	–26.6	–27.5	–26.5	–25.8	2.6	5.2	3.9	2.6	3.5	3.4
Terrestrial angiosperm													
Alnus glutinosa	Leaf	–29.6	–27.0	–28.7	–30.2	–29.9	–28.7	–2.3	–1.6	–2.0	–1.5	–2.3	–2.3
Tanacetum vulgare/*Glaux maritima*	Leaf	–33.4	–30.2	–31.4	–33.1	–31.9	–30.8	–2.5	–1.9	–4.2	–0.1	–3.5	–3.8
Filtering collector (zooplankton)													
Copepoda	Whole animal	–23.2	–23.0	–25.7	–25.3	–22.7	–24.2	6.8	5.9	5.8	7.3	5.2	3.4
Cladocera	Whole animal	–16.1	–18.8	–22.1	n.d.	–21.4	–23.8	1.0	3.3	–2.8	n.d.	0.0	1.4
Filtering collector (bivalve)													
Parvicardium hauniense	Whole animal without shell	–19.5	–19.3	–22.6	–25.5	–17.9	–21.9	3.6	5.5	4.4	5.2	3.6	2.0
Scraper (gastropod)													
Theodoxus fluviatilis	Foot muscle	–12.7	–14.7	–14.7	–16.1	–14.8	–16.8	5.6	6.1	7.3	5.8	4.2	4.9
Radix balthica	Foot muscle	–14.7	–15.6	–14.7	–16.8	–16.4	–17.1	2.7	3.6	1.0	4.2	3.1	1.4
Shredder (crustacean)													
Gammarus spp.	Extremities	–14.1	–16.0	–15.9	–17.3	–18.0	–17.3	2.7	3.0	3.7	4.5	2.5	2.2
Gathering collector													
Insect													
Chironomidae	Whole animal	–15.9	–17.9	–18.6	–14.4	–17.9	–18.3	2.8	4.4	5.1	5.5	3.1	1.8
Crustacean													
Ostracoda	Whole animal	–8.5	–9.1	–7.6	–5.9	n.d.	–8.1	–1.6	4.1	2.6	3.9	n.d.	1.0
Predator													
Insect													
Odonata	Extremities	–14.4	–15.8	–17.1	n.d.	–20.4	–18.9	5.5	4.4	6.2	n.d.	5.4	3.2
Fish													
Cyprinidae	Tail muscle	–14.3	n.d.	–20.5	–19.6	–18.2	–20.0	7.9	n.d.	8.1	8.6	7.9	5.7
Periphyton		–19.0	–17.9	–19.5	–20.1	n.d.	–20.9	1.7	2.6	4.0	3.1	n.d.	1.4
Particulate organic matter (POM)		–20.0	–23.7	–23.5	–21.6	–21.7	–22.8	3.5	4.4	4.3	3.9	5.0	3.1
Sedimentary organic matter (SOM)		–18.4	–19.2	–21.6	–19.1	–19.2	–18.6	1.8	2.0	3.3	2.1	1.5	0.7