Invertebrate communities associated with blue mussel beds in a patchy environment: a landscape ecology approach

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ABSTRACT: Landscape ecology has evolved rapidly as a terrestrial discipline over the past centuries due to an increased concern over habitat loss and fragmentation. Proceedings in the marine realm have been comparatively scarce, even though many key habitats in marine ecosystems are becoming equally fragmented. We sampled the macrofauna associated with blue mussel beds in naturally patchy landscapes of islands and reefs in the non-tidal Baltic Sea and tested for the effect of island area, isolation and reef depth on local species richness and composition. The fauna was also compared among islands and reefs. Contrary to expectations, species richness did not increase with island size, and species diversity was higher on deep reefs compared to shallow reefs and islands protruding from the water. Region and depth also had an effect on species assemblage. Geographical distance to nearest island or reef showed no correlation with species richness but correlated positively with faunal density, i.e. a higher degree of isolation increased density. In accordance with other marine studies, our data, therefore, supports the nearest refuge hypothesis, postulating that mobile invertebrates disperse over areas of non-habitat and then concentrate in isolated habitats because habitats in isolation are the nearest available refuge. We show that terrestrial landscape approaches cannot be directly applied to the study system. This has important implications for the planning of marine protected areas and their management.

KEY WORDS: Habitat area · Isolation · Seascape · Benthic community · Diversity · Baltic Sea

INTRODUCTION

During the last few decades, there has been a growing interest in the application of landscape ecology to predict how ecosystems are changing due to human induced habitat fragmentation and loss of habitat (e.g. Forman & Godron 1981, Pimm et al. 1995, Fahrig 2003). Consequently, patch-occupancy dynamics have been extensively studied in terrestrial habitats and many theories have been developed for these systems. One of the most important of all landscape theories is the theory of island biogeography (MacArthur & Wilson 1967), predicting that species diversity on islands is determined through the balance of factors controlling immigration and extinction rates. Accordingly, species richness increases with growing island size and a closer distance to sources of propagules due to a higher rate of immigration. Tightly linked to island biogeography theory is the concept of metapopulations. This has become a major paradigm in terrestrial community ecology during recent decades, referring to subpopulations that live in discrete patches or islands with their own dynamics, but where individuals disperse among patches (Hanski & Gilpin 1997). The rate of dispersal is affected by aspects of landscape heterogeneity,

with patch size and isolation being among the most important ones. Consequently, patch area and connectivity are considered to be among the most important factors determining species richness and faunal composition with major implications on conservation strategies worldwide (e.g. Tischendorf & Fahrig 2000, Moilanen & Hanski 2001).

Landscape ecology approaches in aquatic environments, so called seascape studies, have not emerged at the same pace despite evidence that the concepts are applicable in many coastal environments and it has been questioned whether the metapopulation concept can be applied to marine landscapes (e.g. Wiens 2002, Grimm et al. 2003). Seascape studies have until now been restricted to a few coastal landscapes, with roughly half of the studies conducted in seagrass landscapes (49%) and a smaller portion in salt marsh environments (32%), coral reefs (11%), mangroves (6%) and oyster reefs (2%) (Boström et al. 2011). Results have been highly variable among habitat types with a lack of general tendencies, as well as partly differing from terrestrial models (Boström et al. 2011). Habitat fragmentation, resulting in smaller patches, increased isolation and increased proportion of edge habitat is common in a large range of shallow marine habitats, not only seagrass and salt marsh habitats, but also in oyster reefs and rocky shore mussel beds throughout the world, both by natural and anthropogenic causes (e.g. Rothschild et al. 1994, Smith et al. 2006). Therefore, habitat- and scale-dependent information on how organisms perceive and respond to changes in marine landscapes is critical to efforts aimed at predicting the effects of habitat change on population abundance.

A big challenge in applying landscape ecology approaches to marine landscapes is to delineate populations and their local scales and to determine what constitutes an insular habitat in the first place (Camus & Lima 2002, Grimm et al. 2003). So far, our understanding of the dynamics of biologically engineered patches such as blue mussel communities, seagrass beds or corals has been largely derived from studies conducted at small spatial scales where the bioengineered patches typically function as insular habitats for faunal communities. On a within-shore scale, patch size, body size or height and density, as well as patch shape have all been found to influence some associated communities (Tsuchiya & Nishihira 1986, Ragnarsson & Raffaelli 1999, Bologna & Heck 2002, Irving & Bertness 2009, Koivisto et al. 2011). Also, patch context and surrounding matrix influence faunal assemblages both in terrestrial and marine systems (Mazerolle & Villard 1999, Ricketts 2001). In addition to small-scale studies, interconnected subregions can be ecologically relevant scales to study population dynamics due to the widespread dispersal within clusters of habitat patches. Such studies are, however, rare in current literature (Bode et al. 2006).

As for terrestrial species, dispersal techniques vary greatly for marine organisms, which might affect their abundance in patches. Some marine species may lack local population dynamics due to pelagic larval stages since larvae are transported over long distances by currents (Gaines et al. 2007), but the majority of the marine fauna are holobenthic and lack regular benthic dispersal. They, therefore, occur in distinct patches, separated by vast areas of unsuitable habitat (Grimm et al. 2003). Despite the importance of understanding dispersal rates and strategies for community ecology, these processes are still poorly known in marine ecosystems (Valanko et al. 2010).

In the northern Baltic Sea, the seascape is comprised of a mosaic of habitats showing a high degree of natural patchiness with islands, islets and underwater rocky reefs of varying sizes separated by deeper waters below the photic zone. Hence, the study area represents a unique natural laboratory where the effects of a variety of physical and biological factors can be determined in an island biogeography theory context. Underwater reefs are relatively common and protected by the EU Habitats Directive Natura 2000 (habitat type 1170; Airaksinen & Karttunen 1998). Despite this, the fauna on these reefs has never been described in the study area, nor are there other comparable published studies from the Baltic Sea. The fauna on these reefs might be very different from that of islands and continuous habitats due to isolation, poor connectivity, the lack of littoral algal belts and, therefore, fewer habitats. The size of the islands and the distance to nearest neighbouring island or reef vary considerably and they are, therefore, optimal for testing the effect of habitat size and isolation on fauna at a seascape level.

We were interested in determining the extent to which the theory of island biogeography can predict how the community structure of the fauna associated with blue mussels (*Mytilus trossulus* × *M. edulis*) will vary between islands of different sizes and reefs of different submersion levels with a varying degree of isolation in 2 areas of the Finnish coastline in the northern Baltic Sea. We tested 4 hypotheses: (1) Mussel beds on bigger islands will support greater levels of species richness than smaller islands and a higher

degree of isolation will lower species richness on islands as postulated by the island biogeography theory. (2) The fauna will differ between reefs of differing depth and reefs versus islands since deeper reefs lack shallow algal belts and the algal communities possibly uphold communities that spread downwards. (3) The mode of dispersal might affect the abundance of species, restricting the abundance of species with direct development compared to species with pelagic phases and (4) depth will influence the faunal communities with different species living at different depths.

MATERIALS AND METHODS

Sample regions

In order to compare faunal composition in islands of differing size and reefs of differing depths, 56 locations from 2 different regions separated by ca. 30 km were sampled in the summer season 2009 (Fig. 1). Region 1, Jussarö (59° 48′ N, 23° 33′ E), is part of the Gulf of Finland, whereas region 2, Western Hangö (59° 55′ N, 22° 50′ E), is part of the Archipelago Sea. Both sites are characterized by high levels of topographic complexity formed by mosaics of islands, islets, rocks and reefs, where ambient physical wave conditions vary considerably over proximate sites (Westerbom & Jattu 2006). Exposure was determined according to Westerbom & Jattu (2006) using the Baardseth index. This index calculates the amount of open water in a landscape around a given site (Baardseth 1970) and has been commonly used in the study area as a measure of wave impact on rocky shore communities (e.g. Ruuskanen et al. 1999, Westerbom & Jattu 2006). The exposure on all sites was low (Baardseth < 2).

Large islands were defined by a diameter ranging from 100 to 500 m above sea surface, small ones ('islets') as small tops (diameter 1 to 50 m) emerging from the water. Shallow reefs were completely submerged under water with their shallowest parts ranging from 1.7 to 3.6 m depth. The shallowest parts of the deep reefs ranged from 4.6 to 5.2 m. Both reef types had a diameter of 1 to 50 m. The island and reef areas were calculated using the 5 m depth curve. The deep reefs lacked the annual and perennial algal belts that are considered to be important elements on the northern Baltic shores (Kraufvelin & Salovius 2004, Wikström & Kautsky 2007). The isolation of each habitat was defined as geographic distance to the nearest habitat, here defined as nearest island or reef shallower than 5 m regardless of size. Current directions were not considered since they are determined by wind and, therefore, run in various directions, lacking a main direction (Alenius et al. 1998). The islands of differing size and both reef types are hereafter referred to as 'island types'.

Sampling technique and processing of samples

Samples of the invertebrate fauna were taken at 2, 3.5 and 5 m depth from each of the island types by SCUBA diving in September 2009. Deep reefs were sampled only at 5 m. Each island type had 14 replicates. The samples were collected by placing a quadrat frame (20 × 20 cm) into dense mussel beds and scraping the entire frame content into an attached fabric sampling bag. These samples were placed in jars and covered by 70% ethanol. To ease the counting of all individuals, the fauna was sorted by size through a series of sieves (mesh sizes 9.5, 4, 2, 1 and 0.5 mm), after which fauna was identified to
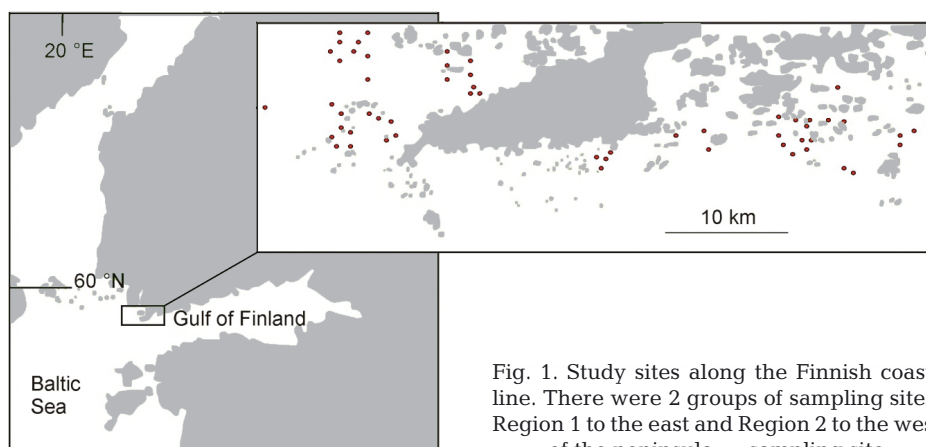

Fig. 1. Study sites along the Finnish coastline. There were 2 groups of sampling sites: Region 1 to the east and Region 2 to the west of the peninsula. ●: sampling site

the lowest taxonomic level possible. The smallest fractions were analysed with the aid of a dissecting microscope (Leica S6E).

Data analysis

To test for differences in species richness between islands and reef types, we used a 2-factor ANOVA with island type and region as fixed factors for each depth separately, followed by a Student-Newman-Keuls (SNK) post-hoc test. Furthermore, to test whether species richness and faunal density are functions of island area or nearest neighbor (NN), multiple regressions using a general linear model (GLM) were used. We also tested whether the relationships vary with depth and whether faunal density and species richness are connected. Data were analyzed as both untransformed and log-transformed data because the relationships were expected to be non-linear. Since the relationship of species richness and area was found to vary with depth, the area effect was tested separately for each depth. Faunal density was found to be a function of species richness, and since the interaction effect of NN and depth could not be excluded, the effect of area and NN for density was tested separately for each depth in a model including NN, area and species richness (all numbers log-transformed). Since the p-value for area exceeded 0.1, the relationship was also tested with a model excluding area. As both NN and species richness were found to have a positive effect on density, the residuals from the regression of density versus species richness against NN, as well as the residuals from the regression of density versus NN against species richness (all numbers log-transformed) were plotted to see whether NN and species richness have independent effects.

All species were categorized into 4 groups of developmental mechanism (planktotrophic, lecithotrophic, direct–internal or external brooding or other) based on Valanko et al. (2010) and Törnroos et al. (2012) and the abundance of the dispersal categories in each island type were tested for differences using a one-way ANOVA. The dispersal ability of members in the direct development or brooding groups was expected to be restricted, whereas taxa with pelagic larvae were expected to be more evenly distributed. Planktotrophic species included all bivalves, *Hydrobia* sp., the barnacle *Balanus improvisus* and 2 polychaete species; lecithotrophic species included 1 gastropod and a few polychaete species as well as Oligochaeta, whereas species with direct

development or internal or external brooding included crustacean species and a few gastropod species (Table 1). Kolmogorov-Smirnov and Levene's tests were used to test if data fulfilled assumptions for parametric testing and, if necessary, data were log-transformed to fulfill these assumptions. Nearest neighbor distances were calculated by measuring the straight-line distances between each island and its nearest habitat using an electronic map and regressed against species richness and faunal density. Furthermore, to test whether species richness among the different depths in the individual locations interconnected, the species richness at different depths from all locations was tested for correlation with a Spearman rank test for the different depth combination pairs separately (2 vs. 3.5 m, 2 vs. 5 m, 3.5 vs. 5 m).

To test if the faunal assemblages differ in the 4 island types, a 2-factor permutational multivariate analysis of variance (PERMANOVA) with island type and region as fixed factors was performed on

Table 1. Species or taxa found in the study with different functional developmental characteristics. Grouping based on Valanko et al. (2010) and Törnroos et al. (2012). *: species may belong to more than one category

Developmental strategy	Taxon
Planktotrophic	*Mytilus edulis*
	Macoma balthica
	Mya arenaria
	Cerastoderma glaucum
	Hydrobia sp.
	Pygospio elegans*
	Balanus improvisus
	Boccardia redeki*
Lecithotrophic	*Theodoxus fluviatilis*
	Hediste diversicolor
	Marenzelleria viridis*
	Oligochaeta
Direct development or internal or external brooding	*Potamopyrgus jenkinsi*
	Limapontia capitata
	Gammarus spp.
	Calliopius laevisculus
	Leptocheirus pilosus
	Corophium volutator
	Idotea sp.
	Iaera spp.
	Mysidae
	Ostracoda
	Turbellaria
	Nemertea
	Hirudinea
	Lymnea peregra
	Fabricia sp.
Other	Chironomidae

Bray Curtis dissimilarities on square root-transformed data for each depth separately. Faunal communities in the different islands or regions were compared using the SIMPER procedure and a canonical analysis of principal coordinates (CAP; Anderson & Willis 2003) where differences were significant. Individual taxa with strong correlations with the ordination axes (≥ 0.3) were plotted as arrows in a biplot (Anderson & Willis 2003). The effect of depth was tested using a single factor PERMANOVA on all data combined and since differences were highly significant between depths, CAP analysis was performed to visually compare the assemblages associated with the different depths.

RESULTS

Species richness was significantly higher on deep reefs compared to large islands and shallow reefs at 5 m as revealed by the ANOVAs followed by the SNK-post hoc (ANOVA $F_{3,55} = 3.87$, p = 0.02). There were no significant differences in the species richness at 2 m or 3.5 m (Fig. 2). The species richness did not increase with island area at any of the depths according to the regressions (Fig. 3); on the contrary, the maximum number of species was higher on the small islands compared to the larger ones at 3.5 m and 5 m (24 vs. 23 at 3.5 m and 25 vs. 24 at 5 m). Region had a significant effect at 3.5 m and 5 m with the Western Hangö area having a higher species richness compared to the Jussarö region (ANOVA $F_{1,41} = 8.8$, p = 0.05; $F_{1,55} = 4.82$, p = 0.03). The distance to nearest neighboring island did not show any relationship with species richness, but was a positive predictor for faunal density at 5 m as seen from the multiple regression of the log-transformed values, i.e. a higher distance increased density (Fig. 4). Also, species richness had a positive effect on density (multiple $R^2 = 0.27$, p ≤ 0.05). The residual plots from the regression of density versus species richness against NN as well as the residuals from the regression of density versus NN against species richness showed that NN and species richness do indeed have distinguishable effects on faunal density with both showing linear relationships (Fig. 5). The distance to nearest neighboring island or reef was slightly higher for both reef types compared to small and large islands (ANOVA, $F_{3,55} = 10.56$, p ≤ 0.001). Species with planktotrophic larvae were significantly least abundant at the large islands (ANOVA, $F_{3,139} = 3.16$, p = 0.03). There were no differences in the

abundance of species with direct development or internal or external brooding among island types.

The PERMANOVA found significant differences in the composition of the species assemblages between the island types at 5 m (pseudo-$F_{3,55} = 2.0$, p = 0.001), but not at the other depths (p > 0.05). According to the pair-wise comparisons, the large island fauna differed from all other island types (p > 0.05 for all pairs). Many grazing species, such as *Iaera* spp., *Tenellia adspersa* and *Leptocheirus pilosus* as well as the polychaete *Marenzelleria viridis* and the bivalve *Macoma balthica* were more associated with the island types, whereas the bivalve *Cerastoderma glaucum* and nematodes were more tightly associ-
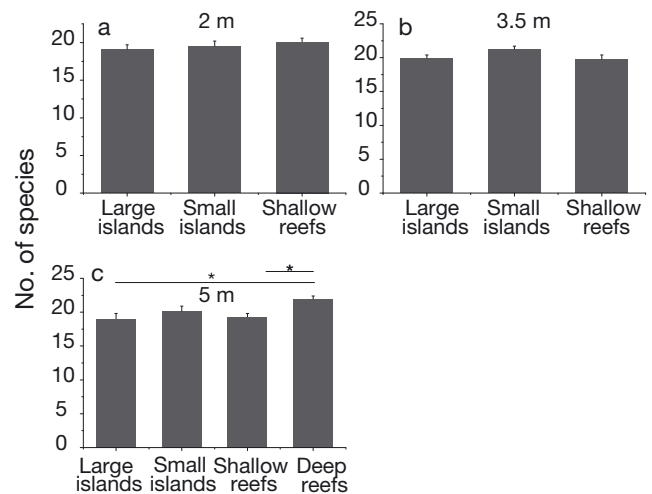
Fig. 2. Species richness in the 4 habitat types (small or large islands, shallow reefs or deep reefs) at (a) 2 m (b) 3.5 m and (c) 5 m. Values are given per sampled square area (400 cm^2). Lines above bars indicate habitat types that significantly differ from each other as revealed by the post-hoc test. *p = 0.05
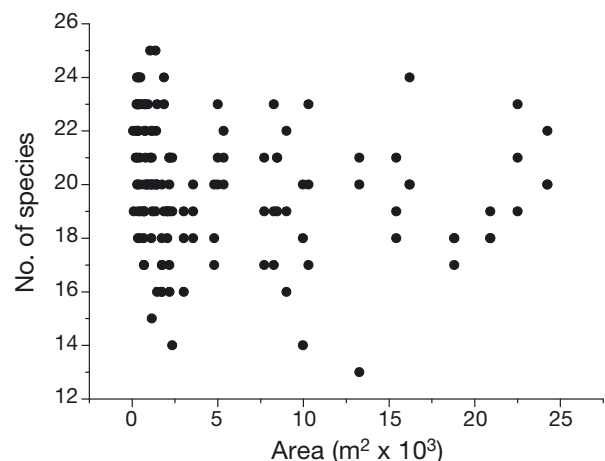
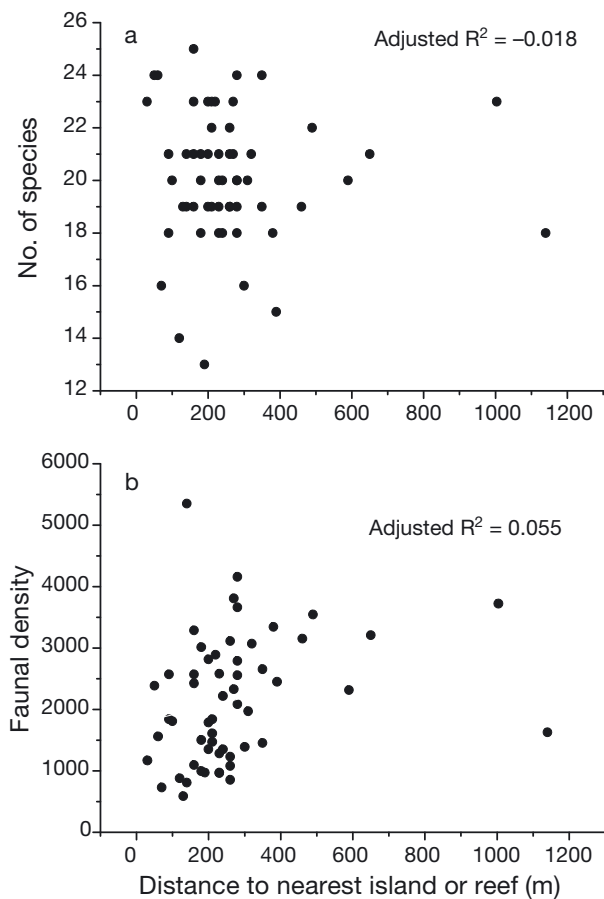Fig. 3. Relationship between habitat area and number of species at 5 m depth. N = 56

Fig. 4. Relationship of (a) species richness and (b) faunal density (all species combined) as number of individuals per sampled patch area (400 cm^2) with distance to nearest neighboring island or reef. Data from 5 m depth (N = 56)

ated with the reefs (Fig. 6). Region also had a significant effect at all 3 depths (pseudo-$F_{1,41}$ = 6.81, p = 0.001; pseudo-$F_{1,41}$ = 8.32, p = 0.001 and pseudo-$F_{1,55}$ = 9.83, p = 0.001 respectively). Still, the compositions of the faunal assemblages were remarkably similar in all island types, also among regions: *Hydrobia* sp., *Balanus improvisus*, *M. balthica*, *Iaera* spp. and *Gammarus* spp. ranked among the 5 most abundant taxa in both regions as revealed by the SIMPER procedure. Depth had a significant effect on the faunal composition (pseudo-$F_{2,139}$ = 4.8, p < 0.001) with all depths differing from each other (p < 0.01 for all). There were more crustacean grazers at the shallow depths, whereas Oligochaeta and bivalves were more common at 5 m (Fig. 7). There were no correlations between species richness at the different depths at individual locations (p > 0.05 for all depth combinations).

DISCUSSION

The theory of island biogeography has remained influential more than 40 yr after publication, although metapopulation theories have largely replaced island biogeography as a framework for describing the dynamics of populations interconnected by occasional migration (Hanski & Gilpin 1997). Surprisingly, in this study, the larger islands did not show a higher species richness compared to the smaller islands (Figs. 2 & 3). On the contrary, the maximum number of species was higher on the smaller islands at the deeper depths. These findings are in contrast with many terrestrial studies (e.g. Simberloff & Wilson 1969, Diamond 1975) and small-scale studies of patches of blue mussels, seagrass and coral reefs (Sale et al. 1994, Hovel & Lipcius 2001, Norling & Kautsky 2008). The result might be a consequence of scale since the study islands were bigger than most previously studied habitats. It is possible that other factors such as physical disturbance, larval
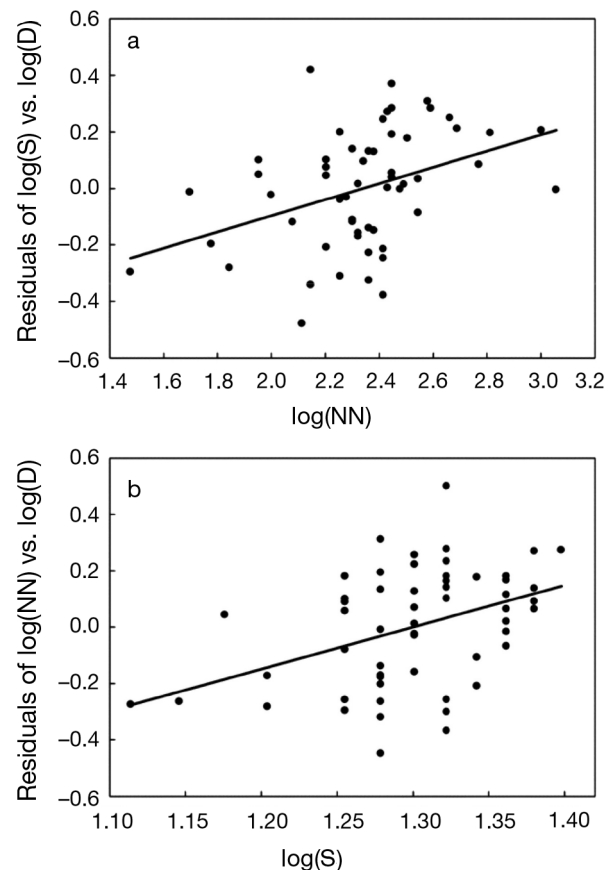

Fig. 5. Residual plots of (a) density (D) versus number of species (S) against nearest neighbor (NN) and (b) D versus NN against S. Data from 5 m depth (N = 56)
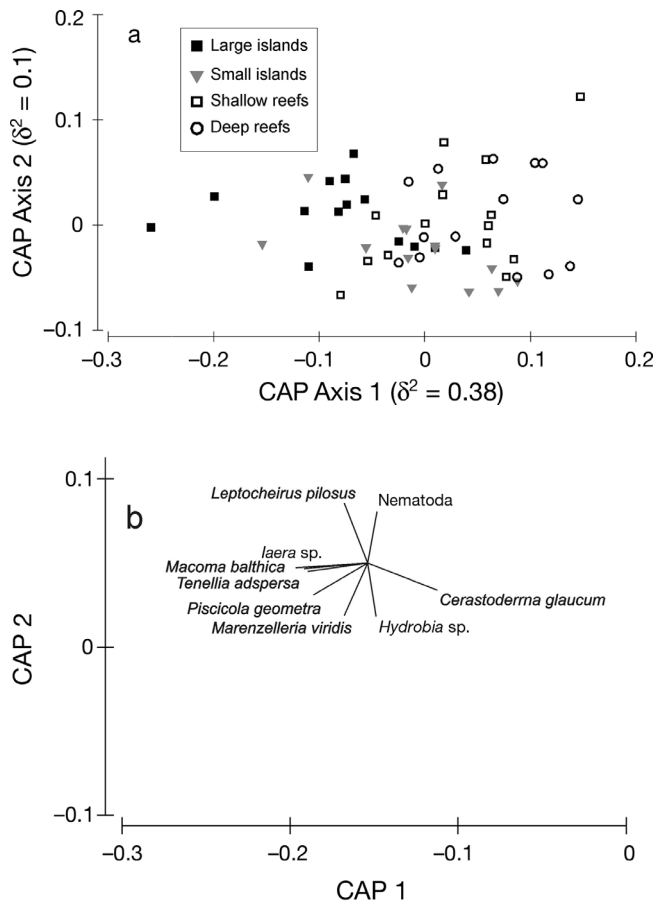
Fig. 6. Canonical analysis of principal coordinates (CAP) plot from the different island types showing (a) canonical axes that best discriminate assemblages at the different islands and (b) correlations of individual taxa with the canonical axes

Isolation had no effect on species richness on the study islands. In contrast, faunal density correlated with increasing distance to nearest neighboring island or reef (Figs. 4 & 5). A greater abundance of invertebrate taxa in habitats that are distant from each other compared to aggregated habitats has also been previously reported (Gunnill 1982, Virnstein & Curran 1986, Russell et al. 2005). The most popular explanation for this inverse pattern compared to terrestrial systems is the 'nearest refuge hypothesis', i.e. that mobile invertebrates disperse over areas of non-habitat and then concentrate in isolated habitats because habitats in isolation are the nearest available refuge (see also Edgar 1992). Since density was also linked to higher species richness, this result may also reflect the higher number of species on the deep reefs. However, as seen from the residual plots (Fig. 5), both NN and species richness had independent effects on the faunal density. Russell et al. (2005) proposed that the colonization success of distant

supply or predation may shape the invertebrate communities beyond a minimum size threshold, which our islands may have exceeded. The higher number of species on the deep reefs compared to large islands (Fig. 2c) was also somewhat surprising since deep reefs lack many structural components, such as filamentous algal- and fucoid belts that are commonly found on shallow reefs and islands, and since structural heterogeneity is generally considered to generate higher diversity (Heck & Wetstone 1977, Downes et al. 1998). On the other hand, physical disturbances such as ice scour may less affect deeper reefs. The overall number of species is also very low in the Baltic Sea (Ojaveer et al. 2010), restricting the species pool and it may well have been that no additional species able to inhabit blue mussel patches exist in the study area, making it impossible for the number of associated species to grow despite an increase in the island area.
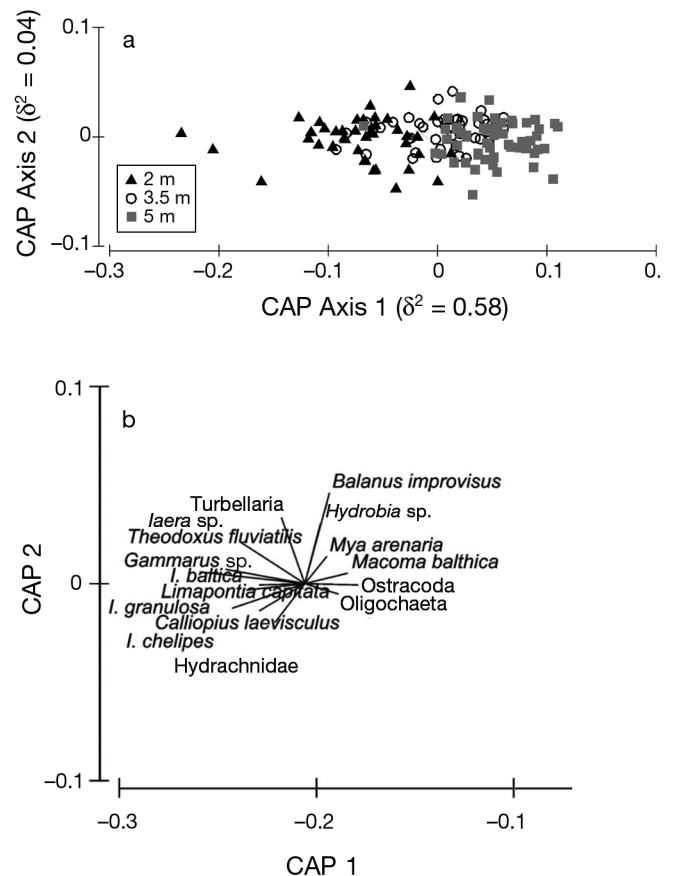

Fig. 7. CAP plot from the different depths showing (a) canonical axes that best discriminate assemblages at the different depths and (b) correlations of individual taxa with the canonical axes

habitats should vary markedly for different groups of taxa, however, we found only few differences in the abundance of highly different taxa groups among island types, showing that most taxa in the study area are good dispersers at the studied scale. The most striking difference was a higher number of some opportunist species such as nematodes on the reefs, whereas many grazing species were more tightly linked to the islands (Fig. 6b), perhaps reflecting a larger amount of suitable habitat for the species on these island types (sediment load, algae etc.) rather than limitations in dispersal. It would be very interesting to further study where the isolation effect begins since we were unable to find any effects on the studied scale. Also, the speed by which the propagules move across islands could provide valuable information.

There are obvious analogues between terrestrial and marine populations with respect to metapopulation approaches, but where the movement between patches is usually low in terrestrial models of metapopulations, the opposite is considered true for marine ecosystems (Botsford et al. 2003). The dispersal of reproductive propagules (immigrants, larvae, asexual buds) is likely to play an important driving role in determining community diversity, invasibility and stability in many systems (Tilman 1997). Water flow plays a direct and important role in determining the local species richness of benthic invertebrate communities by mediating the delivery of species (Palardy & Witman 2011). In marine systems, it is generally assumed that the continuous supply of larvae connects and shapes populations in heterogeneous habitats (Gaines et al. 2007) even though recent genetic studies support the existence of distinct metapopulations for a number of taxa in marine environments where populations show strong local adaptation (Hellberg 2009). In our study, the high number of species in the isolated deep reefs was not limited to species with pelagic larvae. Also, species with direct development or brooding, mostly crustaceans, were equally abundant in the distant deep reef islands, proving that they are capable of migrating freely in this system. Processes affecting dispersal and migration of invertebrates in fragmented landscapes are, without doubt, complex and further testing in the field should be done. Post-larval dispersal, such as swimming, drifting and crawling, is important for spatial patterns of distribution and abundance in the study area with great temporal variability (Valanko et al. 2010). For example, amphipods are highly active swimmers as adults and stochastic wind-wave events might play an impor-

tant role for their dispersal (Commito et al. 1995). It has been suggested that even small groups of individuals, drifting egg masses or even just one fertilized female with direct development may rapidly establish a population if the environment is suitable (Johannesson 1988). Also, rafting acts as an important process in transferring macrofaunal species to novel areas in the study area (Salovius et al. 2005).

There were large and significant differences among depths in the structure of faunal assemblages and some taxa were found almost exclusively at deeper depths (*Fabricia* sp., Oligochaeta), whereas many grazers, such as isopods, amphipods and gastropods were more frequent at shallow depths (Fig. 7b). With increasing water depth, the species assemblage tends to shift from filter feeders and grazers toward communities dominated by deposit feeders and predators (Glockzin & Zettler 2008). Water movement and sedimentation (Airoldi 2003), physical and biological disturbance (Ayling 1981, 1983) and the interplay between biotic and abiotic processes (Smith & Witman 1999) have been suggested to explain depth gradient patterns. The species richness between depths at individual locations did not correlate, suggesting that species composition and abundance in shallow algal habitats have little effect on deeper habitats, perhaps due to local selection that causes vertical zonation patterns. The difference in faunal composition between the 2 study regions may reflect differences in blue mussel population structure apart from different physical conditions. The Jussarö area is characterized by dense mussel patches made up of a large portion of small individuals (2 to 10 mm), whereas the populations in the Archipelago Sea have an older mussel structure, made up of proportionately larger mussels, but with a sparser density (Westerbom et al. 2002). Blue mussel biomass significantly influences species richness in associated communities (Koivisto & Westerbom 2010). Also, ice conditions are less severe in the Archipelago Sea.

Our results have 3 important implications for applying terrestrial landscape ecology principles to marine environments in the study area. (1) General landscape models such as the species–area relationship and connectivity models cannot always be directly applied to aquatic communities due to the high dispersal of many marine animals. This is an important finding since approaches to marine conservation lean heavily on ideas from terrestrial systems. As the populations of most marine species exchange juveniles between sites, small isolated marine protected areas are unlikely to ensure the

persistence of marine metapopulations (Mora et al. 2006), and we suggest that the relationship between animal movements and seascape connectivity should be further looked into. (2) Threshold values might exist beyond which phenomena, such as the islands biogeography theory, no longer have an effect. The theory has commonly been found to apply on studies conducted at smaller, within-shore scales (e.g. Tsuchiya & Nishihira 1985, Koivisto & Westerbom 2010), but was not detected in this study. (3) The invertebrate fauna associated with blue mussels is abundant in most habitat types on hard substrates, enforcing the idea that blue mussels are effective ecosystem engineers regardless of their patch context (see Koivisto & Westerbom 2010 and Koivisto et al. 2011). The high diversity on stony reefs should also be considered when designing marine protected areas in the northern Baltic Sea since shallow, windy archipelago areas are considered as possible locations for wind energy constructions.

LITERATURE CITED

Airaksinen O, Karttunen K (1998) Natura 2000 luontotyyppi-opas. Suomen ympäristö 46. Suomen ympäristökeskus, Helsinki

Airoldi L (2003) The effects of sedimentation on rocky coast assemblages. Oceanogr Mar Biol Annu Rev 41:161–236

Alenius P, Myrberg K, Nekrasov A (1998) The physical oceanography of the Gulf of Finland: a review. Boreal Environ Res 3:97–125

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511–525

Ayling AL (1981) The role of biological disturbance in temperate subtidal encrusting communities. Ecology 62: 830–847

Ayling AL (1983) Factors affecting the spatial distribution of thinly encrusting sponges from temperate waters. Oecologia 60:412–418

Baardseth E (1970) A square-scanning, two stage sampling method of estimating seaweed quantities. Rep Norw Inst Seaweed Res 33:1–41

Bode M, Bode L, Armsworth PR (2006) Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. Mar Ecol Prog Ser 308:17–25

Bologna PAX, Heck KL (2002) Impact of habitat edges on density and secondary production of seagrass-associated fauna. Estuaries 25:1033–1044

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar Ecol Prog Ser 427:191–217

Botsford LW, Fiorenza M, Hastings A (2003) Principles for the design of marine reserves. Ecol Appl 13(Suppl): S25–S31

Camus AP, Lima M (2002) Populations, metapopulations, and the open-closed dilemma: the conflict between operational and natural population concepts. Oikos 97: 433–438

Commito JA, Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ (1995) Dispersal dynamics in a wind-driven benthic system. Limnol Oceanogr 40:1513–1518

Diamond JM (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol Conserv 7:129–146

Downes BJ, Lake PS, Schreiber ESG, Glaister A (1998) Habitat structure and regulation of local species diversity in a stony, upland stream. Ecol Monogr 68:237–257

Edgar GJ (1992) Patterns of colonization of mobile epifauna in a Western Australian seagrass bed. J Exp Mar Biol Ecol 157:225–246

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Syst 34:487–515

Forman RTT, Godron M (1981) Patches and structural components for a landscape ecology. Bioscience 31:733–740

Gaines SD, Gaylord B, Gerber LR, Hastings A, Kinlan BP (2007) Connecting places: the ecological consequences of dispersal in the sea. Oceanography (Wash DC) 20:90–99

Glockzin M, Zettler ML (2008) Spatial macrozoobenthic distribution patterns in relation to major environmental factors – a case study from the Pomeranian Bay (southern Baltic Sea). J Sea Res 59:144–161

Grimm V, Reise K, Strasser M (2003) Marine metapopulations: a useful concept? Helgol Mar Res 56:222–228

Gunnill FC (1982) Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetia fastigiata.* Mar Biol 69:263–280

Hanski IA, Gilpin ME (1997) Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA

Heck KL, Wetstone GS (1977) Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J Biogeogr 4:135–142

Hellberg ME (2009) Gene flow and isolation among populations of marine animals. Annu Rev Ecol Evol Syst 40: 291–310

Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology 82:1814–1829

Irving AD, Bertness MD (2009) Trait-dependent modification of facilitation on cobble beaches. Ecology 90: 3042–3050

Johannesson K (1988) The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. Littorea*)? Mar Biol 99:507–513

Koivisto ME, Westerbom M (2010) Habitat structure and complexity as determinants of biodiversity in blue mussel beds on sublittoral rocky shores. Mar Biol 157: 1463–1474

Koivisto M, Westerbom M, Riihimäki A (2011) Succession-driven facilitation of macrofaunal communities in sublittoral blue mussel habitats. Mar Biol 158:945–954

Kraufvelin P, Salovius S (2004) Animal biodiversity in Baltic rocky shore macroalgae: can *Cladophora glomerata* compensate for lost *Fucus vesiculosus?* Estuar Coast Shelf Sci 61:369–378

MacArthur RH, Wilson E (1967) The equilibrium theory of island biogeography. Princeton University Press, Princeton, NJ

Mazerolle MJ, Villard M (1999) Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6:117–124

Moilanen A, Hanski I (2001) On the use of connectivity measures in spatial ecology. Oikos 95:147–151

Mora C, Andrefouet S, Costello M, Kranenburg C and others (2006) Ecology. Coral reefs and the global network of marine protected areas. Science 312:1750–1751

Norling P, Kautsky N (2008) Patches of the mussel *Mytilus* sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. Aquat Biol 4:89–98

Ojaveer H, Jaanus A, MacKenzie BR, Martin G, and others (2010) Status of biodiversity in the Baltic Sea. PLoS ONE 5:e12467

Palardy JE, Witman JD (2011) Water flow drives biodiversity by mediating rarity in marine benthic communities. Ecol Lett 14:63–68

Pimm SL, Russell GJ, Gittelman L, Brooks TM (1995) The future of biodiversity. Science 269:347–350

Ragnarsson SA, Raffaelli D (1999) Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments. J Exp Mar Biol Ecol 241:31–43

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99

Rothschild BJ, Ault JS, Goulletquer P, Heral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Mar Ecol Prog Ser 111:29–39

Russell BD, Gillanders BM, Connell SD (2005) Proximity and size of neighbouring habitat affects invertebrate diversity. Mar Ecol Prog Ser 296:31–38

Ruuskanen A, Bäck S (1999) Morphological variation of northern Baltic Sea *Fucus vesiculosus* L. Ophelia 50:43–59

Sale PF, Guy JA, Steel WJ (1994) Ecological structure of assemblages of coral reef fishes on isolated patch reefs. Oecologia 98:83–99

Salovius S, Nyqvist M, Bonsdorff E (2005) Life in the fast lane: macrobenthos use temporary drifting algal habitats. J Sea Res 53:169–180

Simberloff DS, Wilson EO (1969) Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278–296

Smith F, Witman JD (1999) Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. Ecology 80:51–69

Smith JR, Fong P, Ambrose RF (2006) Dramatic declines in mussel bed community: Response to climate change? Ecology 87:1153–1161

Tilman D (1997) Community invisibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92

Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. Environ Manag 90:7–19

Törnroos AM, Bonsdorff E (2012) Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. Ecol Appl 22:2221–2236

Tsuchiya M, Nishihira M (1985) Islands of *Mytilus* as habitat for small intertidal animals: effect of island size on community structure. Mar Ecol Prog Ser 25:71–81

Tsuchiya M, Nishihira M (1986) Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. Mar Ecol Prog Ser 31:171–178

Valanko S, Norkko A, Norkko J (2010) Strategies of post-larval dispersal in non-tidal soft-sediment communities. J Exp Mar Biol Ecol 384:51–60

Virnstein RW, Curran MC (1986) Colonization of artificial seagrass versus time and distance from source. Mar Ecol Prog Ser 29:279–288

Westerbom M, Jattu S (2006) Effects of wave exposure on the sublittoral distribution of blue mussels *Mytilus edulis* in a heterogeneous archipelago. Mar Ecol Prog Ser 306:191–200

Westerbom M, Kilpi M, Mustonen O (2002) Blue mussels, *Mytilus edulis*, at the edge of the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea. Mar Biol 140:991–999

Wiens JA (2002) Riverine landscapes: taking landscape ecology into the water. Freshw Biol 47:501–515

Wikström SA, Kautsky L (2007) Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuar Coast Shelf Sci 72:168–176