ECOLOGY

Disturbance-related patterns in unstable rocky benthic habitats of the north-eastern Baltic coast

Kiran Liversage[a] and Jonne Kotta[b*]

[a] Natural Resources South East, Department of Environment, Water and Natural Resources, GPO Box 1046, Mount Gambier, S.A. 5290, Australia
[b] Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia

Abstract. Distinct patterns of benthic flora and fauna are produced when unstable rocky substrata are disturbed by water motion. This study investigated occurrence of disturbance-related patterns in benthic boulder habitats on the north-eastern Baltic coast. Sessile assemblages, mostly algae on tops of boulders and barnacles and bryozoans underneath, were found to differ between small (50–150 cm^2 upperside surface area) and large (200–800 cm^2) boulders. Densities of motile gammaridean amphipods were negatively correlated with boulder size. These patterns may be due to small boulders being displaced by water motion more frequently than large ones. Most of the barnacle shells/tests were remnant empty ones, and the proportion of empty tests and living barnacles was similar underneath small and large boulders, suggesting that degradation/removal of empty tests was not influenced by disturbance associated with boulder size. There was no consistent evidence of algae being affected by boulder size, but the tops of boulders had less algae than the edges, a pattern that is typically associated with high rates of overturning. Confirmation of disturbance as having caused these patterns and thus being an important process for structuring benthic biota in this region could be achieved by further manipulative experimentation.

Key words: boulder reefs, Baltic Sea, *Balanus improvisus*, *Gammarus* spp., filamentous algae, physical disturbance, overturning of boulders.

INTRODUCTION

The generality of ecological processes can be inferred by testing the spatio-temporal extent of patterns known to be caused by those processes (Underwood and Petraitis, 1993; Underwood et al., 2000). Previous uses of this approach have in some cases reduced (e.g. Foster, 1990) and in others increased (e.g. Kelaher et al., 2004) the acknowledged regional-scale generality of processes such as grazing, predation, and competition in marine systems. It is ideal to make observations of patterns as a precursor to more in-depth manipulative examinations (Underwood et al., 2000), especially when comparing dynamics over particularly large scales (e.g.

inter-regional; Coleman et al., 2006) and during initial investigations of previously unstudied systems.

The coast of the Baltic Sea has large areas with unstable cobble/boulder benthos (Malm and Isæus, 2005; Diesing and Schwarzer, 2006). Processes such as grazing and anthropogenic disturbance from nutrient addition are known to be important for the algae on tops of boulders (Hillebrand and Kahlert, 2001; Kotta et al., 2004; Kraufvelin et al., 2006; Korpinen and Jormalainen, 2008). In soft sediment habitats of the Baltic Sea, physical disturbance from sand movement is known to be important (Herkül et al., 2006; Torn et al., 2010). In a laboratory experiment in Sweden, simulated physical disturbances of boulder habitats affected algal and invertebrate assemblages taken from the Kattegat coast (Svensson et al., 2010). This evidence suggests that for unstable rocky habitats in the region, physical dis-

turbance (i.e. movement or overturning of boulders) may be important, as has been demonstrated extensively during field experiments in other regions (Sousa, 1979; McGuinness, 1987b; Smith and Otway, 1997; Maggi et al., 2012). These studies identified various ecological patterns that, in those systems, were experimentally confirmed as being caused by disturbance. For example, McGuinness (1987a) found that boulders of different sizes were overturned by water motion at different frequencies. Such disturbance affects species abundances underneath boulders (McGuinness, 1987b). Overturning of boulders can alter the relative abundances of occupied and empty structures and may serve as a driver of patterns in community structure (Addessi, 1994; Liversage, 2012). Liversage (2012) found that, in the absence of disturbance under boulders, persistent empty calcareous structures made by species such as tube worms and barnacles build up there over time. Addessi (1994) found that regular disturbance of a boulder habitat affects particularly algae, by causing what she described as the "monk's head" pattern: "bald rocks fringed with a crown of biota… these rocks have been overturned so often that very little macrobiota live either on the top or bottom surface of the rock. Only a fringe of biota remains on these rocks". If patterns such as these are observed in other regions, it would suggest actions of physical disturbance processes.

This study aimed to observe if the above-mentioned patterns were occurring for mobile and sessile species underneath and on top of boulders on rocky shores in Estonia. The first hypothesis was that assemblages and abundances of common species would differ between larger and smaller boulders. The second hypothesis concerned persistent calcareous structures produced by sessile invertebrates. A widespread and conspicuous species in the north-eastern Baltic Sea that produces such structures is *Balanus* (*Amphibalanus*) *improvisus* (Durr and Wahl, 2004; Kotta et al., 2006). It can be expected that similar dynamics occur for *B. improvisus* tests as for those of other barnacle species (Reimer, 1976; Silva et al., 2014), and the remnant empty tests of *B. improvisus* can be left on the substratum after death, especially in sheltered habitats such as underneath boulders (Liversage, 2012). When disturbance causes calcareous structures to become exposed, the empty structures are more prone to degradation than occupied ones (Kaehler and McQuaid, 1999). So if smaller boulders are displaced more than larger ones, we would predict that the relative cover of occupied and empty tests will differ on smaller vs larger boulders. Finally, we investigated the generality of the pattern described by Addessi (1994) by testing the hypothesis that the cover of algae would be greater at edges of boulders compared to the cover on boulder tops.

METHODS

Fieldwork was done during May 2014 at rocky shores north of Paldiski and at the Paljassaare Bay conservation area, with three random sites sampled in each of the two areas (Fig. 1). Within the shallow sublittoral zone (approximately 50 cm water depth) at each site, boulders were haphazardly selected (Chapman, 2002) until five boulders were sampled in each of two size categories: small (50–150 cm^2 upperside surface area) and large (200–800 cm^2). These size categories were chosen before data were collected and were based on categories for which differences were found in previous similar research (Grzelak and Kuklinski, 2010). All sampled boulders were separated by at least 1 m, and at each site they were interspersed within a length along the shore of approximately 20 m. Numbers of mobile species were recorded at the time of sampling when boulders were lifted from the water. Only individuals using the boulder as the primary substratum (i.e. rock surface) were counted, so these results do not relate to species using algal biogenic habitats. Counts of amphipods and isopods were attempted before they dropped off the lifted boulders, but some would have been missed, so abundances presented here can be considered as slight underestimates. Densities of mobile species were calculated by dividing counts per boulder by boulder area.
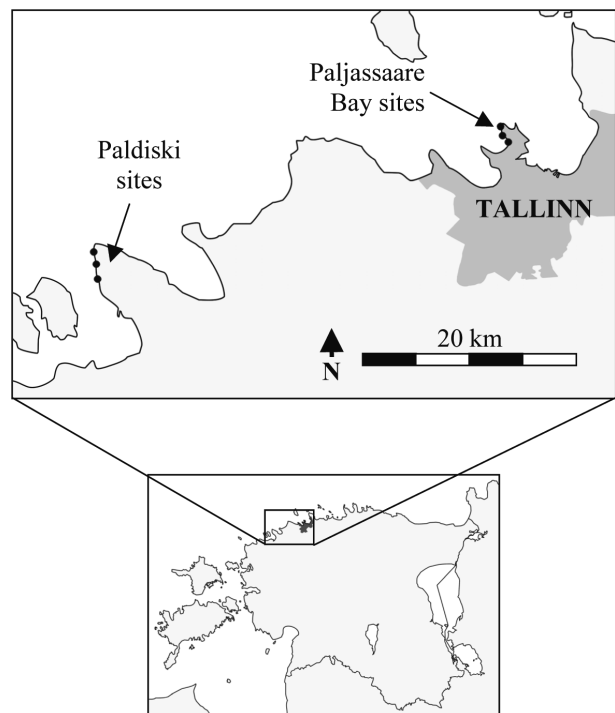

Fig. 1. Map showing the three sites sampled at each of the two locations: Paldiski (lat 59°28′39.9″N, long 24°41′16.3″E) and Paljassaare Bay (lat 59°22′0.8″N, long 24°2′16.8″E).

Each boulder was photographed with a scale bar on the upper- and underside so that the two-dimensional boulder area and percentage cover of sessile species could be later calculated using the program SketchUp. The only types of algae found were the ephemeral filamentous *Cladophora glomerata* with slight additions of *Ulva intestinalis*. Because our hypothesis concerned habitat use by populations of living organisms, we were careful to not include counts of remnant dead structures, especially empty barnacle tests. Although the chambers of some colonies of the bryozoan *Electra crustulenta* were clearly occupied, it was not possible using the photographs to determine whether all colonies had occupied or empty chambers, so this species was not included in the multivariate analysis. A separate univariate analysis was done examining patterns of both dead and living colonies of this species.

The null hypothesis of no difference between assemblages on 50–150 cm^2 vs 200–800 cm^2 boulders was tested with PERMANOVA in PRIMER v6 (Plymouth Marine Laboratory, UK) using Bray–Curtis resemblances and 9999 permutations. The factors were Boulder size (fixed, two levels), Location (random, two levels), and Site (three levels, nested in Location; random). The species that contributed most toward measures of dissimilarity between levels of the fixed factor were identified with Similarity Percentages (SIMPER). All sessile species data were 4th root transformed to harmonize the relative contributions of common and rare taxa and to alleviate problems associated with outlier values present in the untransformed data (Kenkel, 2006). When significant differences were detected between levels of variables, the patterns were assessed graphically using Principle Coordinates Plots (PCO) calculated with PRIMER v6. Patterns of the most abundant non-algal taxa, *Gammarus* spp. and *E. crustulenta*, were investigated individually using univariate PERMANOVA with the same factors as above, except that boulder size was included as a continuous covariable rather than a categorical variable. These resemblances were calculated with the Euclidean distance measure and Type III sums of squares (Anderson et al., 2008). In cases where the covariate was associated significantly with the response variable, the relationship was assessed graphically on scatter plots with linear regression used to plot a trend line. In all analyses, if the *p* values of interaction terms that included a random factor were >0.25, they were eliminated from the analysis to provide a more powerful test for the relevant null hypotheses (Underwood, 1997).

Barnacle tests were observed attached to the substratum in three states: (1) occupied test with intact operculum, (2) empty test with intact side and base plates but operculum missing, (3) base plate with side plates missing. A separate analysis was done for percentage cover of barnacle tests, including the factors

Barnacle test type (occupied, empty, base plate), Boulder size (50–150 cm^2, 200–800 cm^2) and Location. Boulder size was included as a categorical rather than a continuous variable to allow an analysis that can include formal pair-wise (SNK) tests that include the Boulder size variable. To ensure the data were independent, each boulder was randomly assigned to have only one of the three barnacle test types sampled on it. To obtain a sample size of five, data from the three sites were pooled at each location and thus within-location patterns were not assessed. Using ANOVA on GMAV v5 (The University of Sydney), we tested the hypothesis that the relative cover of occupied and empty tests differs on 50–150 cm^2 vs 200–800 cm^2 boulders. This would be interpreted from the analysis as a Barnacle test type × Boulder size interaction. Differences among levels of significant terms were examined using SNK tests.

On the uppersides of boulders, cover of algae was compared between the area around the edge and the area near the top. Edge area was defined as the area on the photographs within 0–33% of the distance from the circumference to the centre point (centroid) of the upperside; the upperside area was the area within 66–100% of that distance. The centroid was estimated visually (Liversage et al., 2012). Percentage covers were measured on scaled photographs imported into SketchUp. Boulder size was included as a continuous covariate, with the factors Position on boulder, Location, and Site, in a univariate PERMANOVA testing the hypothesis that cover is greater at boulder edges.

RESULTS

Sessile assemblages differed between boulders in the small and the large size category (Table 1), and the difference was clearly visualized from the distance of the centroids in the PCO plot (Fig. 2a). This was mostly caused by a greater cover of the filamentous alga *C. glomerata* and a lesser cover of *B. improvisus* on smaller boulders (Table 2). Mobile assemblages were similar between categories at Paljassaare Bay but differed at Paldiski (Table 1; Fig. 2b), which was mostly the result of differences in abundances of gammaridean amphipods (Table 2). Univariate analysis of gammarids indicated a significant correlation between density and boulder surface area (Table 3) with the trend line from linear regression indicating the relationship was negative (Fig. 3). No correlation was found for the other taxon sufficiently abundant to be analysed, *E. crustulenta* (Table 3).

Tests of *B. improvisus* were generally only found on undersides of boulders. Across all boulders, tests on average covered 2.37% of the underside surface area, which equates to 17.23 individuals dm^{-2}. Of the test types empty ones were significantly more prevalent than

Table 1. PERMANOVA of mobile and sessile species assemblages on boulders in the small (50–150 cm^2) and large (200–800 cm^2) size categories from three random sites in each of the sampled two locations in northern Estonia; $n = 5$. Boldface designates significant differences

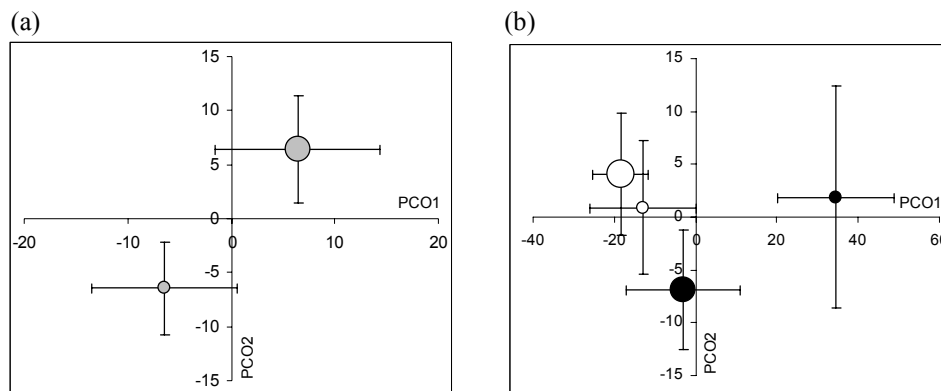| Source	Mobile species assemblages (density)				Sessile species assemblages (% cover)			
	df	MS	*F*	*p*	df	MS	*F*	*p*
Location	1	15 207	14.65	**<0.01**	1	2 710	2.74	>0.1
Boulder size category	1	7 235	1.61	>0.25	1	1 742	4.30	**<0.05**
Site(Location)	4	1 038	1.16	>0.25	4	975	1.71	>0.05
Location × Boulder size category	1	4 495	5.02	**<0.05**	1	391	–	
Boulder size category × Site(Location)	4	706	–		4	232	–	
Residual	52	895			53	423		

– eliminated term.

Fig. 2. Constrained principal coordinates plots of (a) sessile species assemblages pooled from both locations and (b) mobile assemblages at Paldiski (black points) and Paljassaare Bay (white). Points of different sizes represent the centroids ($\pm 95\%$ confidence interval) of assemblages on 50–150 cm^2 (small circles) and 200–800 cm^2 (large circles) boulders; $n = 5$.

Table 2. Contributions of species to measures of dissimilarity for mobile and sessile assemblages underneath boulders in the small (50–150 cm^2) and large (200–800 cm^2) size categories. Percentage cover data were fourth-root transformed for the analysis, but displayed mean abundances are untransformed

Assemblage	Species	Small boulders	Large boulders	Dissimilarity: standard deviation ratio	Per cent contribution to dissimilarity
Mobile (density dm^2)	*Gammarus* spp.	4.64	1.13	1.85	78.65
	Theodoxus fluviatilis	0	0.07	0.4	14.87
	Idotea balthica	0.18	0.01	0.37	6.48
Sessile (% cover)	*Cladophora glomerata*	15.74	12.64	1.09	75.96
	Balanus improvisus	0.01	0.07	0.67	20.60
	Mytilus trossulus	0.013	0.012	0.19	3.43

Table 3. PERMANOVA using Euclidean distances (Anderson et al., 2008) to compare densities of gammarid amphipods and percentage covers of the bryozoan *Electra crustulenta* between boulders from three random sites in each of the sampled two locations, with boulder size as covariate; $n = 5$. Boldface designates significant differences

| Source	*Gammarus* spp. density				*Electra crustulenta* cover			
	df	MS	*F*	*p*	df	MS	*F*	*p*
Boulder size covariate	1	258.08	8.01	**<0.05**	1	14.56	1.73	>0.1
Location	1	352.77	11.88	**<0.01**	1	50.46	4.95	>0.05
Site(Location) Site(Location)	4	25.44	0.79	>0.5	4	13.20	1.57	>0.1
Boulder size covariate × Location	1	113.3	3.52	>0.05	1	25.75	3.05	>0.05
Boulder size covariate × Site(Location)	4	8.248	–		4	6.86	–	
Residual	52	32.22			52	8.43		

– eliminated term.
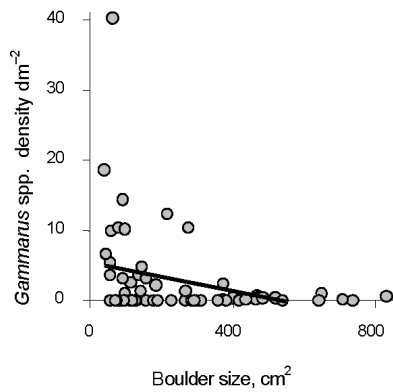
Fig. 3. Correlation between abundance and boulder size for gammarid amphipods. Linear regression was used to visually represent the result from the permutational ANCOVA. Data were pooled from three random sites in each of the two locations; $n = 5$.

occupied tests and remnant base plates (Table 4, Fig. 4a). Although there were more barnacle tests on larger boulders (Fig. 4b), there was no Test type $\times$ Boulder size interaction, which would indicate a difference in relative abundances of the three test types according to boulder size (Table 4).

The univariate analysis of algal cover provided no evidence of variation related to the boulder size covariate (Table 5). Although there was much variability in algal cover on both edges and tops of boulders, on average twice as much algae occurred at edges ($p < 0.05$; Fig. 5, Table 5).

Table 4. ANOVA comparing percentage cover of barnacle tests of three types (occupied test, empty test with side plates remaining, empty test with only base plate remaining) on boulders in two size categories (50–150 cm^2 and 200–800 cm^2) and from two random locations. Cochran's test $C = 0.27$, $p > 0.05$; $n = 5$

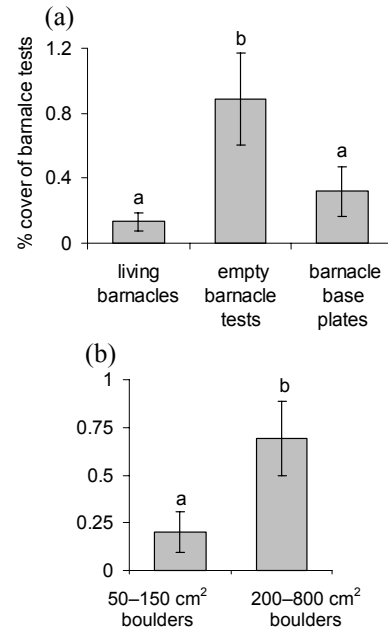| Source	df	MS	F	p
Type of barnacle test	2	0.72	5.53	<**0.01**
Boulder size	1	1.14	8.70	<**0.01**
Location	1	0.38	2.87	>0.05
Type of barnacle test $\times$ Boulder size	2	0.17	1.29	>0.25
Type of barnacle test $\times$ Location	2	0.01	–	
Boulder size $\times$ Location	1	0.18	–	
Type of barnacle test $\times$ Boulder size $\times$ Location	2	0.01	–	
Residual	48	0.13		

– eliminated term.

Fig. 4. Mean ($\pm$SE) cover of *Balanus improvisus* tests that are (a) of different types (occupied, empty with side plates remaining, or empty with only the base plate remaining), and (b) on different sized boulders, from three random sites in each of the two locations. Letters above bars represent treatments found to differ significantly in abundance using SNK tests; $n = 5$.

Table 5. PERMANOVA using Euclidean distances (Anderson et al., 2008) to compare percentage cover of *Cladophora glomerata* between boulders from three random sites in each of the two locations sampled at the position of either their edges or their tops and with boulder size as the covariate; $n = 5$

| Source	df	MS	F	p
Boulder size covariate	1	0.089	0.068	>0.75
Location	1	1.887	1.444	>0.1
Position on boulder	1	5.215	3.991	<**0.05**
Site(Location) Site(Location)	4	1.146	–	
Boulder size covariate $\times$ Location	1	0.283	–	
Boulder size covariate $\times$ Position on boulder	1	0.003	0.002	>0.75
Location $\times$ Position on boulder	1	0.033	–	
Boulder size covariate $\times$ Site (Location)	4	0.463	–	
Site(Location) $\times$ Position on boulder	4	0.383	–	
Boulder size covariate $\times$ Location $\times$ Position on boulder	1	0.000	–	
Boulder size covariate $\times$ Site (Location) $\times$ Position on boulder	4	0.196	–	
Residual	36	1.671		

– eliminated term.
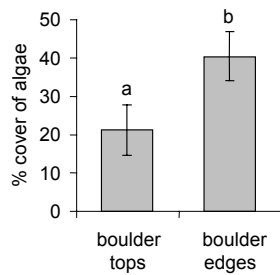
Fig. 5. Mean (±SE) cover of *Cladophora glomerata* on boulders at the edge position (area within 0–33% of the distance from the circumference to the centre point of the upperside) and the position at the top (area within 66–100% of that distance) from three random sites in each of the two locations. Letters above bars represent treatments found to differ significantly in abundance using SNK tests; $n = 5$.

DISCUSSION

In many regions, coastal boulder habitats harbour a particularly great diversity of species including many habitat specialists (Le Hir and Hily, 2005; Chapman, 2011; Liversage and Benkendorff, 2013). From the results of this study and those of Grzelak and Kuklinski (2010) and Wallin et al. (2011), it appears that there are no boulder habitat specialists in the species depauperate regions of the Baltic Sea (i.e. the regions occurring further east of the entrance and in south-west). The boulders sampled harboured many gammaridean amphipods, but this taxon does not require a hard substratum (Lauringson and Kotta, 2006) and would likely be present regardless of the availability of boulder habitats. Important populations of *E. crustulenta* may be using under-boulder habitats, but further observations differentiating living and remnant dead colonies are required before this can be confirmed. Many tests of *B. improvisus* also occurred underneath boulders, but it is not clear whether the presence of empty tests reflects the usefulness of the habitat for the species. For example, the barnacle may have previously used the habitat extensively with a large population size there and a large mortality event may have caused the tests to subsequently become empty. Alternatively, the barnacle may have never used the habitat extensively and only ever recruited there at low rates, but the sheltered under-boulder conditions inhibited the removal of empty tests, causing them to build up over time (Liversage, 2012). Thus further information over larger temporal scales about *B. improvisus* recruitment processes in this habitat is required to answer the question of how extensively the barnacle uses under-boulder habitats.

It would be ideal to consult previous similar studies to help determine the generality of the patterns we found. The hypotheses investigated in previous similar studies that included *B. improvisus* (Grzelak and

Kuklinski, 2010; Wallin et al., 2011) concerned habitat suitability, with distributions of living animals being of interest. These studies reported large densities of *B. improvisus* tests, which were comparable to the total densities of empty + occupied tests we found, but they did not mention the presence of any empty tests. It is not clear if empty tests were not found, or if they were found but not counted, or if counts of living animals may have been confounded by their dead tests. For small sessile species that produce calcareous structures such as *B. improvisus*, it is important that future studies take into account both occupied and empty structures to prevent ambiguity. This is especially true for habitats where empty structures are known to build up, even when living individuals of the species never occurred there in large numbers (Liversage, 2012).

It can be expected that the relationship is positive between rates of disturbance and rates of degradation of empty tests, and that the removal rate of empty tests would be more than for tests with living barnacles (Kaehler and McQuaid, 1999; Liversage, 2012). There-fore, if disturbance varies between small and large boulders, so will the relative abundance of empty and occupied tests. Our results did not support this hypo-thesis, suggesting that any disturbances that may vary between boulder sizes are not important for degradation of remnant *B. improvisus* tests.

The null hypothesis that sessile assemblages are similar on small and large boulders was rejected. The null hypothesis was similarly rejected for the mobile taxon, *Gammarus* spp. However, for whole mobile species assemblages, the inconsistencies in patterns between random locations meant that this null hypothesis was not rejected. It was interesting that this case of random spatial variation of a pattern was the only example we found. The tests of random spatial variation are important to provide information about the spatial generality of patterns (Beck, 1997), and thus inform future studies about the important spatial scales over which to focus the replication of sampling. We found no cases where significant random spatial variation occurred at the scale of sites separated by hundreds of metres, so future studies of patterns of boulder habitats in this region should focus on replicating sampling especially over multi-kilometre spatial scales rather than smaller ones.

When individual species were considered, *B. impro-visus* in particular was associated with the habitat un-derneath large boulders. These observations are con-sistent with the model of Sousa (1979) and McGuinness (1987b) that increased disturbance associated with small boulders alters assemblage structure and reduces abundance of sessile species. The negative relationship we found between *Gammarus* spp. and boulder size has been described previously (Grzelak and Kuklinski, 2010), suggesting that this is a widely general pattern. It may indicate that the taxon is positively influenced by

boulder disturbance, or alternatively, other variables associated with boulder size may influence these species. Such variables may include height above the water/ice surface (McGuinness and Underwood, 1986), the amount of edge habitat (which is favourable to some species; Le Hir and Hily, 2005; Liversage et al., 2012), or effects from other species that are themselves influenced by boulder size. Further research is required to (1) observe directly the frequency of physical disturbance and (2) determine if there is a causal link between disturbance and assemblage patterns.

Boulder size did not appear to affect algae, which may be due to the rapid recruitment rate of these opportunistic filamentous species (Kiirikki and Lehvo, 1997; Kraufvelin et al., 2006) causing them to recover quickly following any disturbance associated with boulder size (McGuinness, 1987a; Bucas et al., 2007). There was, however, evidence of the "monk's head" pattern occurring, typically associated with instability of small boulders (Addessi, 1994). Alternatively, there may have been other potential causes of this pattern such as disturbance from floating ice (Barnes, 1999) or emergence of the top of rocks when the water level was low (McGuinness and Underwood, 1986).

Overall, these observations have raised many questions about processes that may be occurring in Baltic coastal boulder habitats. While patterns suggestive of physical disturbance of boulders were not overabundant, some patterns found indicated that further in-depth investigation of disturbance processes is warranted in Estonian coastal boulder habitats. This is especially true considering the vast extent of this habitat in the country, and the potential for physical disturbance processes to be playing an important role across that extent.

REFERENCES

Addessi, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. *Ecol. Appl.*, **4**, 786–797.

Anderson, M. J., Gorley, R. N., and Clarke, K. R. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth.

Barnes, D. K. A. 1999. The influence of ice on polar nearshore benthos. *J. Mar. Biol. Assoc. UK*, **79**, 401–407.

Beck, M. W. 1997. Inference and generality in ecology: current problems and an experimental solution. *Oikos*, **78**, 265–273.

Bucas, M., Daunys, D., and Olenin, S. 2007. Overgrowth patterns of the red algae *Furcellaria lumbricalis* at an exposed Baltic Sea coast: the results of a remote underwater video data analysis. *Estuar. Coast. Shelf S.*, **75**, 308–316.

Chapman, M. G. 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral. Ecol.*, **27**, 211–228.

Chapman, M. G. 2011. Restoring intertidal boulder-fields as habitat for "specialist" and "generalist" animals. *Restor. Ecol.*, **19**, 1–9.

Coleman, R. A., Underwood, A. J., Benedetti-Cecchi, L., Aberg, P., Arenas, F., Arrontes, J., Castro, J., Hartnoll, R. G., Jenkins, S. R., Paula, J., Della Santina, P., and Hawkins, S. J. 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia*, **147**, 556–564.

Diesing, M. and Schwarzer, K. 2006. Identification of submarine hard-bottom substrates in the German North Sea and Baltic Sea EEZ with high-resolution acoustic seafloor imaging. In *Progress in Marine Conservation in Europe: NATURA 2000 Sites in German Offshore Waters* (Nordheim, H., ed.), pp. 111–125. Springer-Verlag, Berlin.

Durr, S. and Wahl, M. 2004. Isolated and combined impacts of blue mussels (*Mytilus edulis*) and barnacles (*Balanus improvisus*) on structure and diversity of a fouling community. *J. Exp. Mar. Biol. Ecol.*, **306**, 181–195.

Foster, M. S. 1990. Organization of macroalgal assemblages in the Northeastern Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia*, **192**, 21–33.

Grzelak, K. and Kuklinski, P. 2010. Benthic assemblages associated with rocks in a brackish environment of the southern Baltic Sea. *J. Mar. Biol. Assoc. UK*, **90**, 115–124.

Herkül, K., Kotta, J., Kotta, I., and Orav-Kotta, H. 2006. Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonization and sedimentation processes. *Oceanologia*, **48**(S), 267–282.

Hillebrand, H. and Kahlert, M. 2001. Effects of grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. *Limnol. Oceanogr.*, **46**, 1881–1898.

Kaehler, S. and McQuaid, C. D. 1999. Lethal and sub-lethal effects of phototrophic endoliths attacking the shell of the intertidal mussel *Perna perna*. *Mar. Biol.*, **135**, 497–503.

Kelaher, B. P., Castilla, J., and Seed, R. 2004. Intercontinental test of generality for spatial patterns among diverse molluscan assemblages in coralline algal turf. *Mar. Ecol. Prog. Ser.*, **271**, 221–231.

Kenkel, N. C. 2006. On selecting the appropriate multivariate analysis. *Can. J. Plant Sci.*, **86**, 663–676.

Kiirikki, M. and Lehvo, A. 1997. Life strategies of filamentous algae in the northern Baltic Proper. *Sarsia*, **82**, 259–267.

Korpinen, S. and Jormalainen, V. 2008. Grazing and nutrients reduce recruitment success of *Fucus vesiculosus* L. (Fucales: Phaeophyceae). *Estuar. Coast. Shelf S.*, **78**, 437–444.

Kotta, J., Torn, K., Martin, G., Orav-Kotta, H., and Paalme, T. 2004. Seasonal variation in invertebrate grazing on *Chara connivens* and *C. tomentosa* in Kõiguste Bay, NE Baltic Sea. *Helgoland Mar. Res.*, **58**, 71–76.

Kotta, J., Kotta, I., Simm, M., Lankov, A., Lauringson, V., Põllumäe, A., and Ojaveer, H. 2006. Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. *Helgoland Mar. Res.*, **60**, 106–112.

Kraufvelin, P., Salovius, S., Christie, H., Moy, F. E., Karez, R., and Pedersen, M. F. 2006. Eutrophication-induced changes in benthic algae affect the behaviour and fitness of the marine amphipod *Gammarus locusta. Aquat. Bot.*, **84**, 199–209.

Lauringson, V. and Kotta, J. 2006. Influence of the thin drift algal mats on the distribution of macrozoobenthos in Kõiguste Bay, NE Baltic Sea. *Hydrobiologia*, **554**, 97–105.

Le Hir, M. and Hily, C. 2005. Macrofaunal diversity and habitat structure in intertidal boulder fields. *Biodivers. Conserv.*, **14**, 233–250.

Liversage, K. 2012. Ecology of Cryptic Habitats under Intertidal Boulders. PhD thesis. The University of Sidney.

Liversage, K. and Benkendorff, K. 2013. A preliminary investigation of diversity, abundance, and distributional patterns of chitons in intertidal boulder-fields of differing rock type in South Australia. *Molluscan Research*, **33**, 24–33.

Liversage, K., Cole, V. J., McQuaid, C. D., and Coleman, R. A. 2012. Intercontinental tests of the effects of habitat patch type on the distribution of chitons within and among patches in intertidal boulder field landscapes. *Mar. Biol.*, **159**, 2777–2786.

Maggi, E., Bulleri, F., Bertocci, I., and Benedetti-Cecchi, L. 2012. Competitive ability of macroalgal canopies overwhelms the effects of variable regimes of disturbance. *Mar. Ecol. Prog. Ser.*, **465**, 99–109.

Malm, T. and Isæus, M. 2005. Distribution of macroalgal communities in the central Baltic Sea. *Ann. Bot. Fenn.*, **42**, 257–266.

McGuinness, K. A. 1987a. Disturbance and organisms on boulders I. Patterns in the environment and the community. *Oecologia*, **71**, 409–419.

McGuinness, K. A. 1987b. Disturbance and organisms on boulders II. Causes of patterns in diversity and abundance. *Oecologia*, **71**, 420–430.

McGuinness, K. A. and Underwood, A. J. 1986. Habitat structure and the nature of communities on intertidal boulders. *J. Exp. Mar. Biol. Ecol.*, **104**, 97–123.

Reimer, A. A. 1976. Succession of invertebrates in vacant tests of *Tetraclita stalactifera panamensis. Mar. Biol.*, **35**, 239–251.

Silva, A. C. F., Mendonca, V., Paquete, R., Barreiras, N., and Vinagre, C. 2014. Habitat provision of barnacle tests for overcrowded periwinkles. *Mar. Ecol.* doi: 10.1111/maec.12161.

Smith, K. A. and Otway, N. M. 1997. Spatial and temporal patterns of abundance and the effects of disturbance on under-boulder chitons. *Molluscan Research*, **18**, 43–57.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology*, **60**, 1225–1239.

Svensson, J. R., Lindegarth, M., and Pavia, H. 2010. Physical and biological disturbances interact differently with productivity: effects on floral and faunal richness. *Ecology*, **91**, 3069–3080.

Torn, K., Martin, G., Kotta, J., and Kupp, M. 2010. Effects of different types of mechanical disturbances on a charophyte dominated macrophyte community. *Estuar. Coast. Shelf S.*, **87**, 27–32.

Underwood, A. J. 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance.* Cambridge University Press, Cambridge.

Underwood, A. J. and Petraitis, P. S. 1993. Structure of intertidal assemblages in different locations: how can local processes be compared? In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Ricklefs, R. E. and Schluter, D., eds), pp. 38–51. University of Chicago Press, Chicago.

Underwood, A. J., Chapman, M. G., and Connell, S. D. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *J. Exp. Mar. Biol. Ecol.*, **250**, 97–115.

Wallin, A., Qvarfordt, S., Norling, P., and Kautsky, H. 2011. Benthic communities in relation to wave exposure and spatial positions on sublittoral boulders in the Baltic Sea. *Aquat. Biol.*, **12**, 119–128.

Füüsilistest häiringutest tingitud põhjaelustiku levikumustrid Läänemere kirdeosa liikuvatel kivistel põhjadel

Kiran Liversage ja Jonne Kotta

Lainetusest liikuma pandud kividel peaks tekkima omanäoline kooslus. Välivaatluste käigus uurisime, kas selline protsess on oluline ka Läänemere kirdeosa kiviste põhjade koosluste kujunemisel. Suurte (kivi ülemise külje pindala 200–800 cm^2) ja väikeste kivide (50–150 cm^2) põhjakooslused olid statistiliselt erinevad. Väikestel kividel kasvavate suurvetikate ja tõruvähkide levikumustrid vihjasid kivide sagedasele liikumisele. Nimelt oli väiksemate kivide peal vähem vetikaid kui kivide külgedel. Suured kivid olid aga palju ühtlasemalt elustikuga kaetud. Kivide liikumine ei mõjutanud tõruvähkide kestade lagunemist. Samuti oli elusate tõruvähkide asustustihedus kivide all stabiilne, sõltumata kivi suurusest. Täpsete põhjuse ja tagajärje seoste väljaselgitamiseks ning selliste füüsiliste häiringute intensiivsuse mõõdistamiseks on välivaatlusi vaja toetada manipulatiivsete eksperimentaaluuringutega.