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Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient

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ABSTRACT

Foundation species host diverse associated communities by ameliorating environmental stress. The strength of this facilitative effect can be highly dependent on the underlying biotic and abiotic context. We investigated community level patterns of macrofauna associated with and adjacent to the marine foundation species eelgrass (*Zostera marina*) along a hydrodynamic stress gradient. We could demonstrate that the relative importance of this foundation species for its infaunal community increases with environmental variables associated with increasing hydrodynamic stress (depth, sand ripples formation, sediment grain size and organic content). Faunal assemblages in proximity to the *Zostera* patch edges, however, showed no (infauna) or negative (epifauna) response to hydrodynamic stress. Our study highlights that the facilitative outcome of a foundation species is conditional to the faunal assemblage in question and can be highly variable even between positions within the habitat.

Keywords: ecosystem engineer; *Zostera marina*; conditional facilitation; seagrass; habitat modification; foundation species

1. INTRODUCTION

It is increasingly recognized that facilitation by foundation species, and ecosystem engineers, has a profound influence on surrounding communities in both terrestrial and aquatic ecosystems (Dayton 1972, Jones et al. 1994, Bruno and Bertness 2001, Bruno et al. 2003, Ellison et al. 2005). Biogenic habitats such as salt marshes, seagrasses meadows, bivalve reefs and mangrove forests form vast seascapes and provide multiple important ecosystem services, including hosting diverse associated communities (Beck et al. 2001, Boström et al. 2011). By ameliorating e.g. physical exposure or nutrient availability, they promote the occurrence of other local species. Efforts that aim to resolve underpinning mechanisms of positive interactions continue to increase (Michalet and Pugnaire 2016). As such the Stress Gradient Hypothesis (SGH) predicts that facilitation will become more important in stressful than in benign environments (Bertness and Callaway 1994). A broadened understanding of facilitation provided by ecosystem engineers has great relevance for successful conservation and restoration efforts in biogenic habitats (Cordero et al. 2012, Sharma et al. 2016). Although the concept of facilitation is an inherent part of ecological theory and the supporting mechanisms are widely acknowledged, our knowledge of its conditionality remains fragmentary. This has led to discussions about the generality of the SGH (Maestre et al. 2005, Lortie and Callaway 2006, Maestre et al. 2009, Holmgren and Scheffer 2010, He et al. 2013), implying that the outcome of positive species interactions is highly dependent on environmental context and the interacting species in question (Norkko et al. 2006, Kawai and Tokeshi 2007, Bulleri et al. 2011, Jurgens and Gaylord 2016). Moreover, these discussions emphasize that facilitation theory and the underpinning functional relationships need to be studied across a wide range of abiotic and biotic gradients and ecosystems.

Plant-plant interactions in terrestrial environments have received broad attention (Brooker et al. 2008, Bulleri 2009). In comparison, aquatic environments, and most notably marine subtidal habitats, remain understudied in terms of facilitation (Bulleri 2009). The majority of

studies describing the conditionality of facilitation in subtidal habitats have either addressed intraspecific interactions (Wernberg et al. 2010, Bennett and Wernberg 2014, Bennett et al. 2015) or mutualism between two species (Bulleri et al. 2011, Bennett et al. 2015), but the potential facilitation effect of an engineering species on its broader associated community has been widely ignored. Earlier works by Woodin (1981) and Gallagher et al. (1983), for example, highlight the importance of benthic tube-builders for predator refuge and natural succession. Norkko et al. (2006) and Lohrer et al. (2013), have further revealed how environmental conditions can inhibit facilitation of a subtidal benthic ecosystem engineer and result in a decline in associated community abundance and diversity when biotic or abiotic stress increases. This suggests that our understanding of stress amelioration by an ecosystem engineer and its conditionality are insufficient and further attention is needed.

Seagrasses are important ecosystem engineers that possess a pronounced engineering capacity resulting in a strong influence on multiple abiotic and biotic processes and subsequent ecosystem services (Heck and Orth 1980, Fonseca et al. 1982). Seagrasses are, however, simultaneously subjected to a multitude of anthropogenic stressors (Boström et al. 2011) causing local and global declines (Waycott et al. 2009), potentially compromising their future role in marine coastal ecosystems. In accordance with ecological theory, these habitats should be particularly important in maintaining benthic communities and promoting biodiversity in physically stressful environments. As seagrass meadows significantly modify their environment through e.g. attenuation of waves, reduction of current flow and provision of below- and above-ground complexity (Fonseca et al. 1982, Fonseca and Cahalan 1992, González-Ortiz et al. 2016), they are assumed to extend the realized niche of associated invertebrates towards more unfavourable conditions (Bruno et al. 2003).

Here we present a study novel to subtidal facilitation theory by studying species and community level patterns along a physical stress gradient dominated by the foundation species, eelgrass (*Zostera marina*). Specifically, we predicted that *Zostera* patches located

108 along a depth gradient perpendicular to the shoreline will experience more hydrodynamic
109 stress in terms of wave exposure when depth and distance to the shoreline decrease. By
110 comparing invertebrate community variables between the seagrass patch interior, the patch
111 edges and the adjacent bare sediments along this gradient, we aimed to enhance our
112 understanding regarding the conditional outcome of facilitation by an ecosystem engineer.
113 The study system is conceptualized in Fig. 1 illustrating how faunal community variables
114 potentially change with increasing physical exposure. We hypothesized, that:

- 115 1. With increasing exposure, environmental conditions will negatively affect the local
116 community in unprotected bare sediments (Fig. 1a). Facilitation by *Zostera*,
117 simultaneously, will increase in importance for the local benthic community when
118 environmental stress increases (Fig. 1c).
- 119 2. Facilitation will be less pronounced and more variable at seagrass edges compared to
120 the interior, as the edges represent abrupt transitions between vegetated and bare
121 habitats, highly exposed to variable hydrodynamic conditions (Fig. 1b).
- 122 3. Sediment infauna and leaf epifauna will respond differently to the ecosystem
123 engineering by *Zostera*.

Figure 1: Conceptual model of the experimental setup illustrating how the benthic invertebrate community relative to seagrass patches (a: patch interior, b: patch edge, c: adjacent bare sand) and the edge structure of the seagrass patches (photos) are assumed to change along a gradient of decreasing depth and increasing physical exposure. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Photography supplied courtesy of Christoffer Boström (cbostrom@abo.fi, left) and Pekka Tuuri (pekka.tuuri@kolumbus.fi, mid and right).

2. MATERIAL AND METHODS

2.1. Study design and field sampling

Sampling was conducted in a shallow exposed sandy embayment at the Hanko peninsula, SW Finland (Fig. 2). In this region, *Zostera* meadows extend from the shoreline several hundred

Figure 2. Study site with sampling locations (59°49' N; 23°09' E) at the Hanko peninsula, SW Finland, northern Baltic Sea.

meters seawards (1-6 m depth range, Boström et al. 2014). Although there are some small islands in the vicinity, the area is exposed to the predominant southwesterly winds (Valanko et al. 2010). The seagrass in the embayment was comprised of a mosaic of habitat patches within unvegetated sandy sediments. Six separate *Zostera* patches (hereafter P1 - P6, with P1 being located most distant to and P6 closest to the shore) at an interval of min. 25 m were chosen for sampling. The selection criteria for the patches were: 1) to have a diameter of at

least 10 m, 2) to show a distinct seagrass/sand boundary and 3) to be aligned along a depth gradient perpendicular to the shoreline, which served as a proxy for exposure. For each *Zostera* patch three habitats for sampling were defined, which were all located towards the seaward side of each patch: the patch interior >1 m inside from the seagrass/sand boundary (I), the patch edge 0.3 m inside from the seagrass/sand boundary (E), and the adjacent bare sand habitat (B) 1-3 m outside from the seagrass meadow (Fig. 1).

Samples of biotic and abiotic variables were collected by SCUBA diving within one week from the end of August until the beginning of September 2008. For quantification of sediment parameters, five replicate samples of the top 2 cm of the sediment were obtained from each *Zostera* patch in all three habitats using syringes of 2.1 cm diameter. To quantify *Zostera* plant characteristics, three replicate samples were collected at each patch from the edge and interior of the meadow. Below-ground roots and rhizomes were collected by pushing a core (Ø 13.5 cm) into the sediment and collecting all material into a bag. Above-ground plant material was taken with an Ø 29 cm core. The same samples were used to collect mobile leaf epifauna from the *Zostera* interior and edge at each patch. For quantification of benthic infauna, five replicate samples from each habitat (interior, edge, bare sand) at each patch were taken by pushing a core (Ø 5.6 cm) 10 cm into the sediment.

For further quantification of potential wave energy, ten randomly chosen sand ripples were measured in length and height in the bare sand habitat of each patch. The ripple index, i.e. the resulting quotient of length and height relates to the orbital diameter of surface waves at seafloor level (³⁴Clifton and Dingler 1984).

2.2.Laboratory analysis

The grain size distribution of the sediment samples was analyzed by dry sieving methods. The finest fraction (< 1 mm) was further analyzed with a Malvern laser diffraction instrument. Grain sizes were classified into size class fractions according to the Wentworth scale

(Wentworth 1922). Organic content of the sediment was measured as loss on ignition (LOI) in 6 h at 440°C, after drying the samples at 60°C for 48 h.

Root and rhizome samples were rinsed and *Zostera* below-ground and above-ground biomass was determined by weighing after drying to constant weight at 60 °C. Shoots in each sample were counted and average shoot length was calculated based on 10 randomly chosen shoots. Samples of in- and epifauna were sieved over a 0.5 mm sieve, preserved in 70 % ethanol and stained with rose bengal. Macrofauna was subsequently counted and identified to the lowest practical taxonomic level.

2.3. Statistical analyses

Local biotic and abiotic conditions per patch and habitat were assessed by means of plant variables (i.e., shoot density, above-ground biomass, below-ground biomass, shoot length), contribution of grain size classes and sediment LOI. Differences were analyzed using a two-way analysis of variance (ANOVA), with Habitat and Patch as fixed factors. When Habitat × Patch interactions were found, pairwise differences were assessed using Tukey's HSD *post-hoc* multiple comparisons test. To contrast potential differences in facilitative effects between the habitats, mean infaunal and epifaunal abundance and diversity (taxa richness) were subsequently analyzed using Students t-test (contrasting patch edge and patch interior epifauna) and one-way ANOVA (contrasting bare sand, patch edge and patch interior infauna). To meet assumptions for parametric testing, homoscedasticity was tested with the Brown-Forsythe Test and normality of residuals using a Shapiro-Wilk Test. Additionally, histograms, Q-Q plots and variance plots were visually assessed to support assumptions for the use of parametric tests. When necessary, data was appropriately transformed using a square root or natural log+0.5 transformation (see Appendix Table A1). In the case the assumptions for parametric testing were not met, non-parametric equivalent tests (Mann-Whitney *U* test, Kruskal-Wallis Test) were used, followed by Dunn's Test as a corresponding

196 *post-hoc* multiple comparison. All univariate analyses were done using R (R Development
197 Core Team, 2017).

198 The hydrodynamic regime can have strong effects on local sediment properties. Particles
199 of 0.18 mm diameter are expected to be transported first by currents and waves, and thus the
200 proportion of fine sand (0.125-0.2mm, see Wentworth 1922) can give some indication of
201 underlying hydrodynamics (Gray and Elliott 2009). With increasing exposure, sediment
202 organic content typically decreases (Elliott et al. 1998, Samper-Villarreal et al. 2016), while
203 median particle diameter (d_{50}) typically increases (Elliott et al. 1998).

204 To characterize prevailing physical exposure due to wave and current forces along the six
205 habitat patches, we conducted a principal component analysis (PCA) that, additionally to
206 water depth and sand ripple index, took into account d_{50} , LOI and % fine sand outside of the
207 habitat patches. The PCA was performed on a correlation matrix of untransformed data to
208 account for scale differences between parameters. Resulting PC1 scores were used as an
209 adjusted exposure proxy for each habitat patch. This approach has the advantage of returning
210 relative multivariate distances. Thus an integrated relative exposure metric, i.e. an
211 environmental gradient, can be determined across the habitat patches (Ter Braak and Prentice
212 1988). This allows for regression-based techniques, combining potentially co-correlated
213 parameters on hydrodynamics into a latent variable in further analyses (see below).

214 We applied linear regression analysis to assess the functional relationship between the
215 resulting exposure proxy (as described by PC 1) and plant variables at the *Zostera* interior and
216 edge as well as between exposure and the associated fauna in the *Zostera* interior, the edge
217 and the bare sand separately. The ratio between interior and bare sand infauna abundance was
218 then used to assess a potential relative community effect of facilitation along this
219 environmental stress gradient. In order to explore the mechanisms responsible for facilitation,
220 linear regression of fauna with plant and sediment parameters was investigated. Furthermore,
221 dissimilarity percentages (SIMPER) were calculated between each location and patch using

Bray-Curtis measure of similarity on square root transformed abundance data to assess changes in species composition and detect main beneficiaries, i.e. species that benefit from *Zostera* along the gradient (PRIMER 6, Clarke and Gorley 2006).

3. RESULTS

3.1. Environmental characteristics

Analysis of grain size distribution and organic content revealed significant differences among habitats and patches as well as Habitat $\times$ Patch interactions (Appendix Table A1). Grain sizes below 0.5mm increased, while those larger than 0.5mm decreased in proportion towards the patch interior (Fig. 3). Organic content increased towards the patch interior. In all three habitats (patch interior, patch edge, bare sand) the lowest proportion of fines and highest proportion of very coarse sand was found at patch P4.

Figure 3. Average grain size distribution at the *Zostera* interior, *Zostera* edge and adjacent bare sediments examined across the whole exposure gradient (n=30 for each habitat).

The highest proportion of fine and lowest proportion of very coarse sand were observed at the innermost shallowest patch P6 and at the outermost deepest patch P1.

Similarly, median grain size (d_{50} , mm) in all three habitats was highest at P4 and lowest at P1.

Organic content (% LOI) peaked at P1, while lowest proportions of organics were found at P5. Mean values for sediment properties can be found in the Appendix (Table A1).

3.2. Seagrass characteristics

Neither shoot density nor above-ground biomass (AB) showed significant differences between edge and interior and among patches, though a Habitat $\times$ Patch interaction could be detected (Appendix Table A1, Habitat $\times$ Patch interaction; shoot density: $p = 0.049$ and AB: $p = 0.035$). Tukey multiple comparison between means, however, could not reveal pairwise significant differences. Below-ground biomass (BB) was significantly higher in the *Zostera* interior (Appendix Table A1; $p < 0.001$) but showed neither differences among the six patches nor a Habitat $\times$ Patch interaction. Shoot length differed significantly between interior and edge (Appendix Table A1, $p < 0.001$), and among patches ($p < 0.001$) and further showed a Habitat $\times$ Patch interaction ($p < 0.001$). Mean values for plant variables at each patch and habitat are summarized in Appendix Table A2.

3.3. Invertebrate community

Total infaunal abundance differed significantly between the three habitats with the highest abundances in the *Zostera* interior, followed by the edge and lowest abundances in the bare sand (Fig. 4a). Number of taxa was significantly higher in *Zostera* than in the bare sand, but differences between *Zostera* interior and edge could not be detected (Fig. 4b).

In terms of species, the tube-building spionid *Pygospio elegans* had highest abundance in the *Zostera* interior and lowest in the bare sand. The cockle *Cerastoderma glaucum*, the polychaetes *Hediste diversicolor* and *Marenzelleria* spp., and mudsnails *Hydrobia* spp. had

Figure 4. Mean abundance and diversity of infaunal (n=30 for Interior and Edge and n=29 for Bare sand) and epifaunal communities (n=18 for both Interior and Edge) $\pm$ SE. Different letters above bar plots indicate significant differences ($p < 0.05$).

significantly higher abundance in the *Zostera* than in the bare sand, but differences between *Zostera* interior and edge could not be detected for these taxa. Oligochaetes only showed significant differences between *Zostera* interior and the bare sand. The amphipod *Corophium volutator* was absent in the bare sand, although mean abundance did not differ significantly between the interior and edge. The bivalve *Macoma balthica* showed no differences between the habitats. Taxa-specific abundances are summarized in Appendix Fig. A1.

When examined for each patch individually, total infauna abundance in the *Zostera* interior and the bare sand showed contrasting patterns (Fig. 5). Highest infauna abundance in bare sand was found adjacent to the deepest patch P1 and decreased continuously towards patch P5, followed by an increase at P6. On the contrary, infauna abundance in the *Zostera*

Figure 5. Mean infauna abundance $\pm$ SE at *Zostera* patch interior, *Zostera* patch edge and adjacent bare sediments along the depth gradient.

interior was lowest at P1. With decreasing depth, abundance increased, reaching a maximum at patch P4, followed by a decrease for P5 and P6. Infauna abundance at the *Zostera* edge was similar to the *Zostera* interior in the shallow and deep parts but decreased at intermediate depths with the minimum at P4.

Mean abundance and number of taxa of leaf epifauna did not differ between edge and interior (Fig. 4c, d). Further analysis of abundant epifaunal taxa revealed that only the snail *Potamopygrus antipodarum* and the isopod *Idotea balthica* (Appendix Fig. A2) showed significant differences between habitats, with a higher abundance of *P. antipodarum* in the interiors, but higher abundance of *I. balthica* along the edges.

Abundance of epi- and infauna at the six sampling depths could be related to distinct sediment and plant characteristics (Appendix Table A3). The relation to those variables, however, differed considerably, depending on the habitat type. Infaunal abundance in the bare sand correlated negatively with very coarse sand ($r^2=0.268$, $p<0.004$) and positively with

organic content ($r^2=0.205$, $p<0.014$). Infauna abundance at the patch interior in contrast, increased with very coarse sand ($r^2=0.157$, $p<0.030$) and infauna at the patch edge was not related to any sediment characteristics. Linear regression further indicated that infaunal total abundance was not related to any plant characteristics, neither in the *Zostera* patch interior, nor along the patch edges.

Epifauna at the patch edges increased with proportion of fine sand ($r^2=0.451$, $p=0.002$) and organic content ($r^2=0.570$, $p<0.001$), but decreased with very coarse sand ($r^2=0.464$, $p=0.002$), while the epifauna abundance at the patch interior showed no correlation with sediment characteristics. Instead, epifauna abundance at the interior was positively correlated with shoot density ($r^2=0.230$, $p<0.044$) and above-ground biomass ($r^2=0.234$, $p<0.042$), while edge epifauna showed no correlation with plant variables.

3.4. Facilitation along the disturbance gradient

The PCA, used to characterise the exposure gradient, could explain 79.6 % of the variance on the two first axes (Fig. 6). When considered as stand-alone approximations, all variables suggested an increase in physical exposure towards the same direction along component 1 (50.2 %). This pattern indicates the representativeness of this component as a proxy of exposure. Ripple index (-0.49) and d_{50} (0.57) showed strongest correlation with PC1, while % fine sand (-0.34) had the lowest explanation on PC1. Consequently, we used a stress gradient based on the scores from PC1 for further analyses. According to this proxy, exposure increased along the sampling transect from P1 to P4 and declined again towards P6.

Linear regression revealed that none of the plant variables (shoot density, AB, BB, shoot length) were related to the exposure gradient (as described by the PC 1), neither at the patch interior nor at the patch edge. However, both in- and epifauna showed, depending on the habitat position, different responses to physical exposure. Sediment infauna abundance in the

Figure 6. Principal component analysis of sediment parameters (% fine sand, % organic content and d_{50}), depth and ripple index adjacent to the six *Zostera* patches.

bare sand habitat was negatively correlated with physical exposure (Fig. 7a; $r^2=0.31$; $p=0.002$). In contrast, infauna at the *Zostera* interior correlated weakly, but positively with physical stress (Fig. 7c; $r^2=0.15$; $p=0.034$). Infauna along the *Zostera* edge showed no correlation with PC1 (Fig. 7b). Leaf epifaunal abundance at the *Zostera* edge was negatively correlated with the exposure proxy (Fig. 7e; $r^2=0.46$; $p=0.002$), whereas no correlation could be detected for epifauna in the interior of the seagrass patches (Fig. 7d).

Figure 7. Linear regression of total abundance along the exposure gradient, as described by PC1, for the infaunal community at a) the *Zostera* interior, b) the *Zostera* edge and c) the adjacent bare sand; and for the epifaunal community at d) the *Zostera* interior and e) the *Zostera* edge. Regression line and corresponding r^2 and p-values are given where linear regression analysis indicated a significant effect. Samples are shown as mean $\pm$ SE.

While the overall patterns of infauna abundance across the exposure gradient are relatively weak with low explanatory power (albeit significant), an interesting pattern emerges when the ratio of the *Zostera* interior to bare sand abundance, i.e. the relative facilitation ability of *Zostera*, is examined. Linear regression implied that exposure had strong positive effects on the relative facilitation of *Zostera* ($r^2=0.82$, $p=0.014$, Fig. 8a). Interior infaunal

Figure 8. Linear regression of the ratio of *Zostera* interior (I) and bare sand (B) infauna
a) abundance and b) diversity along the exposure gradient (as described by PC1).

abundance at the benign end of the stress gradient was about 1.5 fold the abundance at the adjacent bare sand, but reached almost 4.5 fold bare sand abundance at the stressful end of the gradient. The ratio of taxonomic richness on the other hand did not linearly increase along the gradient ($r^2=0.43$, $p=0.156$, Fig. 8b), but was overall higher at high compared to low exposure.

SIMPER analysis revealed that community dissimilarity between the *Zostera* patch interior and the bare sand was higher at each of the six *Zostera* patches compared to dissimilarities between the edge and the bare sand community, and in particular between the interior and the edge community (Appendix Fig. A3). Taxa contributing most to the overall dissimilarity between interior and bare sand across the entire gradient (46 % dissimilarity) were *P. elegans* (14.2%), *Hydrobia* spp. (11.9 %) and Oligochaeta (11.1 %); all more abundant at the patch interior; (Appendix Table A4). More importantly, the dissimilarity in community composition between patch interior and bare sand significantly increased along the physical stress gradient from 39 % to over 53 % ($r^2=0.67$, $p=0.046$, Fig. 8c, Appendix Fig. A4). The taxa contributing most to the dissimilarity between interior and bare sand at the stressful end of the gradient at P4 (53.5 % dissimilarity) were *C. volutator* (15.6 %), *Hydrobia* spp. (14.7 %) and Oligochaeta (13.8 %); all more abundant in the *Zostera* interior; (Appendix Table A3). Comparing the infaunal community of the *Zostera* interior between the benign and stressful end furthermore showed that while *C. volutator* (16.7 % dissimilarity between P1 and P4), Oligochaeta (13.4 %) and *Hydrobia* spp. (7.7 %) were more abundant, *P. antipodarum* (11.2%) was less abundant under physical stress (Appendix Table A3). On average, dissimilarity between the six patches was significantly higher for the bare sand infauna community (43.01 %), compared to the infauna in the patch interior (35.70 %, $p<0.0001$) and the patch edge (33.55 %, $p<0.0001$, Appendix Table A5). Furthermore, similarity between replicates within the patches was significantly higher in the patch interior (66.14 %, $p=0.049$) and the patch edge (68.14 %, $p=0.008$), compared to the bare sand (60.48 %, Appendix Table A5).

4. DISCUSSION

We examined how the foundation species *Zostera marina* promotes its associated invertebrate community along a physical stress gradient. Our results emphasize the general

relevance of an aquatic engineering plant species for sediment fauna through habitat amelioration and reveal insights into the underlying conditionality. Consistent with past studies, we could find that infauna abundance and taxonomic richness were generally higher in *Zostera* than in nearby unvegetated sediments (Boström and Bonsdorff 1997, Fredriksen et al. 2010). Total abundance thereby increased towards the interior of the *Zostera* patches, and did not show, like occasionally demonstrated, an edge effect, i.e. elevated abundance close to the edges (Bowden et al. 2001, Bologna and Heck 2002). Besides habitat quality, physical disturbance is a crucial mechanism for structuring benthic communities (Probert 1984, Widdicombe and Austen 2001). An approximation for patch-specific exposure was derived by principle component analysis (PCA) of environmental variables likely correlated with hydrodynamic conditions. As shown by studies before, our results indicated that infauna abundance in unvegetated sediments was negatively affected by increasing exposure, waves and currents (Bonsdorff et al. 1995, Valanko et al. 2010). Ecosystem engineers, however, are assumed to increase the realized niche of associated communities (Bruno et al. 2003). In accordance with previous work, we could demonstrate the ameliorating effect of seagrass on hydrodynamics for its associated fauna (Irlandi 1996). The infauna abundance inside *Zostera* patches showed no decline along the exposure gradient, rather our results suggested an increase in abundance with increasing exposure. The relative importance of facilitation by *Zostera* becomes explicit, when directly comparing the infauna community in vegetated and unvegetated sediments. We found that the ratio of *Zostera* interior and bare sand infauna abundance increased monotonically from 1.5 to 4.5 along the gradient of increasing physical exposure. SIMPER analysis showed that simultaneously dissimilarity in community composition between interior and bare sand increased. This implies that not only single species are affected by facilitation, rather it can be inferred that *Zostera* facilitates its whole associated infaunal community through stress amelioration. Thereby, the average community similarity between patches, and between replicates within

patches, was significantly higher in both *Zostera* patch interior and *Zostera* patch edge compared to the bare sand. Thus, the increase in physical stress not just causes a decrease in total abundance, but also alters the infauna community structure in the unprotected bare sand. Through the shelter provided by *Zostera*, on the other hand, the infauna community composition remains comparably stable along the stress gradient.

Gradient approaches are often used where methods of simple patch-mosaic models (e.g. ANOVA) are not appropriate to capture the variability of environmental parameters, e.g. along depth or concentration gradients (McGarigal and Cushman 2005, Hewitt et al. 2007, Cushman et al. 2010). Besides the drawbacks of being of correlative nature and thus lacking direct manipulation, they can be a strong tool revealing insights in underlying functional relations between environmental and community data and related time integrated effects (Hewitt et al. 2007).

Contrary to our predictions, the PCA of environmental parameters along the depth gradient indicated that the realised exposure was not solely dependent on depth, but rather peaked at intermediate depth levels, suggesting a dampening of wave-exposure closer to the shore by the extensive *Zostera* meadows. The distribution of bare sand infauna abundance, i.e. a latent variable for an indirect gradient between more and less favourable conditions (ter Braak and Prentice 1988), matches the approximation of PC1 as an environmental stress gradient for the sediment infaunal community. Overall, other environmental variables such as temperature or light availability are unlikely to cause the observed contrast between bare sand and vegetation, as both are assumed to be highly correlated with depth, yet the exposure proxy deviates from the depth gradient. Moreover, the amelioration effect of *Zostera* on these drivers is limited. Turbidity through sediment resuspension is typically linked to hydrodynamics, and a reduced turbidity within the vegetated patches therefore can be seen as a by-product of the amelioration of hydrodynamics by *Zostera*. Furthermore, the depth differences in this study were limited and thus unlikely to affect other potential causes

such as faunal recruitment patterns of single species. Nonetheless, a positive impact on recruitment success (i.e. increased juvenile survival through mitigation of physical stress) is a facilitative outcome of seagrasses itself.

Although the outcome of facilitative interactions is highly dependent on local abiotic and biotic conditions in any ecological community (Bertness and Callaway 1994, Lenihan 1999, Bruno and Bertness 2001), only a few studies have actually demonstrated this for habitat engineers and their effect on associated communities (Norkko et al. 2006, Wright et al. 2006, Lohrer et al. 2013, Watt and Scrosati 2013, Crotty and Bertness. 2015, McAfee et al. 2016). These examples represent a broad range of different habitats and community types such as marine habitat-forming benthic suspension feeders, intertidal rocky shore seaweeds and cobble beach cord grasses or shrub mounds in terrestrial deserts. Importantly, however, we show for the first time, in a subtidal soft-bottom setting, how amelioration effects are modified by environmental variables related to hydrodynamic exposure. Our overall finding of an increase of the relative importance of facilitation with increasing environmental stress was thereby consistent with results from empirical studies on interspecific (e.g., Callaway et al. 2002, Bennett et al. 2015, López et al. 2016), conspecific (e.g., Bennett et al. 2015, Yang et al. 2016) and trophic (e.g., Daleo and Iribarne 2009) interactions and gives further insights to community-wide effects of habitat engineers in marine environments (McAfee et al. 2016, Watt and Scrosati 2013).

This study further highlights how environmental conditions can affect the relationship between a foundation species and its associated community differently depending on the faunal assemblage in question and proximity to habitat edges. Contrasting to the *Zostera* interior community, infauna living at the habitat edge did not linearly increase with exposure. Instead our results show a decline at high exposure rates, indicating that here a threshold in physical conditions has been reached, at which *Zostera* edges are unable to provide suitable habitat for infauna. Similarly, mobile leaf epifauna declined in abundance with increasing

exposure along the *Zostera* edges, while epifauna was unaffected in the *Zostera* interior. Although in a different setting, exploring facilitation in mussel beds through amelioration of temperature effects, Jurgens and Gaylord (2016) demonstrated that stress amelioration by foundation species can be highly variable within single habitat patches and can even shift to exacerbation at habitat edges. This points out that, depending on underlying abiotic and biotic conditions, an increase of relative importance of facilitation towards stressful environments is not always necessarily true, see Norkko et al. (2006), Kawai and Tokeshi (2007), Fugère et al. (2012), Bakker et al. (2013), Castanho and Prado (2014).

Our results further give indication of mechanisms responsible for the facilitative effect of the foundation species *Zostera*. We have shown that relative facilitation of *Zostera* was not due to changes in structural complexity of the *Zostera* patches per se; i.e. infauna abundance was not correlated with any plant variables. Besides the positive correlation of *Zostera* infauna with exposure was rather weak ($r^2=0.15$), compared to the negative correlation of infauna in the unvegetated sediments ($r^2=0.31$). This indicates that the facilitative effect is first of all attributed to a sheltering potential of *Zostera* along the exposure gradient, i.e. reduction in wave disturbance and current flow, expressed by decreasing sediment grain size and trapping of organic particles towards the patch interior (Boström and Bonsdorff 1997, Hendriks et al. 2008).

Epifauna abundance on the other hand did increase with shoot density and above ground biomass at the *Zostera* interior. This underlines the major relevance of seagrass habitat complexity for epifaunal communities (Boström and Bonsdorff 1997, Carr et al. 2011). However, this pattern was not detected at the edges, where shoot density and above-ground biomass had no effect on epifaunal abundance. Here, total abundance was primarily driven by sediment characteristics, with lowest total abundance at low organic content and high proportion of very coarse sand, further suggesting that close to the edge the occurrence of strong physical forces exceeds the sheltering capacity of *Zostera*.

Habitat edges are defined as sudden transitions between adjacent habitats and play a major role in structuring ecological communities (Strayer et al. 2003). Our results indicate that seagrass patch edges can considerably buffer hydrodynamic forcing (Fonseca et al. 1982, Gambi et al. 1990, Peterson et al. 2004, Temmerman et al. 2005). The substantial changes in hydrodynamic variables, but also biological processes (Boström et al. 2006) that interact at the edges of seagrass patches, influence e.g. recruitment patterns (Carroll et al. 2012) and distributions of predators and prey (Macreadie et al. 2010, González-Ortiz et al. 2014). Seagrass patches have erratically been associated with positive edge effects (Tanner 2005), expressed as an increase in species abundance or diversity (Bowden et al. 2001, Ries et al. 2004, Bologna and Heck 2002, Connolly and Hindell 2006). In this study, however, only the isopod *I. balthica* showed elevated abundances at the edges, implying that edge effects are highly species specific (Tanner 2005), and dependent on environmental context (e.g., hydrodynamic regime).

It has been shown that environmental stress or an additional engineering species can reduce and even inhibit the facilitative relevance of a marine ecosystem engineer for its associated community (Norkko et al. 2006, Lohrer et al. 2013, McAfee et al. 2016). We could demonstrate that underlying mechanisms of facilitation depended on within-habitat position and the faunal assemblage in question. Specifically, we demonstrated strong differences between epifaunal and infaunal assemblages due to different positive feedback mechanisms (Maxwell et al. 2017). Our findings have direct implications particularly for management efforts in degrading biogenic habitats. The ongoing loss of seagrass habitats worldwide (Waycott et al. 2009) and the limited success of restoration programs (van Katwijk et al. 2016) calls for a widespread and sustainable management of these critically important habitats. The results of this study emphasize that conservation efforts should focus particularly on physically stressful environments, as the ecological value in promoting associated communities by seagrass meadows is assumed to be most pronounced here. In line

with these findings, we encourage further experimental efforts to reveal the conditional outcome of facilitation, including both interior and edge habitats for a broad range of foundation species.

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AUTHORS CONTRIBUTIONS

A.N., J.N., T.Y. designed the study; A.N., J.N., T.Y, F.M., S.V., A.J., A.V. performed field sampling; A.J., A.V., J.N., S.V. performed laboratory analysis; L.M. analyzed the data; L.M. drafted the manuscript with substantial input by C.B. and A.N.; T.Y., A.J., F.M., S.V., A.V., C.B., J.N. and A.N. commented and revised the manuscript.

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809 APPENDIX:

810 **Table A1.** Results of two-way ANOVA on sediment and plant characteristics with Patch (P1-
811 P6) and Habitat (*Zostera* interior – *Zostera* edge – Bare sand) as main factors.

Class	Data set	Transformation	Source	Df	SS	MS	F	P
Sediment	Fine	no	Patch	5	0.07129	0.01426	12	<0.0001
			Habitat	2	0.1588	0.07938	66.79	<0.0001
			Patch × Habitat	10	0.03698	0.003698	3.112	0.0024
			Residuals	72	0.08557	0.001188		
	Medium	no	Patch	5	0.1857	0.03713	29.87	<0.0001
			Habitat	2	0.4259	0.213	171.3	<0.0001
			Patch × Habitat	10	0.03789	0.003789	3.047	0.0028
			Residuals	72	0.08952	0.001243		
	Coarse	no	Patch	5	0.09488	0.01898	8.252	<0.0001
			Habitat	2	0.03613	0.01806	7.855	0.0008
			Patch × Habitat	10	0.1248	0.01248	5.428	<0.0001
			Residuals	72	0.1656	0.002299		
	Very coarse	no	Patch	5	0.3499	0.06998	37.8	<0.0001
			Habitat	2	0.9959	0.498	269	<0.0001
			Patch × Habitat	10	0.08792	0.008792	4.749	<0.0001
			Residuals	72	0.1333	0.001851		
	Organics	no	Patch	5	0.016221	0.003244	14.005	<0.0001
			Habitat	2	0.02094	0.01047	45.198	<0.0001
			Patch × Habitat	10	0.005334	0.000533	2.303	0.0211
			Residuals	70	0.016215	0.000232		
Plant	Shoot density	no	Patch	5	181793	36359	1.922	0.1278
			Habitat	1	17885	17885	0.945	0.3406
			Patch × Habitat	5	248874	49775	2.631	0.0493
			Residuals	24	453982	18916		
	Above-ground biomass	Log+0.5	Patch	5	0.484	0.0968	0.677	0.6453
			Habitat	1	0.478	0.4781	3.343	0.08
			Patch × Habitat	5	2.067	0.4134	2.89	0.0351
			Residuals	24	3.433	0.143		
	Below-ground biomass	Log+0.5	Patch	5	1.517	0.3034	2.331	0.0736
			Habitat	1	2.3173	2.3173	17.799	0.0003
			Patch × Habitat	5	0.5374	0.1075	0.826	0.5439
			Residuals	24	3.1245	0.1302		
	Shoot length	no	Patch	5	1135.7	227.1	8.285	0.0001
			Habitat	1	533.2	533.2	19.45	0.0002
			Patch × Habitat	5	903.4	180.7	6.591	0.0005
			Residuals	24	658	27.4		

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814 **Table A2.** Habitat (I=Interior, E=Edge, B=Bare sand) and means of grain size fractions (sand) 1-2mm (very coarse, %), 0.5-1mm (coarse, %), 0.25-0.5 (medium,
 815 %) and 0.1-0.25 (fine, %), organic content (LOI, %), *Zostera* shoot density (shoots m⁻²), *Zostera* above- and belowground biomass (AB and BB, g DW m⁻²),
 816 *Zostera* shoot length (shoot l, cm), depth (m), sand ripple height/length (ripples, mm) and median grain size (*d*₅₀, mm) at the sampling locations P1-6 and as
 817 average (Total). For overall effects between habitats, also significant differences are indicated by superscript letters, based on habitat effect of two-way ANOVA
 818 (p < 0.05).

Patch	Habitat	Grain size (mm)						<i>d</i> ₅₀	LOI	Shoots	AB	BB	Shoot L	Depth	Ripples
		2.00	1.00	0.50	0.125	0.063	<0.063	(mm)	(%)	(m ⁻²)	(g DW m ⁻²)	(g DW m ⁻²)	(cm)	(m)	l/h (mm)
P1	I	6.2%	26.2%	45.2%	19.7%	0.18‰	0.09‰	0.76	0.18	247.3	41.4	176.8	35.8		
	E	8.3%	41.6%	43.9%	7.2%	0.01‰	0.01‰	0.98	0.14	328.0	39.5	76.6	40.6		
	B	22.6%	36.4%	28.9%	2.4%	0.00‰	0.00‰	1.33	0.14					4.1	32.4/5.1
P2	I	10.7%	41.2%	39.9%	7.1%	0.05‰	0.02‰	1.04	0.15	338.1	42.2	127.0	52.6		
	E	9.6%	37.9%	42.4%	7.1%	0.03‰	0.03‰	0.99	0.15	519.8	64.3	110.9	53.5		
	B	31.9%	28.3%	23.9%	0.7%	0.00‰	0.00‰	1.51	0.12					3.8	35.0/6.7
P3	I	12.2%	40.3%	41.5%	8.9%	0.07‰	0.03‰	0.97	0.16	363.4	56.1	135.5	57.5		
	E	24.5%	40.2%	33.2%	3.1%	0.00‰	0.00‰	1.27	0.13	247.3	31.5	120.0	32.2		
	B	40%	39.2%	24.5%	1.7%	0.00‰	0.00‰	1.62	0.13					3.4	41.8/10.9
P4	I	14.2%	40.5%	34.2%	7%	0.29‰	0.05‰	1.10	0.16	459.2	43.3	206.6	47.4		
	E	34.8%	46.7%	23.8%	0.9%	0.00‰	0.00‰	1.54	0.11	524.8	52.0	99.7	43.7		
	B	47.6%	33.6%	17.2%	0.4%	0.00‰	0.00‰	1.90	0.11					3.2	32.3/7.0
P5	I	10.2%	46.2%	38.6%	10.4%	0.23‰	0.05‰	0.96	0.13	540.0	70.2	173.0	47.5		
	E	20.4%	43.4%	30.2%	2.4%	0.02‰	0.00‰	1.29	0.11	247.3	30.9	109.3	34.8		
	B	38.3%	33.8%	21.3%	1.2%	0.01‰	0.00‰	1.60	0.09					3.2	32.9/6.3
P6	I	9.6%	34.8%	42.4%	17.4%	0.19‰	0.04‰	0.82	0.14	439.1	54.2	287.7	42.9		
	E	17.8%	39%	37.2%	10%	0.10‰	0.05‰	1.03	0.13	252.3	25.6	148.3	28.1		
	B	34.9%	34.2%	27.2%	3.4%	0.02‰	0.01‰	1.45	0.11					2.7	32.4/6.2
Total	I	10.5 ^a %	35.3 ^a %	40.3 ^a %	11.7 ^a %	0.17 ^a ‰	0.05 ^a ‰		0.15 ^a	397.83 ^a	51.21 ^a	184.4 ^a	47.3 ^a		
	E	19.2 ^b %	40.1 ^b %	35.1 ^a %	5.1 ^b %	0.03 ^b ‰	0.02 ^b ‰		0.13 ^b	353.26 ^a	40.63 ^a	110.8 ^b	39.7 ^b		
	B	35.9 ^c %	38.6 ^b %	23.8 ^b %	1.6 ^c %	0.01 ^b ‰	0.00 ^b ‰		0.12 ^c						

Table A3. Correlation (numbers correspond to r^2) of a) infauna and b) epifauna abundance with sediment and plant parameters in *Zostera* interior, *Zostera* edge and bare sand. . Statistically significant is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and highlighted in bold.

a) INFAUNA	INTERIOR	EDGE	BARE SAND
SEDIMENT			
Very coarse sand	0.157*	0.062	0.268**
Coarse sand	0.117	0.037	0.134
Medium sand	0.171*	0.071	0.251**
Fine sand	0.121	0.092	0.102
Organic content	<0.001	0.059	0.205*
PLANT			
Shoot density	0.062	0.045	
AB	0.002	0.017	
BB	0.005	0.082	
Shoot length	0.046	0.020	
b) EPIFAUNA	INTERIOR	EDGE	
SEDIMENT			
Very coarse sand	0.002	0.464**	
Coarse sand	0.004	0.150	
Medium sand	0.001	0.573***	
Fine sand	0.008	0.451**	
Organic content	0.022	0.570***	
PLANT			
Shoot density	0.230*	0.014	
AB	0.234*	0.072	
Shoot length	<0.001	0.053	

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840 **Table A4.** Dissimilarities between a) overall *Zostera* interior (I) and bare sand (B). b) patch
 841 P4 *Zostera* interior and patch P4 bare sand. and c) patch P1 (least exposed) and patch P4
 842 (most exposed) *Zostera* interior infaunal communities. For each sub-table corresponding
 843 average contributions of the 4 most pivotal taxa to habitat dissimilarities are listed. While a)
 844 highlights the infaunal taxa generally benefiting from seagrass beds as biogenic habitat, b)
 845 reveals the main taxonomic differences between *Zostera* interior and bare sand habitats at the
 846 most exposed position. Sub-table c) on the other hand outlines the infaunal taxa associated
 847 with *Zostera* that show highest changes in abundance between the least and most exposed
 848 patch.

a) Interior and Bare sand total						
Average dissimilarity =46.00	I	B				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Pygospio elegans</i>	2.99	1.22	6.51	1.50	14.16	14.16
<i>Hydrobia</i> spp.	2.87	1.64	5.46	1.31	11.87	26.02
Oligochaeta	2.57	1.81	5.12	1.40	11.14	37.16
<i>Cerastoderma glaucum</i>	1.60	0.59	4.28	1.46	9.30	46.46

b) Interior high stress (P4) and Bare sand high stress (P4)						
Average dissimilarity = 53.49	I (P4)	B (P4)				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Corophium volutator</i>	2.82	0.00	8.37	1.76	15.64	15.64
<i>Hydrobia</i> spp.	3.76	1.48	7.85	1.57	14.67	30.31
Oligochaeta	3.17	1.49	7.39	1.96	13.81	44.12
<i>Pygospio elegans</i>	2.62	0.68	5.97	1.99	11.16	55.28

c) Interior low stress (P1) and Interior high stress (P4)						
Average dissimilarity = 38.77	I (P1)	I (P4)				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Corophium volutator</i>	0.20	2.82	6.49	1.73	16.73	16.73
Oligochaeta	2.22	3.17	5.19	1.30	13.39	30.11
<i>Potamopyrgus antipodarum</i>	1.78	0.28	4.33	1.37	11.16	41.28
<i>Hydrobia</i> spp.	2.82	3.76	2.98	1.54	7.70	48.97

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851 **Table A5.** ANOVA results for difference in overall community (dis-)similarity between
 852 *Zostera* interior (I), *Zostera* edge (E) and bare sand (B).

Variable	F	P	Tukey HSD
Similarity within patches	6.705	0.0083	I > B*, E > B**
Dissimilarity between patches	40.15	<0.0001	B > I***, B > E***

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Figure A1. Mean abundance of most abundant infauna species in the *Zostera* interior, *Zostera* edge and bare sand habitats (n=30 for Interior and Edge and n=29 for Bare sand) $\pm$ SE. Different letters above bar plots indicate significant differences ($p < 0.05$).

Figure A2. Mean abundance of most abundant epifauna species in the *Zostera* interior and *Zostera* edge (n=18 for each habitat) $\pm$ SE. Significant differences are indicated with * (p<0.05).

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Figure A3. Dissimilarity percentages of the infaunal community between habitats (*Zostera* interior, *Zostera* edge, bare sand) along the 6 *Zostera* patches obtained by SIMPER analysis. The underlying Bray-Curtis measure of dissimilarity is based on square-root transformed abundance data. The patches P1-6 are re-ordered along the exposure gradient (as described by PC1) from least (P1) to most exposed (P4).