Elsevier Editorial System(tm) for Journal of Experimental Marine Biology and Ecology
Manuscript Draft

Manuscript Number:

Title: Biotic structure and sediment stability facilitate benthic trophic diversity in an intertidal soft-bottom ecosystem

Article Type: Full Length Article

Keywords: ecosystem engineers, biotic structure, sediment stability, trophic diversity, Mytilus edulis, Wadden Sea

Corresponding Author: Dr. Els van der Zee,

Corresponding Author's Institution:

First Author: Els van der Zee

Order of Authors: Els van der Zee; Elske Tielens; Sander Holthuijsen; Serena Donadi; Britas Klemens Eriksson; Henk van der Veer; Theunis Piersma; Han Olff; Tjisse van der Heide

Abstract: In intertidal soft-bottom ecosystems, ecosystem engineers such as reef-building bivalves can strongly effect the associated community by providing structure and stabilizing the sediment. Although several engineering species have declined dramatically in the past centuries, the consequences of their loss for the trophic structure of intertidal benthic communities remain largely unclear. In this study, we experimentally test the hypothesis that recovery of aboveground biotic structure and stable sediments, facilitate distinctly different, but trophically more diverse benthic communities, using intertidal mussel beds as a model system. We constructed a large-scale experiment at two intertidal mudflats in the western and the eastern part of the Dutch Wadden Sea, where environmental conditions are distinctly different. At both sites, we crossed the application of anti-erosion mats with the addition of adult mussels to investigate effects of sediment stabilisation and biotic aboveground structure. The anti-erosion mats mainly enhanced species and trophic diversity (i.e. feeding guild richness and diversity) of the infaunal community, while the addition of mussels primarily enhanced species and trophic diversity of the epifaunal community, irrespective of location. The effect size of mussel addition was larger at the site exposed site in the western Wadden Sea compared to the eastern site, probably due to relatively stronger abiotic stress alleviation. We conclude that structure-providing and sediment-stabilizing species such as reef-building bivalves, seagrasses, and tube-worm, form the foundation for trophically diverse benthic communities. In intertidal soft-bottom ecosystems like the Wadden Sea, their conservation and restoration is therefore critical for overall ecosystem functioning.

Biotic structure and sediment stability facilitate benthic trophic diversity in an intertidal soft-bottom ecosystem

Els M. van der Zee[1,2,3,*], Elske Tielens[4], Sander Holthuijsen[1], Serena Donadi[5], Britas Klemens Eriksson[5], Henk W. van der Veer[1], Theunis Piersma[1,2], Han Olff[4] and Tjisse van der Heide[4,6]

[1] Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

[2] Animal Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

[3] Altenburg & Wymenga ecological consultants, Suderwei 2 , 9269 TZ Veenwouden, The Netherlands

[4] Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

[5] Marine Benthic Ecology and Evolution, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

[6] Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University Nijmegen, Faculty of Science, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands.

* corresponding author: emvanderzee@hotmail.com

Abstract

In intertidal soft-bottom ecosystems, ecosystem engineers such as reef-building bivalves can strongly effect the associated community by providing structure and stabilizing the sediment. Although several engineering species have declined dramatically in the past centuries, the consequences of their loss for the trophic structure of intertidal benthic communities remain largely unclear. In this study, we experimentally test the hypothesis that recovery of aboveground biotic structure and stable sediments, facilitate distinctly different, but trophically more diverse benthic communities, using intertidal mussel beds as a model system. We constructed a large-scale experiment at two intertidal mudflats in the western and the eastern part of the Dutch Wadden Sea, where environmental conditions are distinctly different. At both sites, we crossed the application of anti-erosion mats with the addition of adult mussels to investigate effects of sediment stabilisation and biotic aboveground structure. The anti-erosion mats mainly enhanced species and trophic diversity (i.e. feeding guild richness and diversity) of the infaunal community, while the addition of mussels primarily enhanced species and trophic diversity of the epifaunal community, irrespective of location. The effect size of mussel addition was larger at the site exposed site in the western Wadden Sea compared to the eastern site, probably due to relatively stronger abiotic stress alleviation. We conclude that structure-providing and sediment-stabilizing species such as reef-building bivalves, seagrasses, and tube-worm, form the foundation for trophically diverse benthic communities. In intertidal soft-bottom ecosystems like the Wadden Sea, their conservation and restoration is therefore critical for overall ecosystem functioning.

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Introduction

Coastal ecosystems are of great importance to a multitude of marine species and provide crucial services to human society (Barbier, et al., 2011; Beck, et al., 2001; Costanza, et al., 1997; Hodgson and Liebeler, 2002). Ecosystem engineers, species that strongly modify their environment, such as reef-building bivalves, seagrasses and corals (Jones, et al., 1994; 1997), typically play an important role within these ecosystems, because they diversify the landscape by forming complex structures and relieve environmental stress, for instance by attenuating currents and waves (Donadi, et al., 2013; Gutierrez, et al., 2003; Koch, et al., 2009). Due to these habitat modifications, ecosystem engineers typically not only facilitate themselves (Rietkerk, et al., 2004; van de Koppel, et al., 2005; van der Heide, et al., 2007), but also provide a key-habitat for a wide variety of species that depend on them for settlement, refuge or food supply (e.g. Gutierrez, et al., 2003; Nagelkerken, et al., 2000; van der Zee, et al., 2012).

Over the last decades, ecosystem engineer-dominated coastal ecosystems have become severely degraded worldwide, often due to anthropogenic impacts (Barbier, et al., 2008; Lotze, et al., 2006; van Gils, et al., 2006; Waycott, et al., 2009). Moreover, natural recovery of ecosystem engineers is typically slow, unpredictable or absent due to strong internal positive feedbacks, and even active restoration has proven difficult (Eriksson, et al., 2010; Jackson, et al., 2001; Schulte, et al., 2009; van der Heide, et al., 2007). The loss of ecosystem engineers and their lack of recovery often has dramatic implications for many associated species, especially in soft-bottom ecosystems, where solid substrate and aboveground structure are almost exclusively provided by engineering species such as seagrass, tubeworm, mussel and oyster beds (Eriksson, et al., 2010; Hodgson and Liebeler, 2002; Lotze, 2005; Waycott, et al., 2009). Although the importance of engineering species for overall biodiversity has been well established, there is little experimental evidence showing how the loss and recovery of ecosystem engineers affects the trophic structure (i.e. feeding guild richness and diversity) of the benthic community in intertidal soft-bottom ecosystems.

In this study, we empirically test the hypothesis that recovery of aboveground biotic structure and stable sediments facilitates distinctly different, but trophically more diverse intertidal benthic communities, using intertidal mussel beds as a model system. In the Dutch part of the Wadden Sea, one of the world's largest intertidal ecosystems (Compton, et al., 2013; Wolff, 1983), intertidal mussels – ecosystem engineers that create hard substrate, reduce hydrodynamic stress, modify sediment conditions and increase the cohesiveness of the substrata (Donadi, et al., 2013; Gutierrez, et al., 2003; Kröncke, 1996; Widdows and Brinsley, 2002) – covered an area of over 4000 ha at the end of the 1970s. In the beginning of the 1990s, however, intertidal mussel beds disappeared completely due to a combination of overfishing, storms and several years of recruitment failure (Beukema and Cadée, 1996; Dijkema, 1991). In addition to the direct physical removal of mussels, sand extraction and bottom trawling for shrimps (*Crangon crangon*) and edible cockles (*Cerastoderma edule*) also removed sediment-stabilizing species and resuspended the upper layer of the sediment (Kraan, et al., 2007; Piersma, et al., 2001; e.g. Riesen and Reise, 1982; van der veer, et al., 1985). Despite a ban on mechanical dredging for intertidal mussels (1999) and cockles (2005), it took more than a decade for mussels to start to re-establish and even now their recovery is still mainly restricted to the eastern part of the Dutch Wadden Sea (Ens, et al., 2009; Goudswaard, et al., 2009).

To test our hypotheses, we constructed a large-scale experiment, in which we crossed the application of anti-erosion mats with the addition of adult mussels to test for the effects of sediment stabilisation and biotic structure. To investigate whether the treatment effects were consistent across our study system, the experiment was carried out at two different sites with distinctly different conditions and ambient benthic communities (Compton, et al., 2013). The first site was located in the western part of the Dutch Wadden Sea, south of the island Terschelling, and the second was situated in the eastern part of the Dutch Wadden Sea, south of the island Schiermonnikoog. After three months, we investigated treatment effects on the invertebrate community.

2. Methods

2.1. Study area

Large-scale experimental plots were established on the intertidal mudflats of two barrier Islands in the Dutch Wadden Sea. The first site was located in the western part, south of the island of Terschelling (53°21'39.69"N, 5°18'29.18"E) and the second site was located in the eastern part, south of the island of Schiermonnikoog (53°28’3.43”N, 6°14”13.40”E) (Fig. 1). The site at Terschelling has a small tidal range (~0.9 m, based on mean high water levels), is exposed to waves from the southwest, and is typified by relatively clear water and sandy sediment (Table 1). The site at Schiermonnikoog has a somewhat larger tidal range (~1.2 m, based on mean high water levels), is situated in more sheltered conditions, and is characterized by very turbid water and more silty sediments (Table 1). Both sites were located at approximately the same tidal elevation (0.6 to 0.8 m below mean water level), which is similar to the elevation of natural intertidal mussel and oyster beds in the vicinity of the experimental plots (distance: ~1000-2000 m).

2.2. Experimental design

At each site, 12 plots of 20×20 m were established in a line parallel to the gully (distance from the gully ~100-150 m) and with a distance of ~20 m between plots. Plots were divided over three blocks. Within each block, we randomly assigned one replicate of each of the following treatments to the plots: (1) control, (2) addition of a coco-coir mat on the sediment surface to stabilize the sediment, (3) addition of adult mussels to create biotic structure, and (4) addition of a coco-coir mat and adult mussels. Coir mats consisted completely out of coconut fibre and are commonly used to prevent erosion of sediment and seeds on bare soil. The mats were applied by hand, fixated along the edges by digging it in to a depth of ~20 cm and in the middle by inserting 15-cm long biodegradable pins into the sediment. To increase sediment stability and deposition on the coir mat plots, we placed 128 knotted burlap balls (diameter ~10 cm) in each plot at regular distances underneath the mat that reduced water flow velocity between elevations of the balls.

Two-year-old alive mussels (shell length: 51.0 ± 1.0 mm; n=60) were obtained from a natural subtidal mussel bed by mechanical dredging and transported to the site in the beginning of May. Within two days after fishing, 25 circular mussel patches with a ~2.5-m diameter were created at regular distances from each other within each plot, yielding a total cover of around 30% (~2000 kg mussels/plot) – a cover comparable to natural intertidal mussel beds in the Wadden Sea (pers. observ.). Shells of the transplanted mussels were relatively clean with very low numbers of sessile epifauna such as barnacles, most likely due to predation by starfish in the subtidal area (Saier, 2001). In addition, no macroalgae were present on the mussels. The few crabs and starfishes found after dredging were mostly dead. Therefore, the possibility of co-transplanting relevant numbers of species to the experimental mussel plots was minimal.

The experiment lasted from the beginning of May until the beginning of August 2011. After 3 months, the average density of adult mussels within the patches was on Schiermonnikoog 1251 ± 70 mussels m^{-2} and on Terschelling 999 ± 85 mussels m^{-2}. On Schiermonnikoog mussel patches had a 21% cover of the macroalgae *Fucus vesiculosus*, while patches on Terschelling had a 96% cover of the macroalgae *Ulva lactuca*.

2.3. Sediment and benthos sampling

Sediment and benthos samples were collected in the beginning of August 2011. At each control plot, we randomly took sediment and benthos cores. At the coir mat and mussel plots, however, we sampled randomly in the space between the burlap balls and in the mussel patches, respectively. We pooled three 5-cm deep sediment cores with a PVC corer with an area of 7.1 cm^2. Sediment organic matter content in dried sediment (24 h, 70 °C) was estimated as weight Loss On Ignition (LOI; 5 h, 550 °C). Sediment samples were freeze-dried for up to 96 hours till dry. Prior to grain-size analysis, organic matter and carbonate were removed using HCl and H_2O_2. The samples were left overnight at 80 °C to speed up the reaction. Samples were measured in de-gassed Reversed Orsmosis water. Percentage silt (fraction < 63 μm) was determined using a Coulter LS 13 320 particle size analyzer using laser diffraction (780 nm) and PIDS (450 nm, 600 nm and 900 nm) technology. The optical module 'Gray' was used for calculations. Burial depth of the anti-erosion mats was determined with a ruler by 10 random measurements on each coir mat plot in areas without burlap balls. Depth values were averaged per plot afterwards. Two benthos samples were taken within each plot with a stainless steel core with an area of 179 cm^2 down to a depth of 20-25 cm. Samples were sieved over a 1 mm mesh and all fauna was fixed in 4% formalin solution in 2-L bottles for later analyses. In the laboratory, samples were stained with Rose Bengal (CAS 11121-48-5). All fauna were identified to species level and counted. Prior to data analyses, we pooled the two benthos samples and classified all species as either infauna or epifauna species in order to test for treatment effects on the infauna and epifauna community separately (Table S1 & S2).

2.4. Data analyses

To get an overview of the differences in the infaunal and epifaunal assemblages among sites and treatments, we first visualized the treatment effects with non-metric multidimensional scaling ordination models (nMDS) (Kruskall and Wish, 1978) based on the Bray-Curtis dissimilarity matrix (Clarke and Green, 1988). Multivariate analyses were performed on square root transformed data (i.e. for the epifauna data we used $\sqrt{(x+0.1)}$). Differences in the infaunal and epifaunal assemblages among sites and treatments were then analyzed with a distance-based permutational multivariable analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity measures (Anderson, 2001; McArdle and Anderson, 2001).

To further test for treatment effects on community structure, we determined species richness (number of species), species diversity (Shannon diversity index H'), feeding guild richness (number of feeding guilds), feeding guild diversity (Shannon diversity index H') for both the infaunal and epifaunal community. Feeding guilds were based on data extracted from online databases for marine invertebrates (Appeltans, et al., 2012; see Table S3 and S4 for guild list; MarLIN., 2006).

During model selection for the sediment conditions and community diversity, we first selected the best residual error distribution for each model (Gaussian, Poison and negative binomial distributions were tested) and subsequently tested for significance of the random effect 'Block' by analysing all models with generalized linear mixed-effects models (GLMM) and repeating them with generalized linear models (GLM). Models were selected based on AIC comparisons. After model fitting, normality of the residual distribution was checked for normality by using a Shapiro-Wilks test ($p = 0.05$). Both sediment organic matter and silt content were log-transformed to obtain normality of the residual distribution and three-way ANOVA models were used based on AIC comparisons. The model selection procedure also selected three-way ANOVA models for species richness, species diversity, feeding guild richness and feeding guild diversity for the infauna community and epifauna community. All statistical analyses were carried out in R (R Development Core Team 2013). PERMANOVA models and nMDS plots were constructed with the functions *adonis* and *metaMDS*, respectively, in the *vegan* package (Oksanen, et al., 2013). GLMMs and GLMs were constructed with the *glmmadmb* function in *glmmADMB* package (Fournier, et al., 2012). Three-way ANOVA models were constructed using the *aov* functions from the *Stats* package.

3. Results

3.1. Sediment conditions

Sediment organic matter content did not differ between the sites (F=0.05, n=12, p=0.83, Fig. 2A), but silt content was 1.2 times lower at Terschelling than at Schiermonnikoog (F=5.9, n=12, p=0.03, Fig. 2B). The addition of mussels increased organic matter content by 1.6 times (F=47.8, n=12, p<0.001, Fig. 2A) and doubled silt content (F=73.6, n=12, p<0.001, Fig. 2B). The coir mat did not significantly affect either organic matter (F=0.2, n=12, p=0.69, Fig. 2A) or silt content (F=0.0, n=12, p=0.97, Fig. 2B). The coir mat increased suspended sediment deposition, burying the mat under a thin layer of sand (Schiermonnikoog: 33±2 mm; Terschelling: 44±5 mm; mean±SE; n=6).

3.2. Infaunal community

PERMANOVA analyses revealed significant differences in the composition of the infaunal community depending on site, coir mat and mussel additions, which are visualized by nMDS ordination models (Table 2, Fig. 3A). The infauna species *Capitella capitata*, *Hediste* *diversicolor* and *Alitta succinea* were abundant in the mussel plots with and without the coir mat (Table S3). *Scoloplos armiger* was abundant in the control plots and in the coir mat plots and *Lanice conchilega* was abundant in the coir mat plots, mussel plots and in the plots with coir mat and mussels (Table S3). Eleven infaunal species were only found on Terschelling, while six species were exclusive to Schiermonnikoog (Table S3).

Infaunal species richness was significantly affected by coir mat, mussels and site (Fig. 4A, table 3). Species richness was around 1.6 times higher in the coir mat plots, the mussel plots and in the plots with both coir mat and mussels compared to the control plots. On Terschelling, the increase in species richness due to the addition of mussels was 1.9 times stronger than on Schiermonnikoog. Infaunal species diversity was significantly affected by coir mat and site (Fig. 4B; table 3). Diversity was 1.3 times higher in the coir mat plots compared to the plots without coir mats. Furthermore, species diversity was approximately 1.5 times higher on Schiermonnikoog compared to Terschelling, but only in plots without mussel additions. Mussel addition on Terschelling increased species diversity by 1.3 times compared to plots without mussels, while on Schiermonnikoog infaunal diversity was unaffected by mussel addition. Feeding guild richness was 1.5 times higher in the coir mat plots and in the mussel plots compared to the control plots (Fig. 4C; table 3). Feeding guild diversity was significantly affected by coir mat and mussel addition and by the interaction of mussel addition and site (Fig. 4D; table 3). Feeding guild diversity was around 1.5 times higher in the coir mat plots and in the mussel-addition plots compared to control plots. Guild diversity was 2 times higher in plots where both coir mat and mussels were added compared to control plots. On Terschelling, the increase in feeding guild diversity due to the addition of mussels was 1.7 times stronger than on Schiermonnikoog.

3.3. Epifaunal community

PERMANOVA analyses revealed clear differences in the composition of the epifauna community depending on mussel addition, which are visualized by nMDS ordination models (Table 2, Fig. 3B). The most abundant epifauna species (i.e. *Balanus crenatus*, *Carcinus maenus*, *Gammarus locusta* and *Mytilus edulis* spat) were strongly structured by mussel addition and site (Table S4). Four epifauna species were exclusive to Terschelling, while three species were only found on Schiermonnikoog (Table S4). Further analyses showed that epifauna species richness was significantly affected by mussels and site (Fig. 5A; table 3). Species richness was 14 times higher in the plots with mussel addition compared with plots without mussel additions. On Terschelling, the increase in species richness due to the addition of mussels was 1.4 times stronger than on Schiermonnikoog. Epifauna species diversity was also significantly affected by mussels (Fig. 5B; table 3). Species diversity was 1.1 times higher in the plots with mussel additions compared with the plots without mussel additions and the increase in species diversity due to the addition of mussels was 1.3 times stronger on Terschelling than on Schiermonnikoog. Furthermore, addition of mussels on top of the coir mats yielded a 1.2 times higher diversity compared to mussel plots on Terschelling, while on Schiermonnikoog, diversity in these plots was 1.1 times lower compared to mussel plots. Feeding guild richness was significantly affected by mussel addition (Fig. 5C; table 3), with 8 times higher values in the plots with mussels compared to the plots without mussels. Feeding guild diversity was 9.5 times higher in the plots with mussel addition compared to the plots without mussel addition (Fig. 5D; table 3). On Terschelling, the increase in guild diversity due to the addition of mussels was 2 times stronger than on Schiermonnikoog (Fig. 5D; table 3).

4. Discussion

In coastal soft-bottom systems, the direct physical removal of ecosystem engineers in combination with mechanical dredging activity itself can result in a reduced availability of hard substrate and stable sediment with potentially dramatic implications for the associated community (Ferns, et al., 2000; Piersma, et al., 2001; Thrush and Dayton, 2002; Thrush, et al., 1996). Here, we experimentally demonstrate that stable sediments and aboveground structure are two important properties of structure-providing organisms that facilitate distinctly different, and trophically more diverse, intertidal benthic communities.

Sediment stabilization through the application of anti-erosion coir mats stimulated the development of the infaunal community by increasing species and trophic diversity. The mats prevented erosion and increased suspended sediment deposition, burying the mats under a 33-mm layer of sand (van der Heide, et al., 2014). Moreover, as we did not detect any changes in sediment organic matter and silt content, these results suggest that sediment stabilization, rather than sediment composition, enhanced diversity. Depending on location, the addition of mussels slightly increased infaunal diversity or had no effect at all. However, this treatment did cause a shift in infaunal species composition, probably due to deposition of faeces and pseudofaeces (Kautsky and Evans, 1987; Pearson and Rosenberg, 1978; Ragnarsson and Raffaelli, 1999). Furthermore, the addition of adult mussels strongly stimulated the development of the epifaunal community by increasing epifaunal species and trophic diversity, most likely due to the availability of substrate (Gutierrez, et al., 2003; Norling and Kautsky, 2007; Thiel and Dernedde, 1994). The effects of mussel addition on species richness are consistent with previous experimental studies in intertidal soft-bottom systems (Beadman, et al., 2004; Kochmann, et al., 2008; Norling and Kautsky, 2007; Ragnarsson and Raffaelli, 1999). However, by including more functionally-informative metrics of community structure, we show that mussel addition not only influences the benthic community structure by species enrichment, but also by enhancing the number and diversity of feeding guilds. This suggests that by sustaining more or different species and feeding guilds, stable sediments and mussel beds have the potential to alter the number and strength of biotic interactions among species such as predation and competition, thereby affecting overall ecosystem functioning.

Despite the environmental background differences between the communities of the western (Terschelling) and eastern (Schiermonnikoog) Dutch Wadden Sea, the overall effects of our treatments were similar. Nevertheless, the positive effect size of the mussel treatments on the infaunal and epifaunal community was significantly larger at Terschelling. These more pronounced positive effects on the more exposed and sandy site of Terschelling supports the idea that facilitation by ecosystem engineers becomes more important when environmental stress increases (Bertness and Callaway, 1994; Bruno, et al., 2003; Crain and Bertness, 2006). Mussels affect the infaunal community mainly by increasing substrate cohesiveness and reducing hydrodynamic stress (reviewed by Widdows and Brinsley, 2002), resulting in more suitable substrate for larval settlement (Commito, et al., 2005), which seems particularly important at the exposed site of Terschelling. The epifaunal community, on the other hand, is most strongly affected by mussels through provision of aboveground attachment substrate, and shelter from water movement and desiccation (e.g. Stephens and Bertness, 1991; Thiel and Dernedde, 1994). Also these effects are likely more important at Terschelling than at Schiermonnikoog. The differential site effect on the epifaunal community is probably further enhanced by the much higher coverage of epibenthic macroalgae (*Ulva lactuca*) at Terschelling that profit from the relatively high water clarity at this site. These algae, that are attached to the mussels, further increase habitat complexity, but may also serve as an additional food source (e.g. Goecker and Kall, 2003).

Although it has been widely acknowledged that the loss of ecosystem engineers caused a loss of associated species and a homogenization of the Wadden Sea landscape (Lotze, 2005; Reise, 2005; Reise, et al., 1989), the actual consequences for the trophic structure of the intertidal soft-bottom community remained largely unclear. Our results show that structure-providing and sediment-stabilizing ecosystem engineers such as mussels, but likely also engineering effects generated by seagrasses, tube-worms and oysters (Friedrichs, et al., 2000; Gutierrez, et al., 2003; Orth, 1977; Volkenborn, et al., 2009; Widdows, et al., 1998) may strongly affect the trophic structure of the intertidal benthic community by increasing the number and diversity of feeding guilds. This suggests that ecosystem engineers may form the foundation for a trophically diverse ecosystem and illustrates the importance of protecting and restoring them.

Our findings can have important implications for ecosystem-based management and large-scale restoration strategies of intertidal soft-bottom ecosystems. We suggest that the loss of stable sediments and substrates, caused by removal of ecosystem engineers or mechanical dredging, will negatively affect the trophic structure of the benthic community of the Wadden Sea. This study contributes to the growing awareness that the use of facilitative interactions is important in conservation efforts and that ecosystem engineers should be considered as one of the first target species for conservation (Boogert, et al., 2006; Byers, et al., 2006; Crain and Bertness, 2006).

Acknowledgements

We thank Natuurmonumenten, Staatsbosbeheer and many volunteers for their help with setting up the experiment. This study was carried out within project 'Waddensleutels', funded by the 'Waddenfonds'. In addition, EZ, SD and BKE were financially supported by grant 839.08.310 of the NWO-ZKO programme.

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Tables

Table 1. Description of environmental conditions for the site in the western part of the Dutch Wadden Sea (Terschelling) and for the site in the eastern part (Schiermonnikoog). For each site, we obtained sediment silt and organic matter content, tidal elevation and amplitude, diffuse light attenuation, particulate organic carbon and chlorophyll concentration of the water, maximum current velocity, orbital velocity (with NW and W wind direction) and average fetch length. Light attenuation, particulate organic carbon and cholorphyll concentrations were calculated over the monthly composites of May, June and July 2011 from the Modis Ocean satellite.

	West Terschelling	**East Schiermonnikoog**
Silt content (%<63µm)	2.3	3.0
Sediment organic matter content (%)	0.58	0.64
Elevation (m NAP)	-0.8	-0.6
Tidal amplitude (m)	0.9	1.2
Diffuse light attenuation at 490nm (m^{-1})	0.58	1.03
Particulate organic carbon (mg/m^3)	552.33	893.90
Chlorophyll concentration (mg/m^3)	8.76	14.85
Maximum current velocity (ms^{-1})	0.55	0.60
Wave action - Orbital velocity (ms^{-1}) NW	0.21	0.14
Wave action - Orbital velocity (ms^{-1}) W	0.32	0.25
Average fetch length (km)	29.9	9.3

Table 2. F-values and significance levels of PERMANOVA based on Bray-Curtis dissimilarities for treatment effects on the infauna and epifauna community. Significance levels: * p<0.05, ** p<0.01, *** p<0.001. Degrees of freedom: 24 in total; 16 residual.

Treatments	**Infauna**	**Epifauna**
Coir	3.4 (*)	1.4
Mussels	20.1 (***)	85.5 (***)
Site	9.7 (***)	2.3
Coir × Mussels	1.8	1.4
Coir × Site	1.4	2.1
Mussels × Site	1.5	1.9
Coir × Muss. × Site	0.7	1.8

Table 3. F-values and significance levels of all treatments and their interactions for species richness (S), species diversity (H'), feeding guild richness (F_S) and feeding guild diversity (F_H') of the infauna and epifauna community. Significance levels: * p<0.05, ** p<0.01, *** p<0.001. Degrees of freedom: 24 in total; 16 residual.

	Infauna				**Epifauna**			
Treatments	**S**	**H'**	**F_S**	**F_H'**	**S**	**H'**	**F_S**	**F_H'**
Coir	8.1 (*)	23.4 (***)	4.0	18.2 (***)	2.6	1.8	2.3	1.7
Mussels	13.1 (**)	2.3	4.0	6.0 (*)	243.4 (***)	43.0 (***)	168.1 (***)	73.7 (***)
Site	9.6 (**)	18.8 (***)	2.3	2.5	16.0 (**)	1.5	2.3	1.9
Coir × Mussels	11.3 (**)	4.2	9.0 (**)	0.0	0	1.0	0.8	0.9
Coir × Site	0.6	0.1	0.3	0.4	0.2	0.9	0.1	0.4
Mussels × Site	17.1 (***)	34.9 (***)	2.3	7.3 (*)	10.2 (**)	9.0 (**)	0.1	4.5 (*)
Coir × Muss. × Site	0.1	0.3	0.3	3.1	0.2	3.9(*)	0.1	1.9

Figure legends

Figure 1. Map with locations of the experimental plots in the western Dutch Wadden Sea at Terschelling and in the eastern Dutch Wadden Sea at Schiermonnikoog (black squares). White areas represent water, intermediate gray areas represent tidal flats exposed during low tide and land is represented by dark gray.

Figure 2. Organic matter (**A**) and silt content (**B**) for each treatment (Mean ± SE, n = 3).

Figure 3. Non-metric multi-dimensional scaling (nMDS) for differences among treatments for the infauna (**A**) and epifauna (**B**) community. Coir mat and mussel treatments are represented by the darkgrey polygons, sites by the lightgrey polygons and samples by the white circles (CTR=Control, C=Coir, M=Mussel, C*M=Coir*Mussel, WEST=Terschelling, EAST=Schiermonnikoog). A stress value below 0.2 indicates a reliable ordination.

Figure 4. Treatment effects on species richness (**A**), species diversity (**B**), feeding guild richness (**C**) and feeding guild diversity (**D**) of the infauna community (Mean ± SE, n=3). ‘

Figure 5. Treatment effects on species richness (**A**), species diversity (**B**), feeding guild richness (**C**) and feeding guild diversity (**D**) of the epifauna community (Mean ± SE, n=3).

Figure 1
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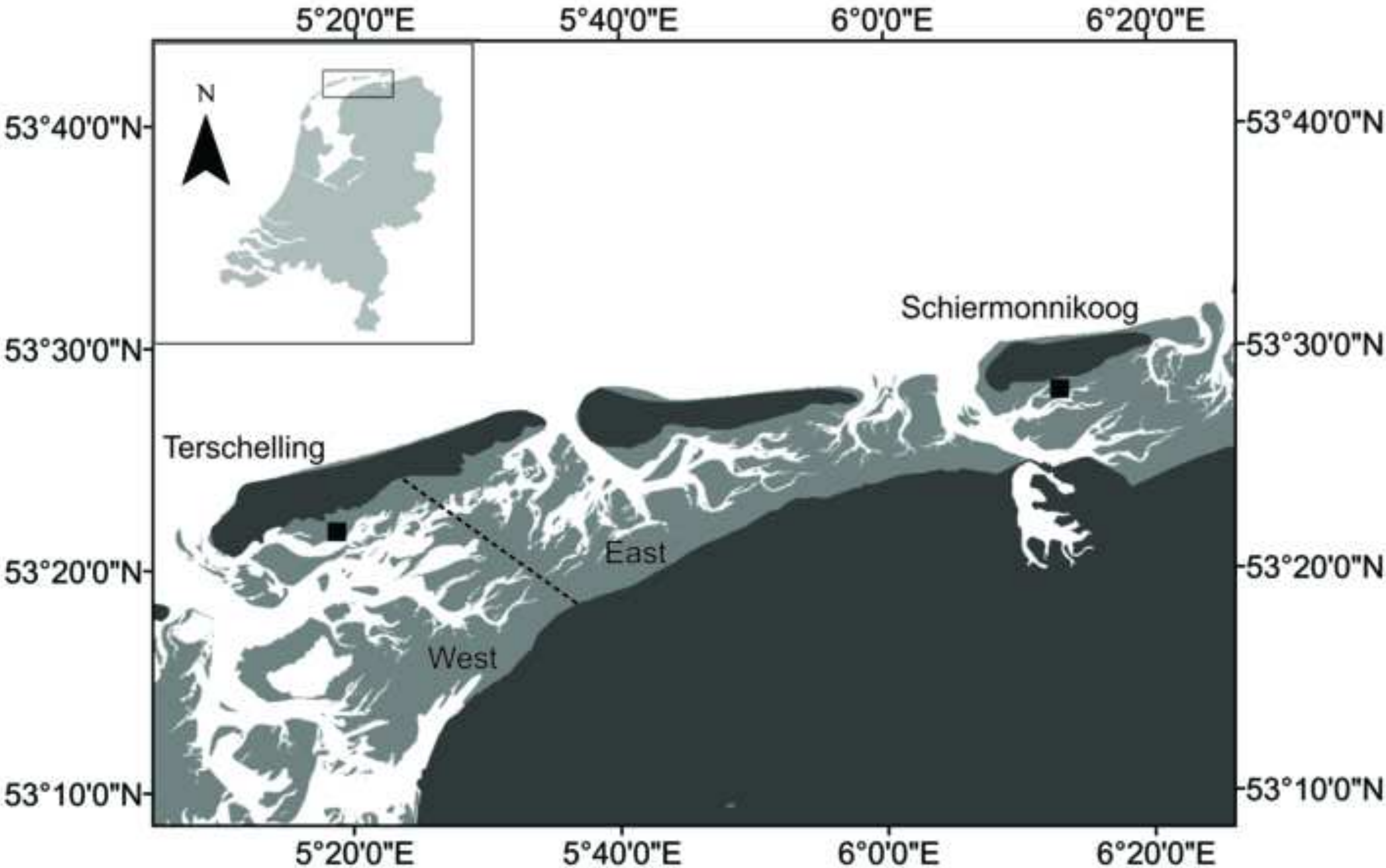

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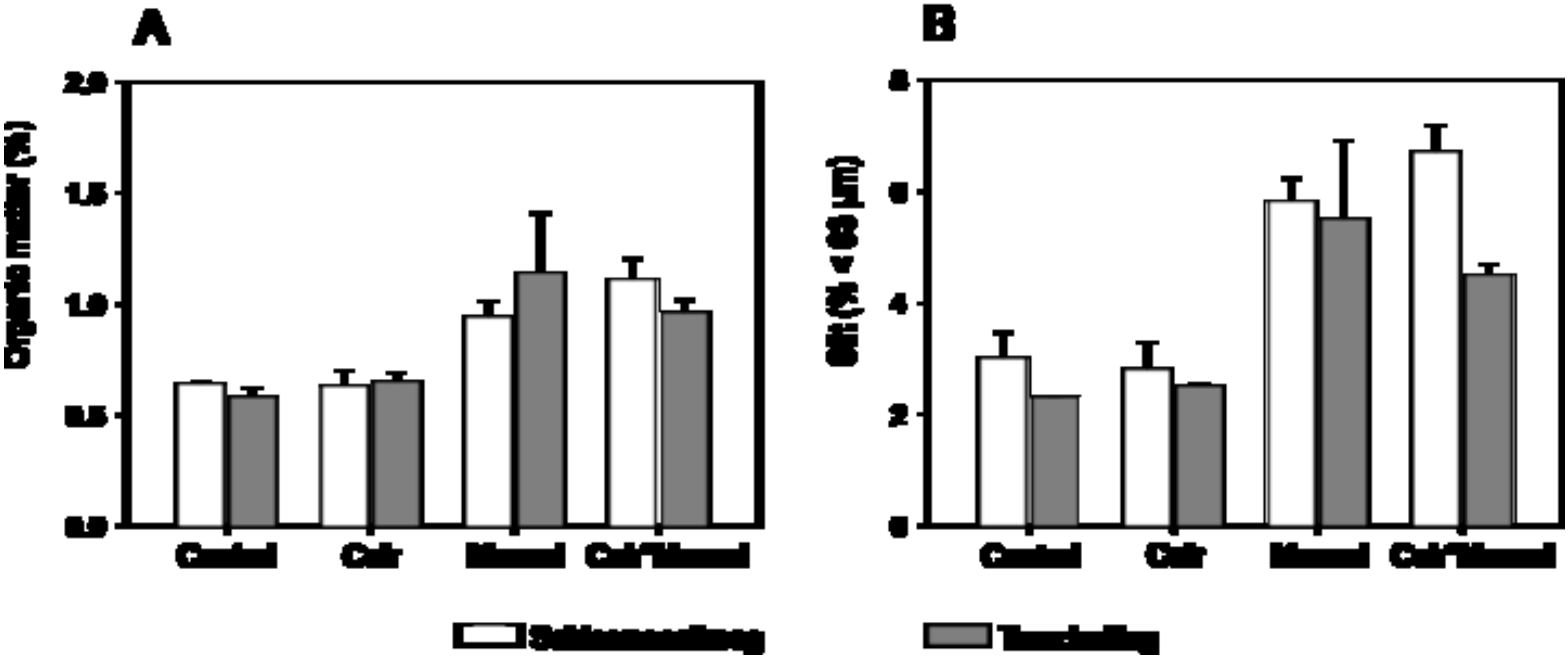

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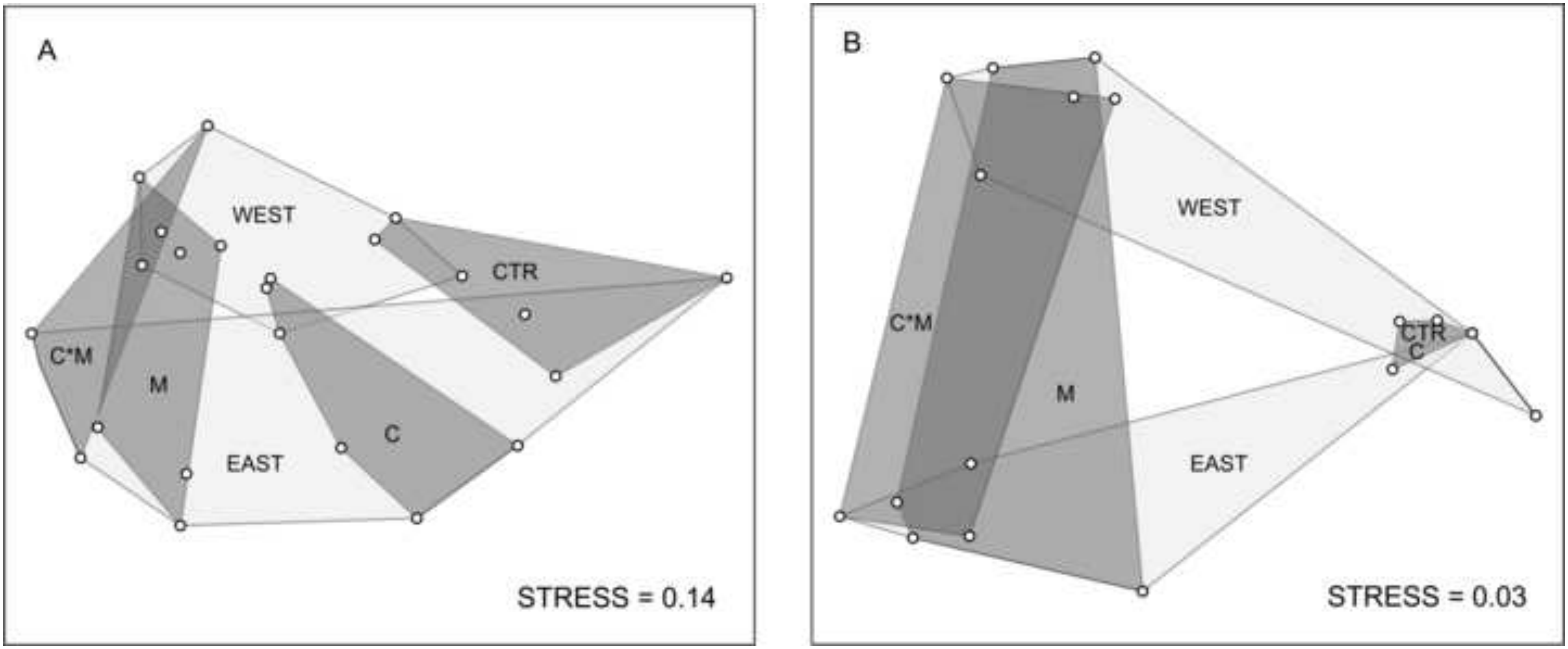

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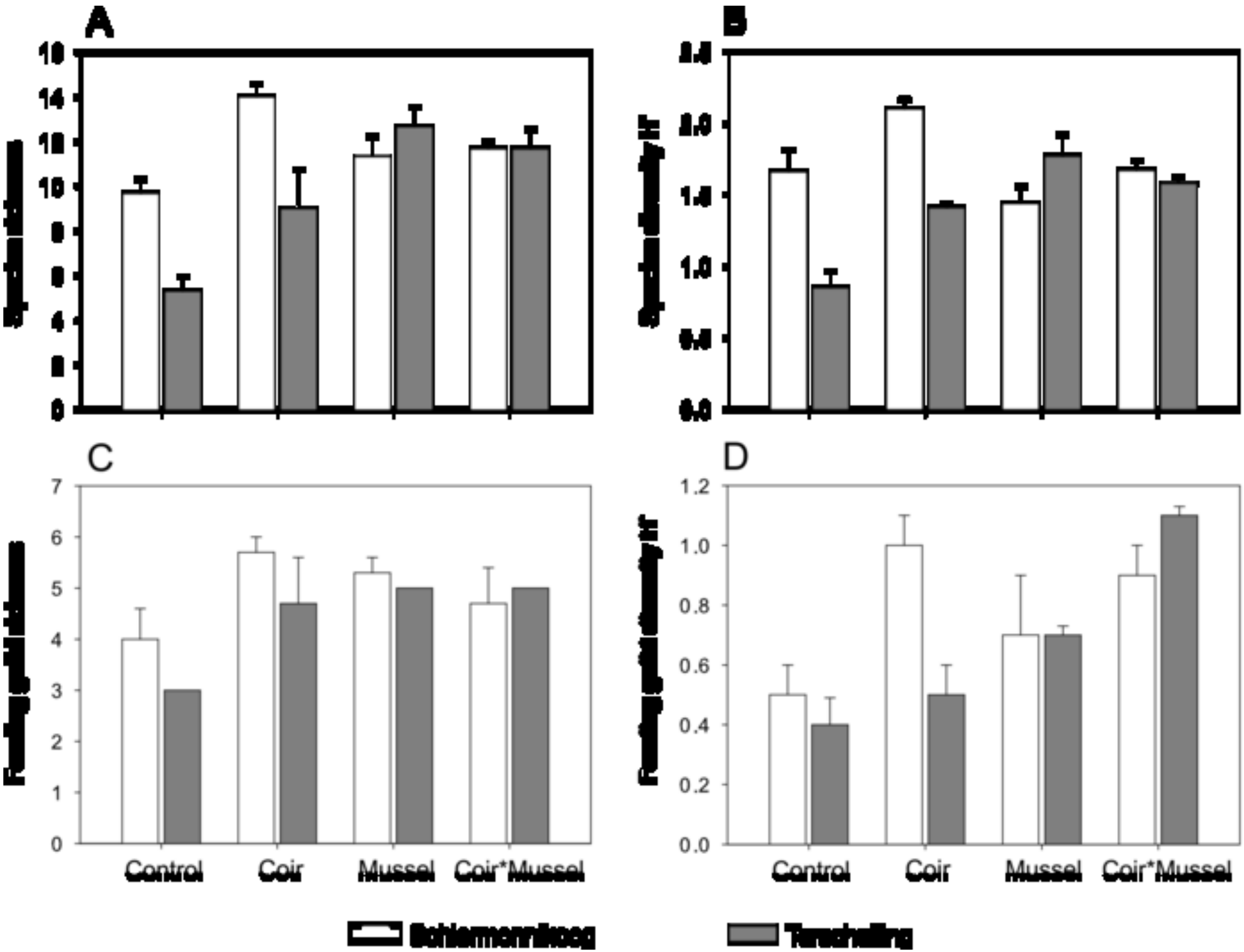

Figure 5

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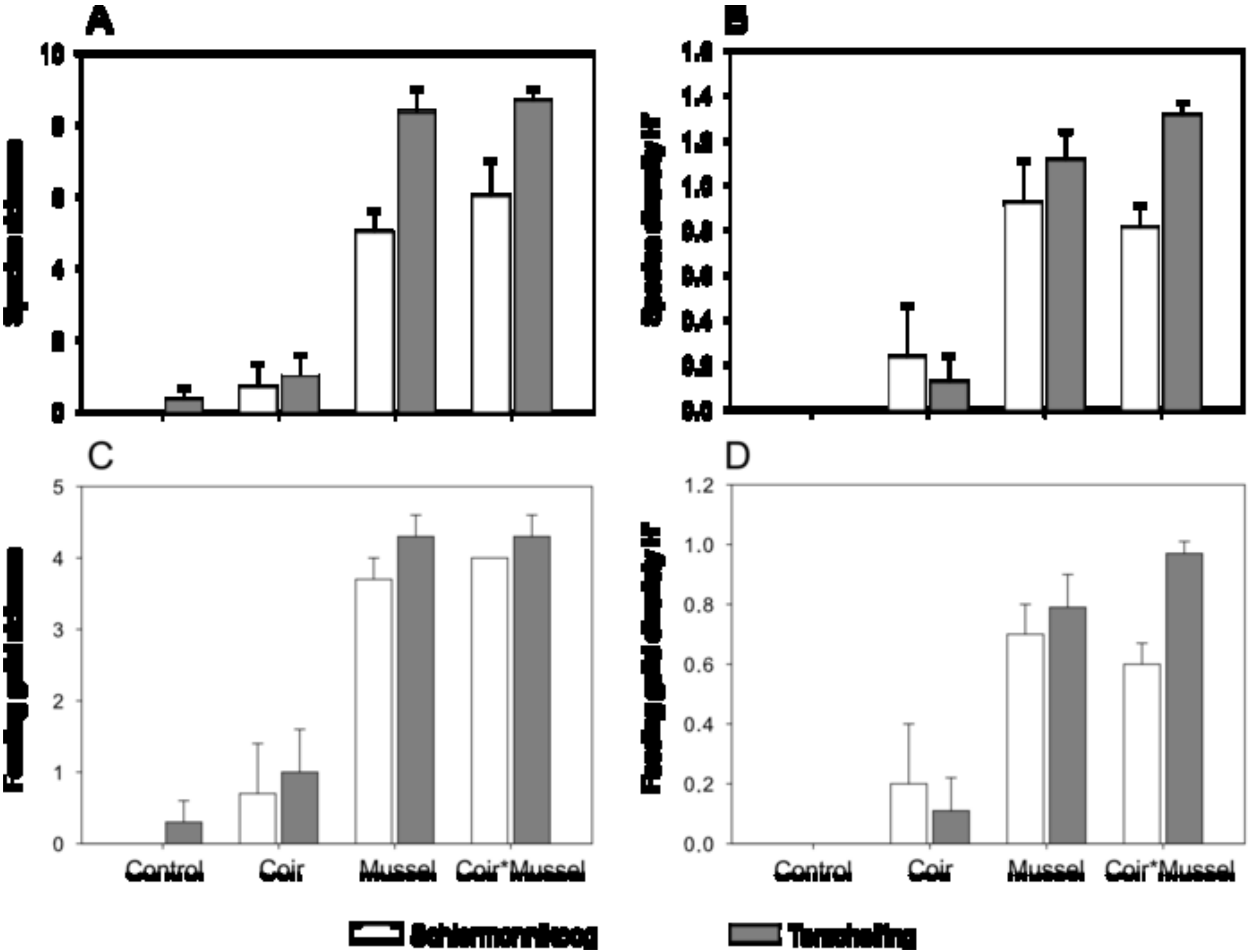

Supplementary Material

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