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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.

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

3
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23

24 **Abstract**

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

45

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47 *edulis*, Wadden Sea

48 **Introduction**

49 Coastal ecosystems are of great importance to a multitude of marine species and provide crucial
50 services to human society (Barbier, et al., 2011; Beck, et al., 2001; Costanza, et al., 1997;
51 Hodgson and Liebeler, 2002). Ecosystem engineers, species that strongly modify their
52 environment, such as reef-building bivalves, seagrasses and corals (Jones, et al., 1994; 1997),
53 typically play an important role within these ecosystems, because they diversify the landscape by
54 forming complex structures and relieve environmental stress, for instance by attenuating currents
55 and waves (Donadi, et al., 2013; Gutierrez, et al., 2003; Koch, et al., 2009). Due to these habitat
56 modifications, ecosystem engineers typically not only facilitate themselves (Rietkerk, et al.,
57 2004; van de Koppel, et al., 2005; van der Heide, et al., 2007), but also provide a key-habitat for
58 a wide variety of species that depend on them for settlement, refuge or food supply (e.g.
59 Gutierrez, et al., 2003; Nagelkerken, et al., 2000; van der Zee, et al., 2012).

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

72 (i.e. feeding guild richness and diversity) of the benthic community in intertidal soft-bottom
73 ecosystems.

74 In this study, we empirically test the hypothesis that recovery of aboveground biotic
75 structure and stable sediments facilitates distinctly different, but trophically more diverse
76 intertidal benthic communities, using intertidal mussel beds as a model system. In the Dutch part
77 of the Wadden Sea, one of the world's largest intertidal ecosystems (Compton, et al., 2013;
78 Wolff, 1983), intertidal mussels – ecosystem engineers that create hard substrate, reduce
79 hydrodynamic stress, modify sediment conditions and increase the cohesiveness of the substrata
80 (Donadi, et al., 2013; Gutierrez, et al., 2003; Kröncke, 1996; Widdows and Brinsley, 2002) –
81 covered an area of over 4000 ha at the end of the 1970s. In the beginning of the 1990s, however,
82 intertidal mussel beds disappeared completely due to a combination of overfishing, storms and
83 several years of recruitment failure (Beukema and Cadée, 1996; Dijkema, 1991). In addition to
84 the direct physical removal of mussels, sand extraction and bottom trawling for shrimps
85 (*Crangon crangon*) and edible cockles (*Cerastoderma edule*) also removed sediment-stabilizing
86 species and resuspended the upper layer of the sediment (Kraan, et al., 2007; Piersma, et al.,
87 2001; e.g. Riesen and Reise, 1982; van der veer, et al., 1985). Despite a ban on mechanical
88 dredging for intertidal mussels (1999) and cockles (2005), it took more than a decade for mussels
89 to start to re-establish and even now their recovery is still mainly restricted to the eastern part of
90 the Dutch Wadden Sea (Ens, et al., 2009; Goudswaard, et al., 2009).

91 To test our hypotheses, we constructed a large-scale experiment, in which we crossed the
92 application of anti-erosion mats with the addition of adult mussels to test for the effects of
93 sediment stabilisation and biotic structure. To investigate whether the treatment effects were
94 consistent across our study system, the experiment was carried out at two different sites with
95 distinctly different conditions and ambient benthic communities (Compton, et al., 2013). The first

96 site was located in the western part of the Dutch Wadden Sea, south of the island Terschelling,
97 and the second was situated in the eastern part of the Dutch Wadden Sea, south of the island
98 Schiermonnikoog. After three months, we investigated treatment effects on the invertebrate
99 community.

100

101 **2. Methods**

102 **2.1. Study area**

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

115

116 **2.2. Experimental design**

117 At each site, 12 plots of 20×20 m were established in a line parallel to the gully (distance from
118 the gully ~100-150 m) and with a distance of ~20 m between plots. Plots were divided over three

119 blocks. Within each block, we randomly assigned one replicate of each of the following
120 treatments to the plots: (1) control, (2) addition of a coco-coir mat on the sediment surface to
121 stabilize the sediment, (3) addition of adult mussels to create biotic structure, and (4) addition of
122 a coco-coir mat and adult mussels. Coir mats consisted completely out of coconut fibre and are
123 commonly used to prevent erosion of sediment and seeds on bare soil. The mats were applied by
124 hand, fixated along the edges by digging it in to a depth of ~20 cm and in the middle by inserting
125 15-cm long biodegradable pins into the sediment. To increase sediment stability and deposition
126 on the coir mat plots, we placed 128 knotted burlap balls (diameter ~10 cm) in each plot at
127 regular distances underneath the mat that reduced water flow velocity between elevations of the
128 balls.

129 Two-year-old alive mussels (shell length: 51.0 ± 1.0 mm; $n=60$) were obtained from a
130 natural subtidal mussel bed by mechanical dredging and transported to the site in the beginning of
131 May. Within two days after fishing, 25 circular mussel patches with a ~2.5-m diameter were
132 created at regular distances from each other within each plot, yielding a total cover of around
133 30% (~2000 kg mussels/plot) – a cover comparable to natural intertidal mussel beds in the
134 Wadden Sea (pers. observ.). Shells of the transplanted mussels were relatively clean with very
135 low numbers of sessile epifauna such as barnacles, most likely due to predation by starfish in the
136 subtidal area (Saier, 2001). In addition, no macroalgae were present on the mussels. The few
137 crabs and starfishes found after dredging were mostly dead. Therefore, the possibility of co-
138 transplanting relevant numbers of species to the experimental mussel plots was minimal.

139 The experiment lasted from the beginning of May until the beginning of August 2011.
140 After 3 months, the average density of adult mussels within the patches was on Schiermonnikoog
141 1251 ± 70 mussels m^{-2} and on Terschelling 999 ± 85 mussels m^{-2} . On Schiermonnikoog mussel

142 patches had a 21% cover of the macroalgae *Fucus vesiculosus*, while patches on Terschelling had
143 a 96% cover of the macroalgae *Ulva lactuca*.

144

145 **2.3. Sediment and benthos sampling**

146 Sediment and benthos samples were collected in the beginning of August 2011. At each control
147 plot, we randomly took sediment and benthos cores. At the coir mat and mussel plots, however,
148 we sampled randomly in the space between the burlap balls and in the mussel patches,
149 respectively. We pooled three 5-cm deep sediment cores with a PVC corer with an area of 7.1
150 cm². Sediment organic matter content in dried sediment (24 h, 70 °C) was estimated as weight
151 Loss On Ignition (LOI; 5 h, 550 °C). Sediment samples were freeze-dried for up to 96 hours till
152 dry. Prior to grain-size analysis, organic matter and carbonate were removed using HCl and
153 H₂O₂. The samples were left overnight at 80 °C to speed up the reaction. Samples were measured
154 in de-gassed Reversed Osmosis water. Percentage silt (fraction < 63 µm) was determined using a
155 Coulter LS 13 320 particle size analyzer using laser diffraction (780 nm) and PIDS (450 nm, 600
156 nm and 900 nm) technology. The optical module ‘Gray’ was used for calculations. Burial depth
157 of the anti-erosion mats was determined with a ruler by 10 random measurements on each coir
158 mat plot in areas without burlap balls. Depth values were averaged per plot afterwards. Two
159 benthos samples were taken within each plot with a stainless steel core with an area of 179 cm²
160 down to a depth of 20-25 cm. Samples were sieved over a 1 mm mesh and all fauna was fixed in
161 4% formalin solution in 2-L bottles for later analyses. In the laboratory, samples were stained
162 with Rose Bengal (CAS 11121-48-5). All fauna were identified to species level and counted.
163 Prior to data analyses, we pooled the two benthos samples and classified all species as either
164 infauna or epifauna species in order to test for treatment effects on the infauna and epifauna
165 community separately (Table S1 & S2).

166

167 **2.4. Data analyses**

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

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

182 During model selection for the sediment conditions and community diversity, we first
183 selected the best residual error distribution for each model (Gaussian, Poisson and negative
184 binomial distributions were tested) and subsequently tested for significance of the random effect
185 'Block' by analysing all models with generalized linear mixed-effects models (GLMM) and
186 repeating them with generalized linear models (GLM). Models were selected based on AIC
187 comparisons. After model fitting, normality of the residual distribution was checked for
188 normality by using a Shapiro-Wilks test ($p = 0.05$). Both sediment organic matter and silt content
189 were log-transformed to obtain normality of the residual distribution and three-way ANOVA

190 models were used based on AIC comparisons. The model selection procedure also selected three-
191 way ANOVA models for species richness, species diversity, feeding guild richness and feeding
192 guild diversity for the infauna community and epifauna community. All statistical analyses were
193 carried out in R (R Development Core Team 2013). PERMANOVA models and nMDS plots
194 were constructed with the functions *adonis* and *metaMDS*, respectively, in the *vegan* package
195 (Oksanen, et al., 2013). GLMMs and GLMs were constructed with the *glmmadmb* function in
196 *glmmADMB* package (Fournier, et al., 2012). Three-way ANOVA models were constructed using
197 the *aov* functions from the *Stats* package.

198

199 **3. Results**

200 **3.1. Sediment conditions**

201 Sediment organic matter content did not differ between the sites ($F=0.05$, $n=12$, $p=0.83$, Fig. 2A),
202 but silt content was 1.2 times lower at Terschelling than at Schiermonnikoog ($F=5.9$, $n=12$,
203 $p=0.03$, Fig. 2B). The addition of mussels increased organic matter content by 1.6 times ($F=47.8$,
204 $n=12$, $p<0.001$, Fig. 2A) and doubled silt content ($F=73.6$, $n=12$, $p<0.001$, Fig. 2B). The coir mat
205 did not significantly affect either organic matter ($F=0.2$, $n=12$, $p=0.69$, Fig. 2A) or silt content
206 ($F=0.0$, $n=12$, $p=0.97$, Fig. 2B). The coir mat increased suspended sediment deposition, burying
207 the mat under a thin layer of sand (Schiermonnikoog: 33 ± 2 mm; Terschelling: 44 ± 5 mm;
208 mean \pm SE; $n=6$).

209

210 **3.2. Infaunal community**

211 PERMANOVA analyses revealed significant differences in the composition of the infaunal
212 community depending on site, coir mat and mussel additions, which are visualized by nMDS
213 ordination models (Table 2, Fig. 3A). The infauna species *Capitella capitata*, *Hediste*

214 *diversicolor* and *Alitta succinea* were abundant in the mussel plots with and without the coir mat
215 (Table S3). *Scoloplos armiger* was abundant in the control plots and in the coir mat plots and
216 *Lanice conchilega* was abundant in the coir mat plots, mussel plots and in the plots with coir mat
217 and mussels (Table S3). Eleven infaunal species were only found on Terschelling, while six
218 species were exclusive to Schiermonnikoog (Table S3).

219 Infaunal species richness was significantly affected by coir mat, mussels and site (Fig.
220 4A, table 3). Species richness was around 1.6 times higher in the coir mat plots, the mussel plots
221 and in the plots with both coir mat and mussels compared to the control plots. On Terschelling,
222 the increase in species richness due to the addition of mussels was 1.9 times stronger than on
223 Schiermonnikoog. Infaunal species diversity was significantly affected by coir mat and site (Fig.
224 4B; table 3). Diversity was 1.3 times higher in the coir mat plots compared to the plots without
225 coir mats. Furthermore, species diversity was approximately 1.5 times higher on
226 Schiermonnikoog compared to Terschelling, but only in plots without mussel additions. Mussel
227 addition on Terschelling increased species diversity by 1.3 times compared to plots without
228 mussels, while on Schiermonnikoog infaunal diversity was unaffected by mussel addition.
229 Feeding guild richness was 1.5 times higher in the coir mat plots and in the mussel plots
230 compared to the control plots (Fig. 4C; table 3). Feeding guild diversity was significantly affected
231 by coir mat and mussel addition and by the interaction of mussel addition and site (Fig. 4D; table
232 3). Feeding guild diversity was around 1.5 times higher in the coir mat plots and in the mussel-
233 addition plots compared to control plots. Guild diversity was 2 times higher in plots where both
234 coir mat and mussels were added compared to control plots. On Terschelling, the increase in
235 feeding guild diversity due to the addition of mussels was 1.7 times stronger than on
236 Schiermonnikoog.

237

238 3.3. Epifaunal community

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

260

261

262 **4. Discussion**

263 In coastal soft-bottom systems, the direct physical removal of ecosystem engineers in
264 combination with mechanical dredging activity itself can result in a reduced availability of hard
265 substrate and stable sediment with potentially dramatic implications for the associated
266 community (Ferns, et al., 2000; Piersma, et al., 2001; Thrush and Dayton, 2002; Thrush, et al.,
267 1996). Here, we experimentally demonstrate that stable sediments and aboveground structure are
268 two important properties of structure-providing organisms that facilitate distinctly different, and
269 trophically more diverse, intertidal benthic communities.

270 Sediment stabilization through the application of anti-erosion coir mats stimulated the
271 development of the infaunal community by increasing species and trophic diversity. The mats
272 prevented erosion and increased suspended sediment deposition, burying the mats under a 33-mm
273 layer of sand (van der Heide, et al., 2014). Moreover, as we did not detect any changes in
274 sediment organic matter and silt content, these results suggest that sediment stabilization, rather
275 than sediment composition, enhanced diversity. Depending on location, the addition of mussels
276 slightly increased infaunal diversity or had no effect at all. However, this treatment did cause a
277 shift in infaunal species composition, probably due to deposition of faeces and pseudofaeces
278 (Kautsky and Evans, 1987; Pearson and Rosenberg, 1978; Ragnarsson and Raffaelli, 1999).
279 Furthermore, the addition of adult mussels strongly stimulated the development of the epifaunal
280 community by increasing epifaunal species and trophic diversity, most likely due to the
281 availability of substrate (Gutierrez, et al., 2003; Norling and Kautsky, 2007; Thiel and Darnedde,
282 1994). The effects of mussel addition on species richness are consistent with previous
283 experimental studies in intertidal soft-bottom systems (Beadman, et al., 2004; Kochmann, et al.,
284 2008; Norling and Kautsky, 2007; Ragnarsson and Raffaelli, 1999). However, by including more
285 functionally-informative metrics of community structure, we show that mussel addition not only

286 influences the benthic community structure by species enrichment, but also by enhancing the
287 number and diversity of feeding guilds. This suggests that by sustaining more or different species
288 and feeding guilds, stable sediments and mussel beds have the potential to alter the number and
289 strength of biotic interactions among species such as predation and competition, thereby affecting
290 overall ecosystem functioning.

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

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

320 Our findings can have important implications for ecosystem-based management and
321 large-scale restoration strategies of intertidal soft-bottom ecosystems. We suggest that the loss of
322 stable sediments and substrates, caused by removal of ecosystem engineers or mechanical
323 dredging, will negatively affect the trophic structure of the benthic community of the Wadden
324 Sea. This study contributes to the growing awareness that the use of facilitative interactions is
325 important in conservation efforts and that ecosystem engineers should be considered as one of the
326 first target species for conservation (Boogert, et al., 2006; Byers, et al., 2006; Crain and Bertness,
327 2006).

328

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333 the NWO-ZKO programme.

334

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- 520

1 **Tables**

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

	West Terschelling	East Schiermonnikoog
Silt content (%<63 μ m)	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

10

11 **Table 2.** F-values and significance levels of PERMANOVA based on Bray-Curtis
12 dissimilarities for treatment effects on the infauna and epifauna community. Significance
13 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 \times Mussels	1.8	1.4
Coir \times Site	1.4	2.1
Mussels \times Site	1.5	1.9
Coir \times Muss. \times Site	0.7	1.8

14

15

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

Treatments	Infauna				Epifauna			
	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

20

21

1 **Figure legends**

2

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

7

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

9

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

15

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

18

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

21

22

Figure 1
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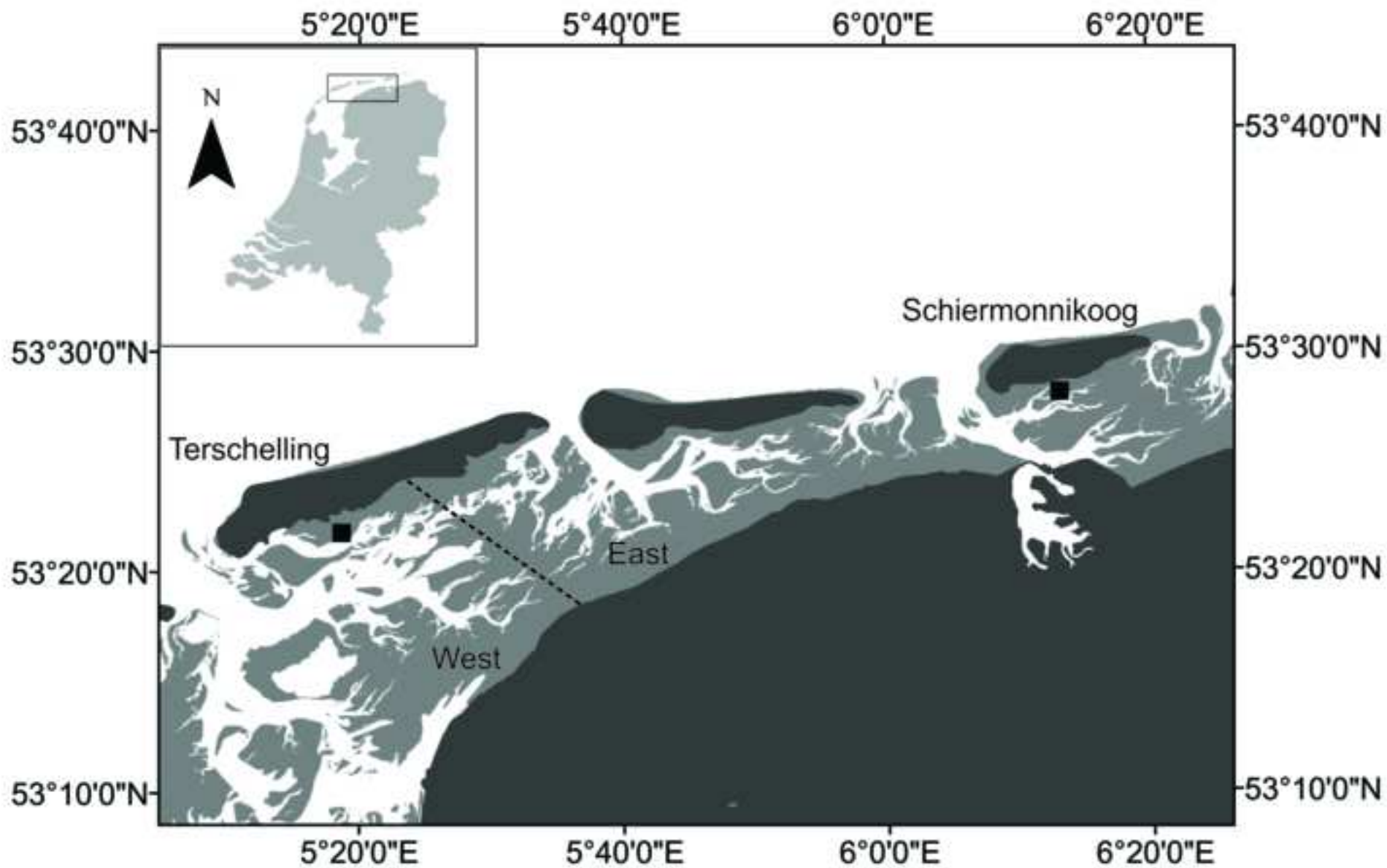


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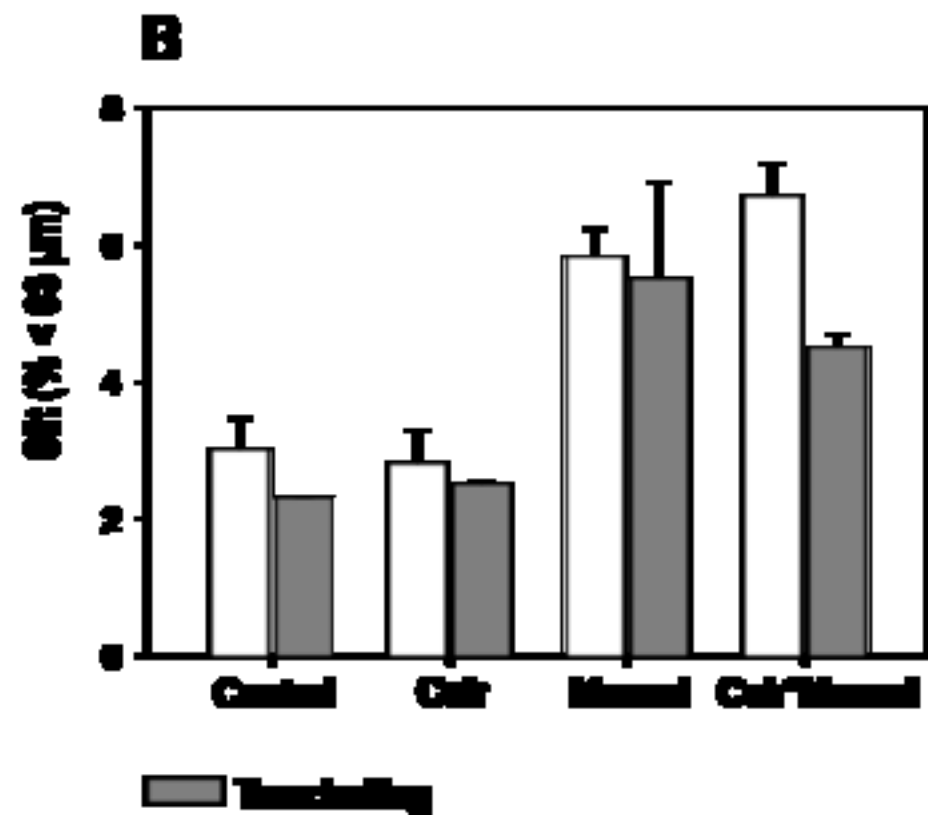
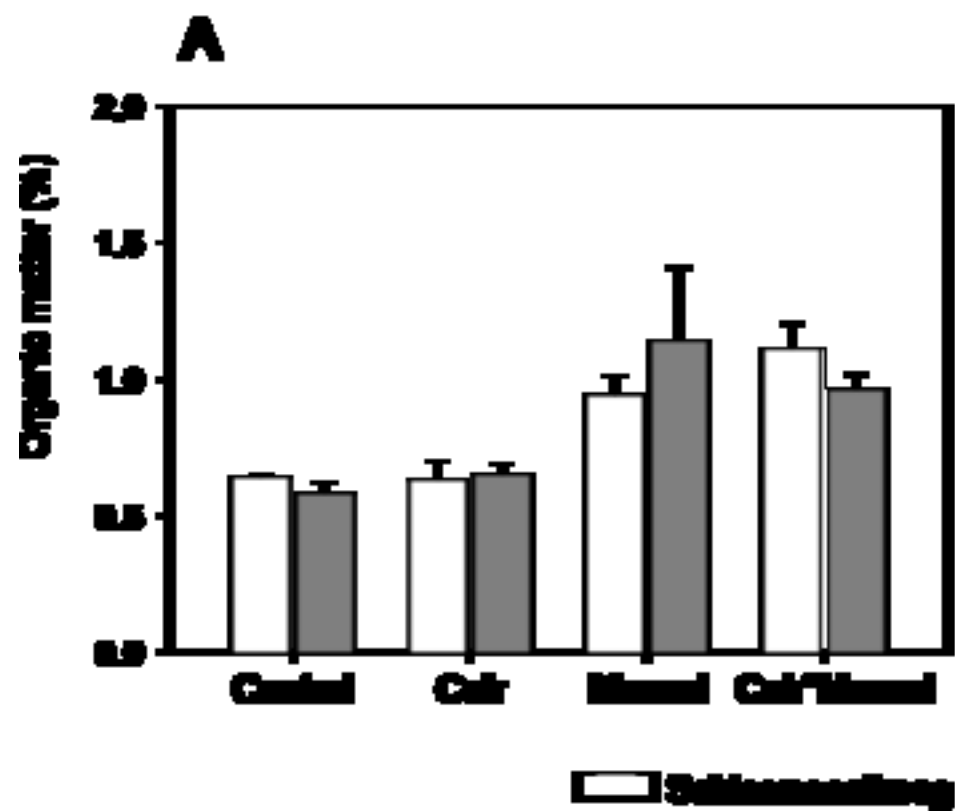


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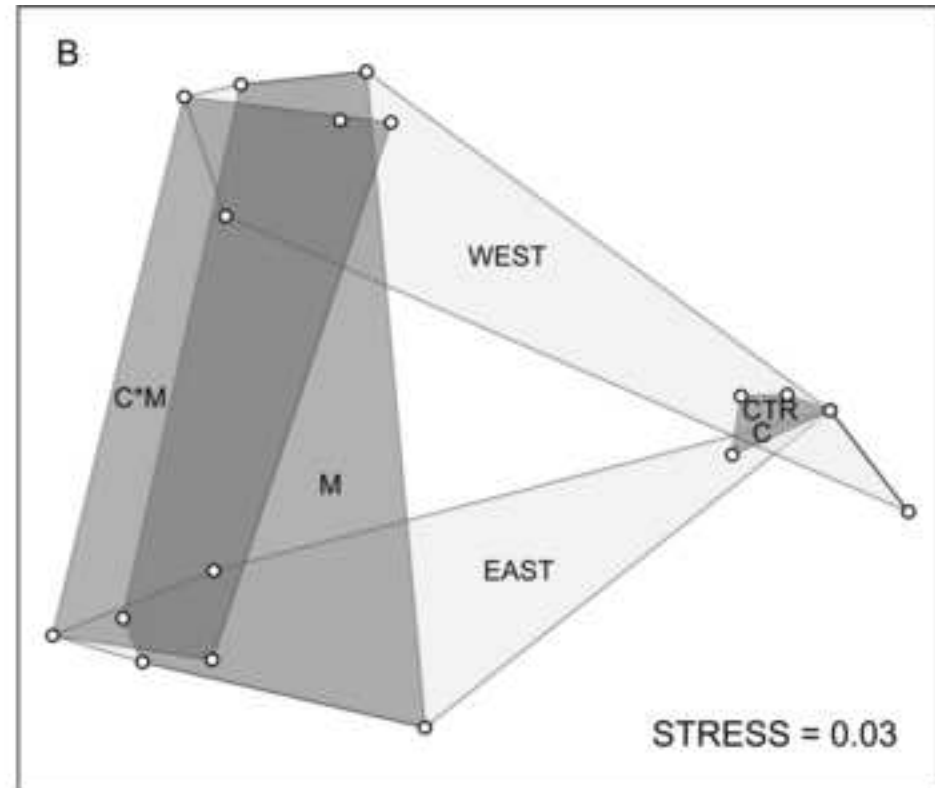
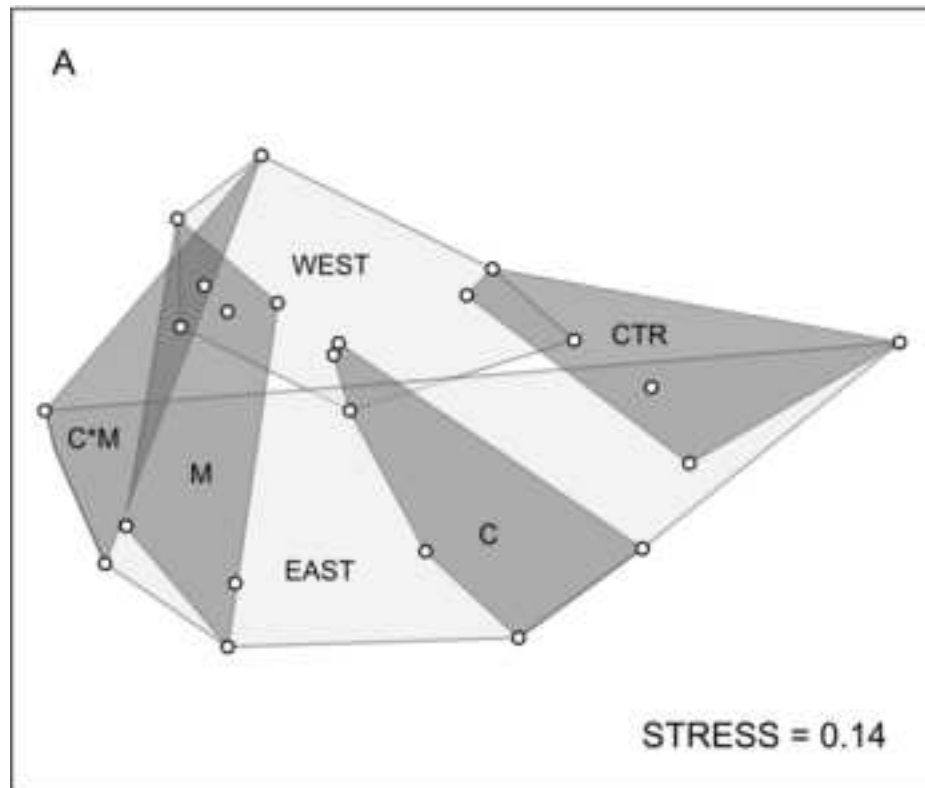
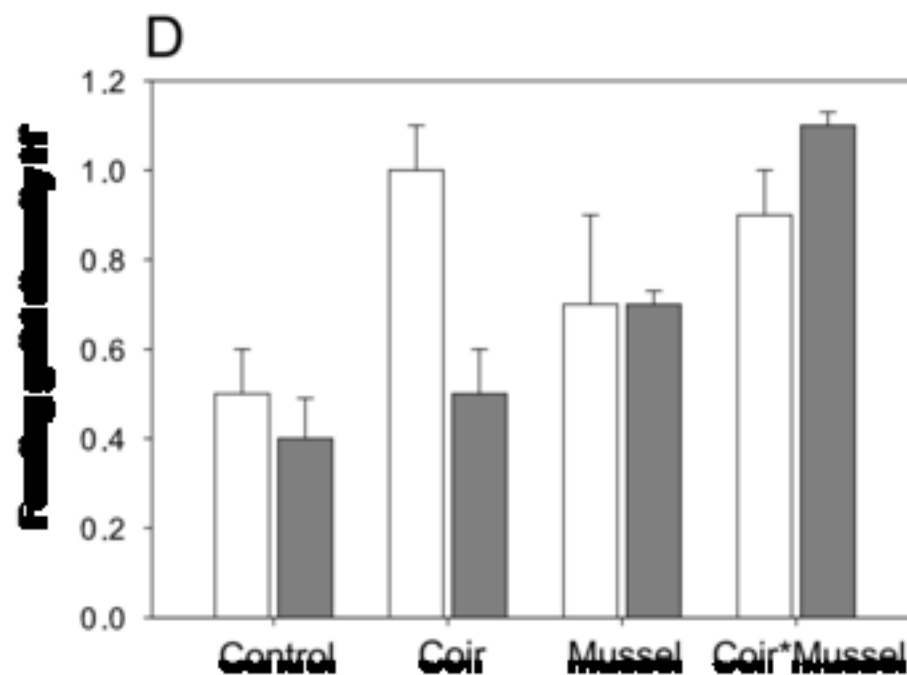
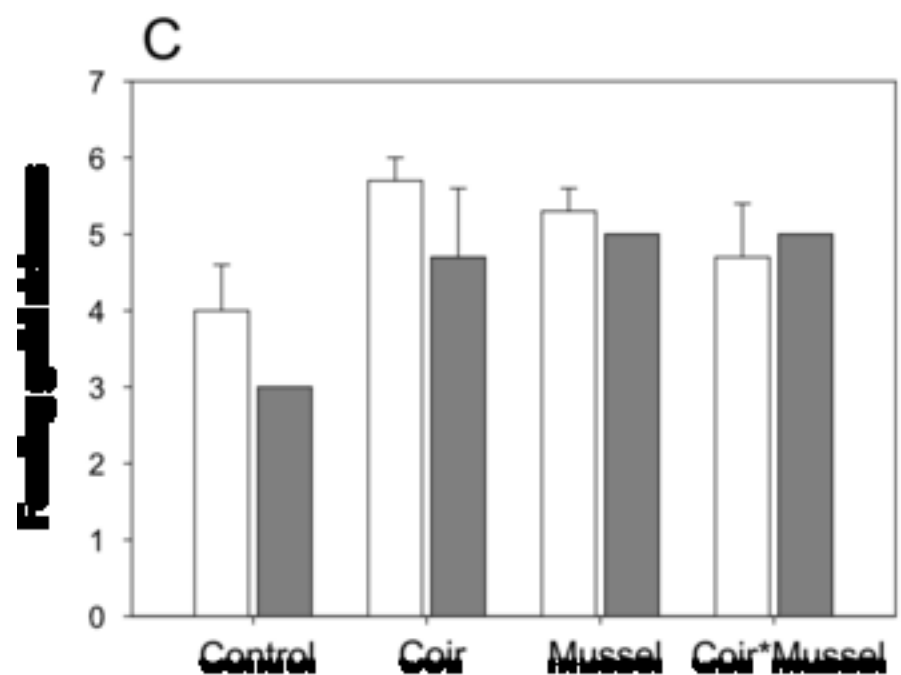
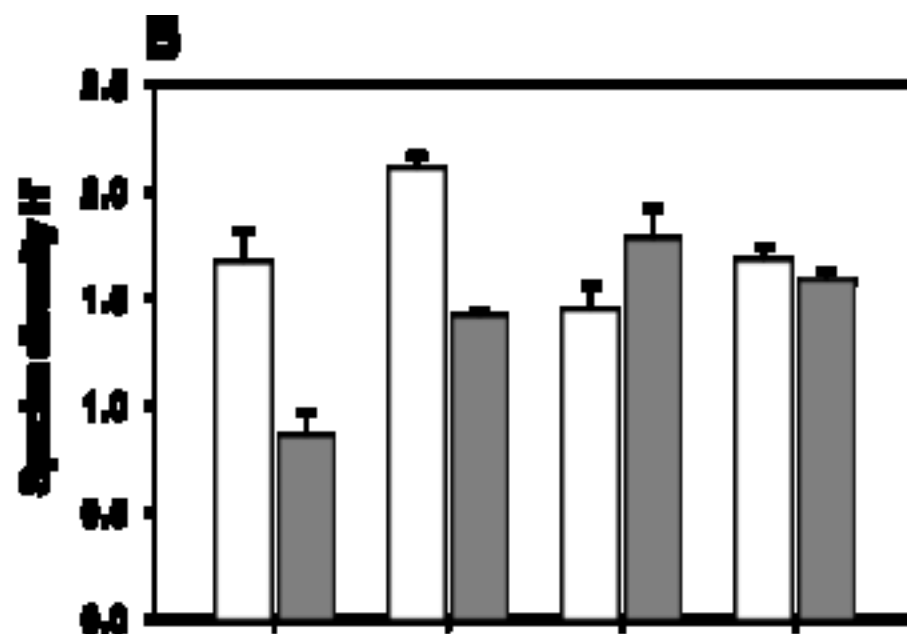
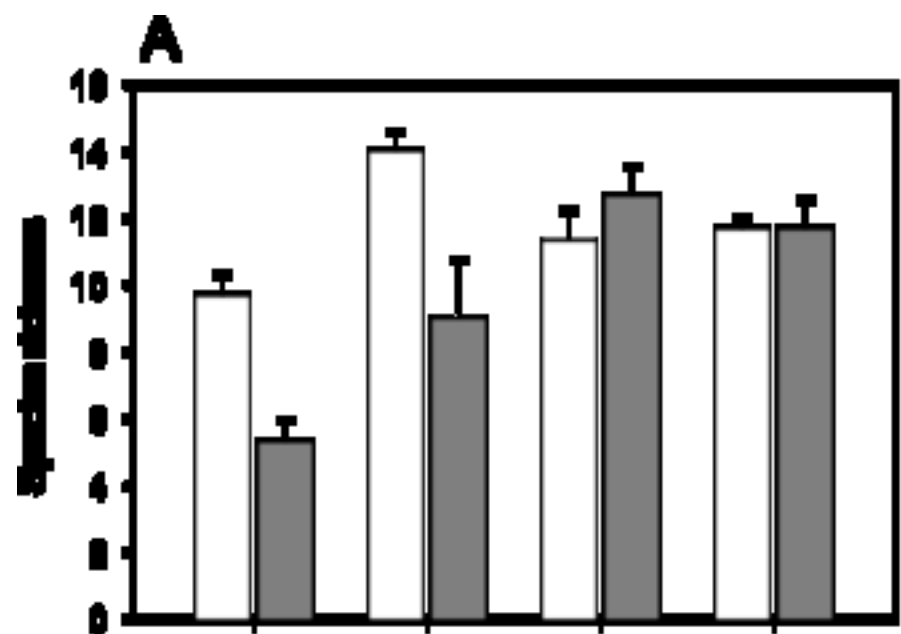


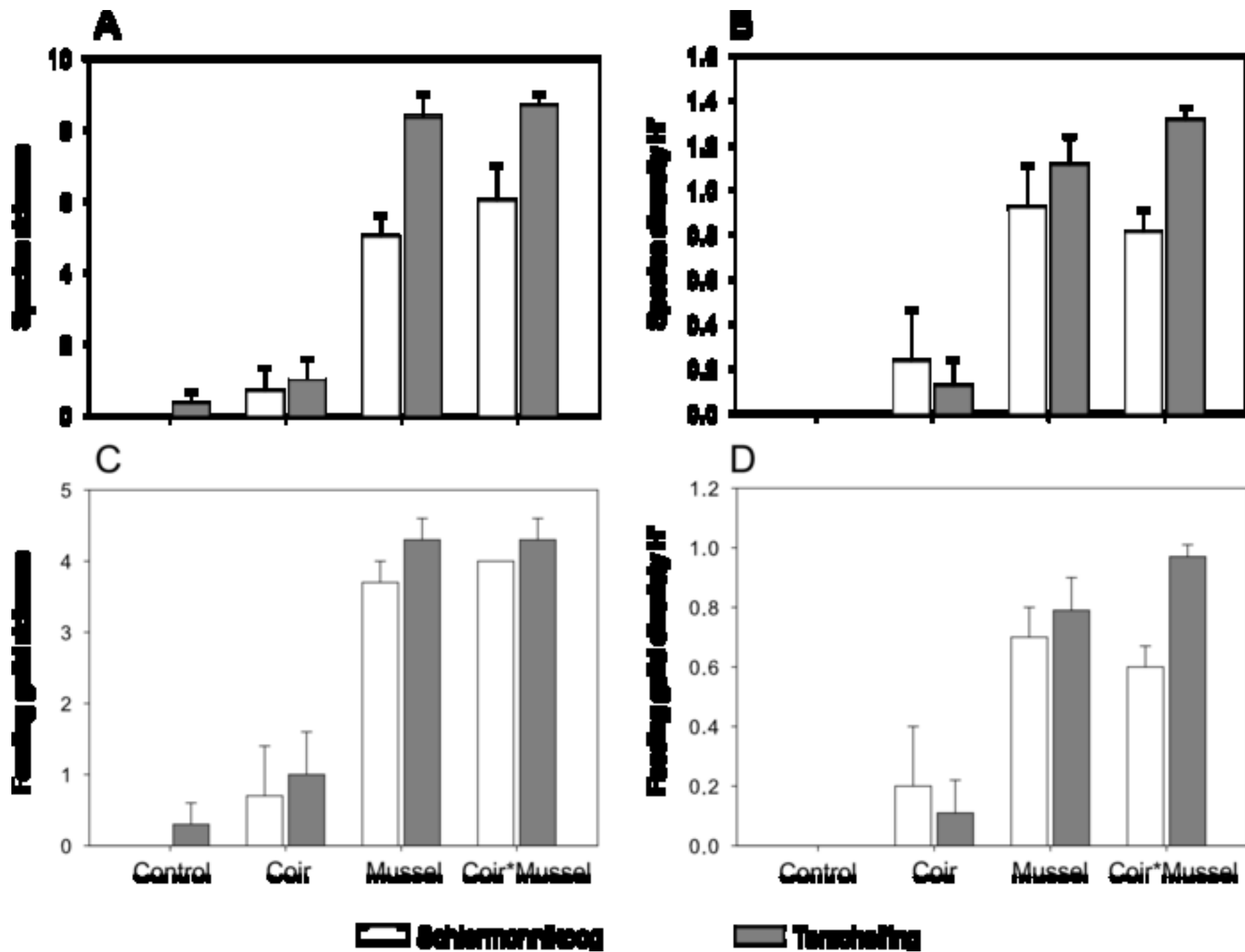
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■ Terechling

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