



Royal Netherlands Institute for Sea Research

This is a preprint of:

de Paoli, H.C.; van der Heide, T.; van den Berg, A.; Silliman, B.R.; Herman, P.M.J.; & van de Koppel, J. (2017). Behavioral self-organization underlies the resilience of a coastal ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 8035-8040

Published version: <https://dx.doi.org/10.1073/pnas.1619203114>

Link NIOZ Repository: www.vliz.be/nl/imis?module=ref&refid=286629

[Article begins on next page]

The NIOZ Repository gives free access to the digital collection of the work of the Royal Netherlands Institute for Sea Research. This archive is managed according to the principles of the [Open Access Movement](#), and the [Open Archive Initiative](#). Each publication should be cited to its original source - please use the reference as presented.

When using parts of, or whole publications in your own work, permission from the author(s) or copyright holder(s) is always needed.

1 Classification: BIOLOGICAL SCIENCES, Ecology

2 **Title: Behavioral self-organization underlies the resilience of**
3 **a coastal ecosystem**

4

5 Authors: H el ene de Paoli ^a Helene.de.paoli@nioz.nl
6 Tjisse van der Heide ^{b,c} T.vanderheide@science.ru.nl
7 Aniek van den Berg ^a Aniek.van.den.Berg@nioz.nl
8 Brian Silliman ^d Brian.silliman@duke.edu
9 Peter M.J. Herman ^{a,c,e} Peter.Herman@deltares.nl
10 Johan van de Koppel ^{a,b} Johan.van.de.Koppel@nioz.nl
11

12 Affiliations: a: Department of Estuarine and Delta Systems, Royal Netherlands Institute of Sea
13 Research and Utrecht University, P.O. Box 140, 4400 AC Yerseke, The Netherlands
14 b: Community and Conservation Ecology Group, Centre for Ecological and
15 Evolutionary Studies (CEES), University of Groningen, P.O.Box 1103,99700 CC
16 Groningen, The Netherlands
17 c: Department of Aquatic Ecology and Environmental Biology, Institute for Water and
18 Wetland Research, Radboud University Nijmegen, Faculty of Science,
19 Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands
20 d: Division of Marine Sciences and Conservation, Nicholas School of the
21 Environment, Duke University, Beaufort, NC, USA
22 e: Unit Marine and Coastal Systems, Deltares, P.O. Box 177, 2600MH Delft, The
23 Netherlands
24

25 Corresponding author: H el ene de Paoli.
26 Royal Netherlands Institute for Sea Research and Utrecht University
27 Korringaweg 7
28 4401NT Yerseke
29 The Netherlands
30 e.mail: helene.de.paoli@nioz.nl
31 Tel. 1: + 31 631 934 295
32 Tel. 2: + 31 113 577 300
33 Fax: +31 113 573 616
34

35

36 ***Abstract (250 words max)***

37 Self-organized spatial patterns occur in many terrestrial, aquatic and marine ecosystems.
38 Theoretical models and observational studies suggest self-organization is critical for enhanced
39 ecosystem resilience. Yet, experimental tests of this cross-ecosystem theory are lacking. In this study,
40 we experimentally test the hypothesis that self-organized pattern formation improves the persistence
41 of mussel beds (*Mytilus edulis*) on intertidal flats. In natural beds, mussels generate self-organized
42 patterns at two different spatial scales: regularly-spaced clusters of mussels at cm-scales driven by
43 behavioral aggregation, and large-scale regularly-spaced bands at m-scales driven by ecological
44 feedback mechanisms. To test for the relative importance of these two spatial scales of self-
45 organization on mussel bed persistence, we conducted field manipulations in which we factorially
46 manipulated small- and/or large-scale patterns. Our results revealed that both forms of self-
47 organization enhanced the stability of mussel beds after settlement, relative to non-organized beds.
48 Small-scale, behaviorally driven cluster patterns were found to be most crucial for persistence and thus
49 resistance to wave disturbance, while large-scale patterns facilitated reformation of small-scale
50 patterns if mussels were dislodged. This study provides experimental evidence that self-organization
51 can be paramount to enhancing ecosystem persistence and that this effect emerges from the interplay
52 between large-scale ecological, and small-scale behavioral self-organization. We conclude that
53 ecosystems hinging upon such interactions are likely to benefit greatly from conservation and
54 restoration actions that explicitly harness the power of self-organization to increase ecosystem
55 resistance to disturbance.

56

57 ***Significance Statement (120-word-maximum):***

58 Theoretical models suggest that spatial self-organization enhances the resistance of ecosystems to
59 disturbance. However, experiments investigating this important prediction are lacking. Our paper
60 provides clear experimental evidence that spatial self-organization profoundly increases the ability of
61 ecosystems to persist in the face of disturbance. The mechanisms underlying this positive impact of
62 self-organization is driven by the synergistic interaction between ecological and behavior processes.
63 Specifically, large-scale banded patterns in mussel beds created by ecological feedback processes
64 facilitate fast behavioral aggregation of individual mussels into clumps, in turn improving mussel
65 survival. Our study emphasizes the potential of harnessing spatial self-organization to enhance
66 restoration success and persistence of threatened ecosystems.

67

68 \body

69 **Introduction**

70 Formation of regular spatial patterns by habitat-forming organisms, such as clumping and banding,
71 have been observed in many different ecosystems, from forests (1) to savannahs (2, 3), peat lands (4-
72 6) and intertidal ecosystems (7-10). Theoretical studies have highlighted that local ecological
73 interactions can explain the formation of large-scale spatial patterns through a process called spatial
74 self-organization (9, 11, 12) (Figure 1). In this process, regular patterns can emerge when organisms
75 improve their growth conditions locally through habitat modification, while inhibiting conspecifics at
76 a larger scale due to competition for resources or other growth restricting interactions (5, 7, 9, 10, 13-
77 19). Other theoretical (6, 13) and a small number of comparative studies (2, 9) predict that formation
78 of self-organized patterns enhances ecosystem persistence and stability (20-23). The ubiquity of self-
79 organized spatial patterns across ecosystems worldwide (24) suggests that self-organization could be
80 of universal importance in shaping ecosystem persistence and their resistance to increasing
81 anthropogenic stressors (25)

82 Despite well-developed theory predicting that self-organization can enhance ecosystem resistance to
83 disturbance, there is currently no experimental evidence supporting this idea in any real world
84 situation. This lack of experimental support does not only hold back further theoretical advance, but
85 also hampers its real-world application, potentially explaining why self-organization theory has so far
86 had very limited impact in conservation or restoration practices. For instance, the practice of dune
87 restoration still applies an even spread of *Ammophila arenaria* plant propagules, disregarding the
88 strong patchy to patterned distribution of *Ammophila* in many naturally emerging dune systems.
89 Similarly, *Spartina alterniflora* propagules are typically planted at a constant and dispersed distance in
90 salt marsh restoration projects, eliminating facilitation between outplants and reducing overall yield
91 (25, 26). To further both fundamental, and conservation and restoration science regarding self-
92 organization, there is thus an urgent need for experimental tests of the emergent effects of spatial self-
93 organization on ecosystems stability and persistence, using manipulative techniques.

94

95 In this paper, we investigated the importance of spatial self-organization on the persistence of mussel
96 beds in sandy intertidal ecosystems. Mussels in soft-sediment ecosystems form very large (1 to >10
97 ha) highly patterned beds, in which self-organization occurs at two different scales (9, 13, 27). At a
98 small scale, mussels make string-shaped clusters that form reticulate patterns (5-10cm wide, Figure
99 1C) as a result of behavioral aggregation – a process equivalent to the physical process of phase
100 separation (28). At larger scales, mussels organize in regularly-spaced bands (5-10m wavelength,
101 Figure 1D) perpendicular to water flow as a consequence of local facilitation and larger-scale
102 competition for pelagic algae (13). Comparative studies and theoretical models highlight the potential
103 importance of pattern formation for mussel survival (9) and the persistence of mussel beds on tidal
104 flats that are regularly exposed to intense wave action and predation (29-31). Mussel beds are thus a
105 highly tractable system in which to test the general idea that self-organization can enhance ecosystem
106 persistence. In addition, if this prediction holds, it has direct implications for the management and
107 restoration of mussel beds, which act as keystone habitat for provisioning of biodiversity (32) as well
108 as being a marine food source.

109 Using manipulative experiments, we tested whether spatial self-organization affects the persistence of
110 mussel beds on intertidal flats, under the natural influence of wave action and predation. In the
111 summer and in autumn of 2012, we created artificial mussel beds with small-scale and large-scale
112 spatial patterns, similar to the patterns found in natural conditions, and determined their effect on the
113 persistence of the mussels. This was tested with four different spatial-organization treatments: beds
114 with small-scale clusters, large-scale bands, bands and clusters combined and a control treatment
115 consisting of randomly scattered mussels (Figure 2). To identify the mechanistic processes behind the
116 differences in persistence in the experiment, we performed an analysis of mussel behavior in both the
117 laboratory and the field. First, we analyzed how mussel movement on sandy substrates was affected by
118 mussel density in both the laboratory and the field. In addition, we compared mussel behavior on
119 sandy and rocky substrate in the laboratory. Our results provide important and novel insights into the
120 importance of spatial self-organization for ecosystem resilience and how self-organization can be used
121 to improve the restoration and conservation of natural ecosystems.

122 **Results**

123 Manipulation of the spatial patterns in artificial mussel beds revealed strong positive effects of self-
124 organization on mussel bed persistence. During the first six days, cover in the control beds, which
125 lacked any form of self-organization, decreased twice as fast (4.98 ± 1.68 se per day) relative to the
126 plots with either small-scale or large-scale patterns, or both (0.87 ± 0.19 se per day, Figure 3A and
127 3B), with significant effects of both large-scale banding ($F_{2,43}=4.32$; $p<0.02$), and small-scale
128 clustering ($F_{1,43}=16.42$; $p<0.001$). Moreover, we found a strong interaction between the two scales of
129 patterning ($F_{2,43}=5.17$; $p<0.01$), indicating that the large-scale banded patterns facilitated the formation
130 of clusters. The experimental results were consistent in both June and October, with the overall
131 positive effect of clustering and banding being slightly stronger in October ($F_{1,43}=6.88$; $p<0.02$). We
132 observed that the loss rate of mussels decreased strongly over time ($F_{1,43}=253.66$; $p<0.001$), most
133 likely because most of the remaining mussels in the treatments had organized into clusters after the
134 first few days (Fig. 3C and D). This result highlights the importance of cluster formation for the
135 resilience of mussel beds following experimental disturbance.

136 We conducted behavioral experiments in both the laboratory and in the field to unravel the importance
137 of active mussel movement in cluster formation. The behavioral experiments revealed that limited
138 ability of mussels to move and aggregate on sand – crucial in determining clump size – underlies
139 lower resistance of mussels in unpatterned beds. The number of mussels in clumps was significantly
140 enhanced by both the simulated clustering and banding treatments ($\chi^2=78.44$; $p<0.001$ and
141 $\chi^2=106.59$, $p<0.001$, respectively) compared to the controls where average clump size was up to 3
142 times smaller. Moreover, we found a significant interaction between both treatments ($\chi^2=38.28$,
143 $p<0.001$), as both the banding and the clustering treatments similarly facilitated aggregation (Fig.
144 4A). In addition, we also identified a significant interaction between the clustering treatment and the
145 experimental setting ($\chi^2=11.10$, $p<0.001$), as the effect of clustering was marginally lower in the
146 field compared to laboratory conditions. Apart from forming smaller clumps, we also found 2 to 7
147 times more individual mussels out of clumps in the controls as illustrated by a significant effect of the
148 clustering and banding treatments, as well as their interaction, on the number of isolated mussels

149 ($F_{1,32}=34.96$, $p<0.001$; $F_{1,32}=43.93$, $p<0.001$; $F_{1,32}=16.88$, $p<0.001$, respectively; Fig. 4B). Similar to
150 clump size, we also found a significant interaction between bands, clusters and the location
151 ($F_{1,32}=7.65$, $p=0.009$), because effects of self-organization were comparable but slightly lower in the
152 field.

153 When the movement of mussels on sand is compared to that on rock in the laboratory, results show
154 that the inability of mussels to move and aggregate on sand is the key limitation explaining the low
155 persistence of mussels in the control treatments, where patterns were absent. The clustering and
156 banding treatments had no significant effect on mussel movement in terms of their average velocity,
157 but mussels were found to move better on stone than on sand ($F_{1,609}=109.23$, $p<0.001$; Fig. 5).
158 Furthermore, we found significant two-way interactions between banding and substrate, and clusters
159 and substrate ($F_{1,609}=16.91$, $p<0.001$; $F_{1,609}=29.57$, $p<0.0001$, respectively), as well as a three-way
160 interaction between banding, clustering and substrate ($F_{1,609}=15.12$, $p<0.0001$). Overall, these results
161 highlight that when isolated, individual mussels can double their movement velocity when on rock,
162 allowing for a fast behavioral response to isolation, is in agreement to observations in prior studies (9,
163 28). In contrast, the movement of mussels on sand is lowered by 26% to 39% when they are isolated.
164 This highlights that when they are alone and on sand, mussels experience significant restrictions in
165 their movement, preventing them to form the clumps that are essential for survival, and explaining the
166 low persistence within the unpatterned mussel treatment, where mussels were scattered over the entire
167 experimental area.

168 ***Discussion***

169 Theoretical models predict that self-organized spatial patterns can have important emergent
170 consequences for the functioning of ecosystems and their ability to resist disturbance (2, 6, 13, 21, 24,
171 33, 34). However, experimental validation of these emergent effects is lacking, restricting
172 advancement and refinement of this cross-ecosystem theory as well as the application of self-
173 organization concepts in the management and restoration of degraded ecosystems (25). In this paper,
174 we experimentally demonstrate that in mussel beds, self-organization processes enhance mussel
175 resistance to disturbance and thus the stability of this diversity-enhancing ecosystem on intertidal flats

176 (35). This positive feedback occurs because of a synergistic interaction between self-organization
177 processes occurring at two separate spatial scales. Without any form of self-organization, i.e. when
178 fully dispersed, field experiments demonstrate that the loss of mussels from the bed is 2.5 to 5 times
179 higher compared to beds where mussels were aggregated in patterns of any sort. Here, small-scale,
180 behavior-driven patterns proved crucial for mussel persistence, and the large-scale banded patterns
181 facilitated aggregation at the small scale. In-depth laboratory analyses identify behavioral self-
182 organization at small spatial scale as the determining factor for the persistence of mussels on the beds;
183 inability to move and aggregate into clumps in the treatments without any self-organization was found
184 to underlie the high losses experienced in this treatment. Hence, our results provide unambiguous
185 experimental support for the emergent effects of spatial self-organization in mussel bed ecosystem,
186 and highlight the mechanisms that are behind this phenomenon.

187 Biological complexity at different spatial scales, driven by a multitude of behavioral, population-
188 level or ecosystem-level processes, is a defining characteristic of natural ecosystems. A recent
189 theoretical study highlighted that the interplay between two different self-organization processes,
190 created spatial patterns at two different scales in mussel beds, which proved a crucial factor defining
191 mussel bed persistence (21). Our results provide experimental validation of this prediction. The
192 formation of small-scale self-organized patterns proved to be crucial for mussel persistence, as clumps
193 increase resistance to disturbance - dislodgement and predation (9, 36-39). In our experiment, the
194 large-scale spatial patterns were found to stimulate the formation of small-scale cluster patterns
195 essential for survival: without large-scale banded patterns, clump formation was hampered, leading to
196 excessive mussel losses. When aggregated into bands, mussels could aggregate and form the cluster
197 patterns by using each other as a foothold, a behavior that becomes impossible when fully dispersed
198 due to the low overall density. Hence, we observed a clear interaction between two scales of pattern
199 formation in driving mussel bed persistence.

200 An unexpected result from our experiments was the clear importance of rapidly emerging
201 behavioral self-organization in determining the persistence of mussel bed. Most studies of regular
202 patterns in ecosystems suggest a scale-dependent interplay of facilitation and competition as the

203 underlying process (5, 7, 10, 13, 14), a slow form of pattern formation that is akin to Turing's activator-
204 inhibitor principle (40, 41). In mussels, however, the formation of small-scale patterns results from a
205 behavioral process that is more similar to the physical process of phase separation (28). Phase
206 separation occurs for instance during the formation of alloys, where separation between different types
207 of molecules creates spatial patterns at sub-millimeter scale, which boosts the material strength of
208 alloys such as steel and bronze (42). Our results highlight that the patterns resulting from the
209 behavioral self-organization in mussels (49) similarly determine the "strength" of mussel beds to resist
210 predation and wave action. This highlights the importance of behavioral self-organization, driven by
211 fast movement processes, as an underappreciated and understudied driver of ecosystem persistence.

212 Our study adds to a growing body of papers – theoretical or empirical – pointing at the importance
213 of facilitation and self-organization for the resilience (43, 44), and productivity (45), and biodiversity
214 of natural ecosystems (35). In many – if not most – human-modified ecosystems, the natural spatial
215 structure is altered or lost to mowing, drainage, dredging and other forms of interference. Moreover, in
216 the coming decades, many ecosystems are expected to face further increases in disturbance as a result
217 of global change (46, 47). Our results highlight that restoration of natural communities in these
218 human-altered and homogenized ecosystems could be facilitated if 1) the original spatial structure is
219 restored or conserved, or 2) the self-organization processes that generate these spatial patterns are
220 restored to their former functioning. This requires a change in management perspectives and
221 restoration approaches. It is likely insufficient to focus on improving abiotic conditions and removing
222 dispersal barriers, as these do not recover the facilitative processes that are characteristic to foundation
223 species such as mussels, cordgrasses or marram grass (25, 26). Instead, restoration approaches should
224 also aim to restore the functioning of internal positive feedback interactions to facilitate the
225 persistence of the involved species. This can be done by recovering or approximating the self-
226 organized spatial configuration of the ecosystem that has to be restored. Our study suggests that
227 harnessing the emergent effects of spatial self-organization can make an important difference in the
228 restoration of many marine and non-marine ecosystems, such as salt marshes (25), seagrass beds (48) or
229 arid bushlands (49).

230 There has been a recent global surge in promoting habitat restoration as a critical conservation
231 approach to deal with both climate change and habitat degradation. At the 2014 United Nations
232 Climate Summit, all nations present pledged to actively restore 350 million acres of degraded
233 ecosystems by 2030. Critical to the success of this global pledge is (1) the facilitation of regrowth of
234 ecosystems in degraded areas, and (2) the continued persistence of those systems once they are
235 initially established. Although restoration of habitats dominated by ecosystem engineers has been
236 prioritized (50-54), large-scale restoration attempts of ecosystems such as coral reefs, shellfish reefs,
237 seagrasses, is currently very costly and of limited success (55-59). As many of these ecosystems are
238 characterized by self-organized spatial patterns generated by habitat forming species, we argue that
239 harnessing positive interactions and the resulting self-organization processes will be critical in
240 developing more successful restoration and conservation practices (25, 26, 46, 47, 60). Our paper
241 provides a strong empirical basis for such a new premise by experimentally demonstrating the
242 importance of self-organization in mussel bed restoration. Moreover, it highlights the importance of
243 the interplay of behavioral and ecological processes in driving ecosystem resilience. This points at the
244 need for an integrated perspective on ecosystem restoration that not only addresses limitation in
245 organism establishment, but integrates the impact of organism behavior in terms of their effect on
246 ecosystem resilience (21).

247 ***Materials and Methods***

248 *Ecological field experiment*

249 To study the effect of self-organization on mussel bed persistence, we set up an experiment in which
250 we tested the importance of pattern formation on the persistence of transplanted mussels in artificial
251 beds. We tested for the effect of large-scale self-organization (bands) and small-scale self-organization
252 (clusters) in a full-factorial design and then measured how treatments affected the persistence of the
253 bed in the weeks after transplantation.

254 We set up the experimental beds (3x5m) on the tidal flats near Schiermonnikoog, the eastern
255 island of the Dutch Wadden Sea (Figure 6) in an area at the same elevation as natural beds (-0.5m,
256 coordinates: 53°27'9.91"N,6°8'50.07"E). Using mussels from a nearby intertidal mussel bed, 12 plots

257 were constructed using an overall density of 2,7 kg/m² (40kg in total), which is similar to densities
258 found in natural mussel beds (9). We applied four different spatial treatments in these experimental
259 beds. The large-scale self-organization was represented by 2 bands of 1 by 3m. Within these bands,
260 mussels were aggregated by hand in string and cluster patterns to reflect small-scale self-organization.
261 In the first treatment (control, Figure 2A), all scales of self-organization were present. In the second
262 treatment (Figure 2B), only clusters were made, and no large-scale, banded patterns were used. In the
263 third treatment (Figure 2C), only bands were made, within which the mussels were fully dislodged.
264 Finally, in the control treatment (Figure 2D), neither large- and small-scale self-organization was
265 implemented, and mussels were randomly dispersed on the plot. Plots were positioned along the low-
266 water line, and the bands were orientated perpendicular to the dominant flow direction. The entire
267 experiment was replicated 4 times in space yielding 16 beds in total. To test for generality over time,
268 the experiment was conducted twice, once in summer (June 2012), and once in autumn (October
269 2012). To measure the change of mussel cover in time, we took aerial pictures at a daily basis during
270 the first 6 days, and once every 12 days after that, using a camera mounted on a telescopic pole.
271 Pictures were transformed in black (mussels) and white (bare sand) images using Image J software.
272 The proportion of black pixels was determined using image J, to provide us with an estimate of mussel
273 cover for each plot. The development of cover over time was used as a measure of mussel persistence.

274 *Behavioral experiments*

275 To investigate to what extent mussel movement behavior contributes to the observed differences in
276 self-organization and subsequent persistence, we studied how mussel aggregative movement varied
277 with the various densities of conspecifics in the different treatments. We first studied mussel
278 aggregation both under natural and controlled conditions. In a second experiment, we analyzed
279 aggregative movement in controlled laboratory conditions.

280 Mesocosm experiment: In the mesocosm, small artificial beds (40x40cm) were set up in two polyester
281 tanks (120x80cm). As in the previous experiment, 4 spatial treatments were used with 4 replicates per
282 treatment. To reflect the conditions within the bands of the large-scale self-organization treatment used
283 in the field, we used a high density of 5.6 kg/m². To reflect conditions without bands, we lowered the

284 density to 2.5 kg/m². Both densities are within the range of densities found in natural mussel beds (9).
285 In both densities, we mimicked small-scale self-organization by aggregating mussels by hand in
286 clumps in half of the units. In the other half, small-scale self-organization was removed by manually
287 detaching the mussels and placing them randomly on the bed.

288 Early observations suggested that mussels appeared more restricted in their movement on
289 sediment compared to the stone surfaces that had been used in prior experiments (Van de Koppel et al
290 2008, De Jager et al 2011). For this reason we replicated the entire experiments on both solid and
291 sandy substrate. The experiments were carried out in 80x120x10 cm tanks with a constant supply of
292 fresh seawater. Each 100 L tank was divided in 2 equal areas on which treatment was randomly
293 applied to create 4 small artificial mussel beds were created. The bottom of the tanks was covered with
294 either 5-cm layer of sand or a 50x50cm stone tile. Mussels were collected from wooden poles at the
295 beach near Vlissingen (The Netherlands) a few days prior to the start of the experiment. Before the
296 start of the experiments, the mussels were dislodged and added to one of the treatments. Each
297 experiment was repeated 3 times.

298 Field experiment: Finally, to test whether laboratory results were an accurately reflected natural
299 conditions, we repeated the part of laboratory experiment that concerned manipulation of mussels on
300 sandy substrate. Pilot experiments revealed that visibility nearby the artificial beds on
301 Schiermonnikoog was too limited to allow for reliable underwater camera observations. The
302 experiment was therefore moved to a tidal flat in the Eastern Scheldt, in the South of the Netherlands
303 (51°27'44.85"N,4°4'51.75"E, Figure 6), where water clarity was much higher. We used the same plot
304 size (~40x40-cm clumps within 50x50-cm plots) and aggregation treatments as in the laboratory and
305 collected the mussels from the same site a few days prior to the start of the experiment. The
306 experiment was set up in November 2013 and replicated 2 times.

307 Data collection: We tracked mussel aggregation and movement in the laboratory using Canon
308 powershot D10 cameras that were mounted over each tank. For the field, we used Canon powershot
309 S90 cameras within a Ikelite 6242.95 underwater housing (www.ikelite.com). The cameras took

310 pictures every minute for 180 minutes. For each picture, we applied a pixel to cm conversion
311 coefficient based on the distance of the camera from the bed and its angle. To analyze the effect of the
312 treatments on the level of aggregation we counted the number of clumps, the number of mussels
313 within the clumps, and the number of isolated mussels after 24 hours. In the lab, mussel movement
314 velocity was quantified for 10 random mussels in each experimental unit. Images were processed in
315 Image J and Matlab to determine the change in position (x,y coordinates) of the mussels, from which
316 the distance travelled per unit of time was calculated.

317 *Statistical Analyses*

318 Ecological field experiment: All of statistical tests were run in R version 3.2.2. Loss of mussels in the
319 ecological experiment was studied including 2 different periods: during the first 6 days of experiment
320 and during the remaining part of experiment. We used analysis of variance (ANOVA) with the four
321 self-organization treatments, period (first 6 days or remaining days), and sampling month as fixed
322 factors.

323 Mussel aggregation analyses: Differences in clump size (i.e. the number of mussels in a clump) was
324 analyzed using a Generalized Linear Model with a negative binomial distribution, using banding,
325 clustering and location (field or mesocosm) as fixed factors. The percentage of single, detached
326 mussels was analyzed using ANOVA with banding, clustering and location (field or mesocosm) as
327 fixed factors. The percentage of loose mussels was square root-transformed in order to obtain a normal
328 distribution of the model residuals.

329 Aggregative movement analyses: Differences in movement on sandy versus rocky substrate were
330 tested using an ANOVA, with the aggregation treatments and substrate as fixed factors. The data were
331 square root-transformed in order to obtain normality of the model residuals.

332

333 *Acknowledgements:*

334 We thank the Silliman lab for comments on earlier versions of this manuscript. We would like
335 to acknowledge Sander Holthuijsen and all the volunteers for their dedicated work in the
336 field. This work is part of the Waddensleutels and Mosselwad projects, both funded by the
337 Waddenfonds.

338

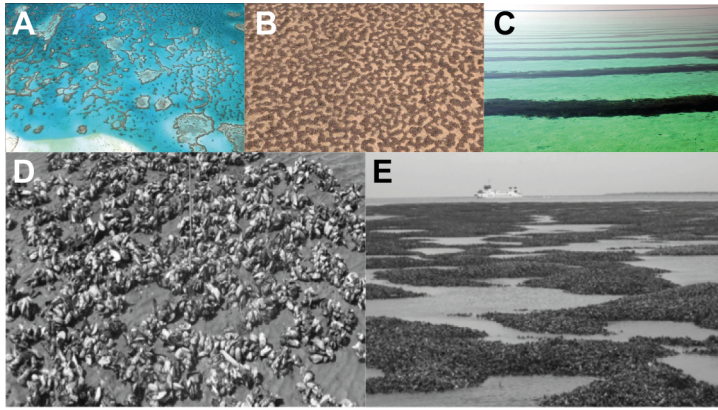
339 **References**

- 340
- 341 1. Bekker MF & Malanson GP (2008) Linear forest patterns in subalpine environments.
- 342 *Progress in Physical Geography* 32(6):635-653.
- 343 2. Pringle RM, Doak DF, Brody AK, Jocqué R, & Palmer TM (2010) Spatial pattern enhances
- 344 ecosystem functioning in an African savanna. *PLoS biology* 8(5):e1000377.
- 345 3. Scanlon TM, Caylor KK, Levin SA, & Rodriguez-Iturbe I (2007) Positive feedbacks
- 346 promote power-law clustering of Kalahari vegetation. *Nature* 449(7159):209-212.
- 347 4. Foster D, King G, Glaser P, & Wright H (1983) Origin of string patterns in boreal
- 348 peatlands.
- 349 5. Eppinga MB, de Ruiter PC, Wassen MJ, & Rietkerk M (2009) Nutrients and Hydrology
- 350 Indicate the Driving Mechanisms of Peatland Surface Patterning. *Am Nat* 173(6):803-
- 351 818.
- 352 6. Rietkerk M, Dekker SC, de Ruiter PC, & van de Koppel J (2004) Self-Organized Patchiness
- 353 and Catastrophic Shifts in Ecosystems. *Science* 305(5692):1926-1929.
- 354 7. van de Koppel J & Crain CM (2006) Scale - Dependent Inhibition Drives Regular Tussock
- 355 Spacing in a Freshwater Marsh. *The American Naturalist* 168(5):E136-E147.
- 356 8. Weerman EJ, Herman PM, & Van de Koppel J (2011) Top-down control inhibits spatial
- 357 self-organization of a patterned landscape. *Ecology* 92(2):487-495.
- 358 9. van de Koppel J, *et al.* (2008) Experimental Evidence for Spatial Self-Organization and Its
- 359 Emergent Effects in Mussel Bed Ecosystems. *Science* 322(5902):739-742.
- 360 10. Van Der Heide T, *et al.* (2010) Spatial self-organized patterning in seagrasses along a
- 361 depth gradient of an intertidal ecosystem. *Ecology* 91(2):362-369.
- 362 11. Reichenbach T, Mobilia M, & Frey E (2007) Mobility promotes and jeopardizes
- 363 biodiversity in rock-paper-scissors games. *Nature* 448(7157):1046-1049.
- 364 12. Klausmeier CA (1999) Regular and irregular patterns in semiarid vegetation. *Science*
- 365 284(5421):1826-1828.
- 366 13. van de Koppel J, Rietkerk M, Dankers N, & Herman PMJ (2005) Scale-dependent feedback
- 367 and regular spatial patterns in young mussel beds. *Am. Nat.* 165(3):E66-E77.
- 368 14. Weerman EJ, *et al.* (2010) Spatial self-organization on intertidal mudflats through
- 369 biophysical stress divergence. *Am Nat* 176(1):E15-32.
- 370 15. Rietkerk M, *et al.* (2002) Self - organization of vegetation in arid ecosystems. *The*
- 371 *American Naturalist* 160(4):524-530.
- 372 16. Sherratt J, Lambin X, Thomas C, & Sherratt T (2002) Generation of periodic waves by
- 373 landscape features in cyclic predator-prey systems. *Proceedings of the Royal Society of*
- 374 *London. Series B: Biological Sciences* 269(1489):327-334.
- 375 17. Liu C, *et al.* (2011) Sequential establishment of stripe patterns in an expanding cell
- 376 population. *Science* 334(6053):238-241.
- 377 18. Anderson KE, Hilker FM, & Nisbet RM (2012) Directional biases and resource-
- 378 dependence in dispersal generate spatial patterning in a consumer-producer model.
- 379 *Ecology Letters* 15(3):209-217.
- 380 19. de Jager M, *et al.* (2014) How superdiffusion gets arrested: ecological encounters explain
- 381 shift from Lévy to Brownian movement. *Proceedings of the Royal Society B: Biological*
- 382 *Sciences* 281(1774):20132605.
- 383 20. Buschbaum C, *et al.* (2009) Mytilid mussels: global habitat engineers in coastal
- 384 sediments. *Helgoland Mar. Res.* 63(1):47-58.
- 385 21. Liu Q-X, *et al.* (2014) Spatial pattern formation at multiple scales drives the resilience of
- 386 mussel bed ecosystems. *Nature Communication* 5:5234; DOI: 5210.1038/ncomms6234.
- 387 22. Van de Koppel J, Herman PMJ, Thoolen P, & Heip CHR (2001) Do alternate stable states
- 388 occur in natural ecosystems? Evidence from a tidal flat. *Ecology* 82(12):3449-3461.
- 389 23. Weerman EJ, *et al.* (2010) Spatial Self - Organization on Intertidal Mudflats through
- 390 Biophysical Stress Divergence. *The American Naturalist* 176(1):E15-E32.

- 391 24. Rietkerk M & van de Koppel J (2008) Regular pattern formation in real ecosystems.
392 *Trends in Ecology & Evolution* 23(3):169-175.
- 393 25. Silliman BR, *et al.* (2015) Facilitation shifts paradigms and can amplify coastal
394 restoration efforts. *Proc Natl Acad Sci U S A* 112(46):14295-14300.
- 395 26. Halpern BS, Silliman BR, Olden JD, Bruno JP, & Bertness MD (2007) Incorporating
396 positive interactions in aquatic restoration and conservation. *Front. Ecol. Environ.*
397 5(3):153-160.
- 398 27. Liu QX, *et al.* (2014) Pattern formation at multiple spatial scales drives the resilience of
399 mussel bed ecosystems. *Nature communications* 5: Article number: 5234
400 doi:5210.1038/ncomms6234.
- 401 28. Liu Q-X, *et al.* (2013) Phase separation explains a new class of self-organized spatial
402 patterns in ecological systems. *Proceedings of the National Academy of Sciences*
403 110(29):11905-11910.
- 404 29. de Paoli H, *et al.* (2015) Processes limiting mussel bed restoration in the Wadden-Sea. *J*
405 *Sea Res* 103:42-49.
- 406 30. van der Heide T, *et al.* (2014) Predation and habitat modification synergistically interact
407 to control bivalve recruitment on intertidal mudflats. *Biol Conserv* 172:163-169.
- 408 31. van der Zee EM, *et al.* (2015) Habitat modification drives benthic trophic diversity in an
409 intertidal soft-bottom ecosystem. *J Exp Mar Biol Ecol* 465:41-48.
- 410 32. Silliman BR, *et al.* (2011) Whole-Community Facilitation Regulates Biodiversity on
411 Patagonian Rocky Shores. *PLoS One* 6(10).
- 412 33. Kéfi S, *et al.* (2007) Spatial vegetation patterns and imminent desertification in
413 Mediterranean arid ecosystems. *Nature* 449(7159):213-217.
- 414 34. Gilad E, von Hardenberg J, Provenzale A, Shachak M, & Meron E (2004) Ecosystem
415 Engineers: From Pattern Formation to Habitat Creation. *Physical Review Letters*
416 93(9):098105.
- 417 35. Christianen M, *et al.* (2016) Biodiversity and food web indicators of community recovery
418 in intertidal shellfish reefs. *Biol Conserv* in press.
- 419 36. Reimer O & Tedengren M (1997) Predator - induced changes in byssal attachment,
420 aggregation and migration in the blue mussel, *Mytilus edulis*. *Marine & Freshwater*
421 *Behaviour & Phy* 30(4):251-266.
- 422 37. Bertness MD & Grosholz E (1985) Population dynamics of the ribbed mussel, *Geukensia*
423 *demissa*: the costs and benefits of a clumped distribution. *Oecologia* 67:192-204.
- 424 38. Hunt HL & Scheibling RE (2002) Movement and wave dislodgment of mussels on a wave-
425 exposed rocky shore. *Veliger* 45(4):273-277.
- 426 39. Hunt HL & Scheibling RE (2001) Patch dynamics of mussels on rocky shores: Integrating
427 process to understand pattern. *Ecology* 82(11):3213-3231.
- 428 40. Turing AM (1952) The chemical basis of morphogenesis. *Philosophical Transactions of*
429 *the Royal Society of London B, Biological Sciences* 237:37-72.
- 430 41. Meinhardt H (1982) *Models of Biological Pattern Formation* (Academic Press, San Diego,
431 CA).
- 432 42. Cahn JW & Hilliard JE (1958) Free energy of a nonuniform system. I. Interfacial free
433 energy. *The Journal of Chemical Physics* 28:258.
- 434 43. Van de Koppel J, Rietkerk M, Dankers N, & Herman PMJ (2005) Scale-dependent
435 feedback and regular spatial patterns in young mussel beds. *American Naturalist*
436 165(3):E66-E77.
- 437 44. Liu QX, *et al.* (2014) Pattern formation at multiple spatial scales drives the resilience of
438 mussel bed ecosystems. *Nature communications* 5.
- 439 45. Pringle RM, Doak DF, Brody AK, Jocque R, & Palmer TM (2010) Spatial Pattern Enhances
440 Ecosystem Functioning in an African Savanna. *Plos Biology* 8(5).
- 441 46. Knutson TR, *et al.* (2010) Tropical cyclones and climate change. *Nature Geoscience*
442 3(3):157-163.

- 443 47. Emanuel K, Sundararajan R, & Williams J (2008) Hurricanes and global warming: Results
444 from downscaling IPCC AR4 simulations. *Bulletin of the American Meteorological Society*
445 89(3):347-367.
- 446 48. Hughes AR, Williams SL, Duarte CM, Heck Jr KL, & Waycott M (2008) Associations of
447 concern: declining seagrasses and threatened dependent species. *Front. Ecol. Environ.*
448 7(5):242-246.
- 449 49. Rochefort L, Quinty F, Campeau S, Johnson K, & Malterer T (2003) North American
450 approach to the restoration of Sphagnum dominated peatlands. *Wetlands Ecology and*
451 *Management* 11(1-2):3-20.
- 452 50. Byers JE, *et al.* (2006) Using ecosystem engineers to restore ecological systems. *Trends in*
453 *Ecology & Evolution* 21(9):493-500.
- 454 51. Crain CM & Bertness MD (2006) Ecosystem engineering across environmental gradients:
455 Implications for conservation and management. *Bioscience* 56(3):211-218.
- 456 52. Fortes MD (1991) Seagrass-mangrove ecosystems management: A key to marine coastal
457 conservation in the ASEAN region. *Marine Pollution Bulletin* 23(0):113-116.
- 458 53. Carls MG, Harris PM, & Rice SD (2004) Restoration of oiled mussel beds in Prince
459 William Sound, Alaska. *Marine Environmental Research* 57(5):359-376.
- 460 54. McLeod IM, Parsons DM, Morrison MA, Le Port A, & Taylor RB (2012) Factors affecting
461 the recovery of soft-sediment mussel reefs in the Firth of Thames, New Zealand. *Marine*
462 *and Freshwater Research* 63(1):78-83.
- 463 55. Piersma T, *et al.* (2001) Long-term indirect effects of mechanical cockle-dredging on
464 intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology* 38(5):976-990.
- 465 56. Hiddink JG (2003) Effects of suction-dredging for cockles on non-target fauna in the
466 Wadden Sea. *Journal of Sea Research* 50(4):315-323.
- 467 57. Lenihan HS & Peterson CH (1998) How habitat degradation through fishery disturbance
468 enhances impacts of hypoxia on oyster reefs. *Ecological Applications* 8(1):128-140.
- 469 58. Bouma T, Olenin S, Reise K, & Ysebaert T (2009) Ecosystem engineering and biodiversity
470 in coastal sediments: posing hypotheses. *Helgoland Mar. Res.* 63(1):95-106.
- 471 59. Badalamenti F, Carlo G, D'Anna G, Gristina M, & Toccaceli M (2006) Effects of Dredging
472 Activities on Population Dynamics of *Posidonia oceanica* (L.) Delile in the Mediterranean
473 Sea: The Case Study of Capo Feto (SW Sicily, Italy). *Hydrobiologia* 555(1):253-261.
- 474 60. Dai A (2011) Drought under global warming: a review. *Wiley Interdisciplinary Reviews:*
475 *Climate Change* 2(1):45-65.

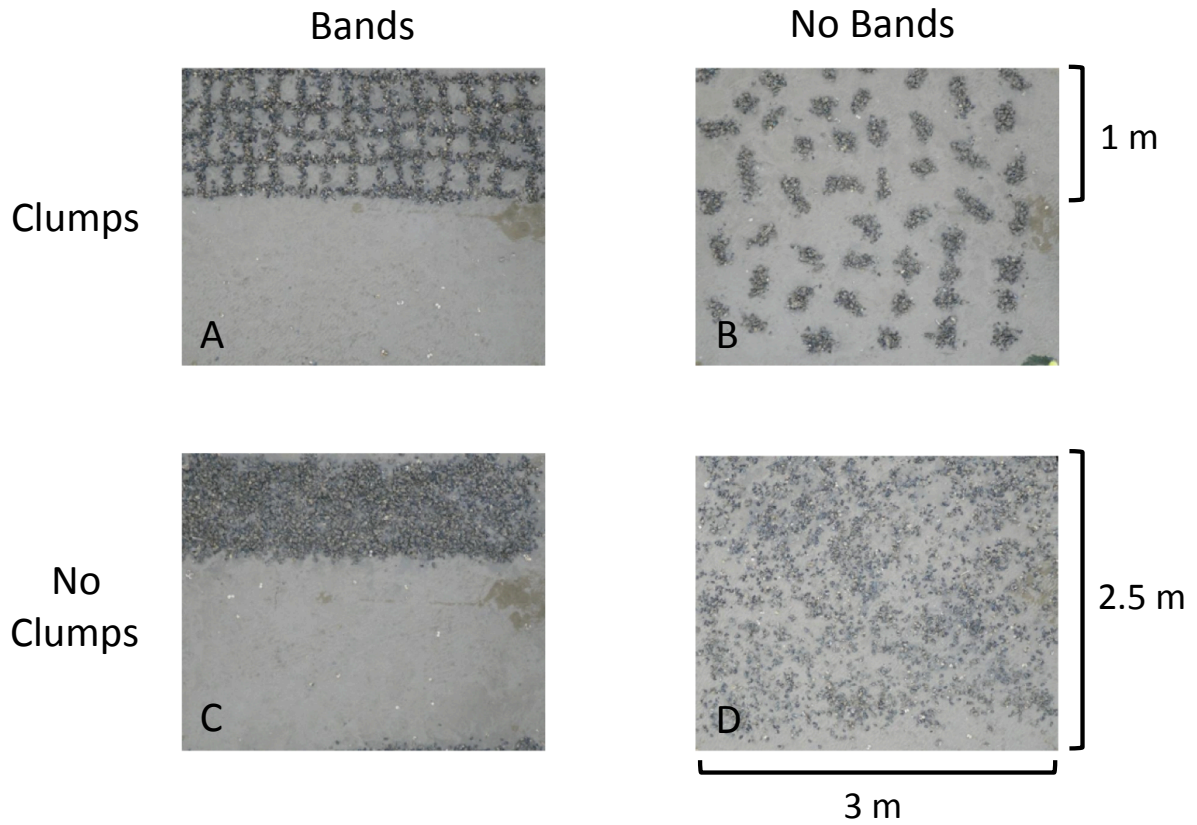
476



477

478 Figure 1: Observations of self-organization in different ecosystems. A: Spotted pattern of in coral reefs
479 in Australia (© Google Earth). B: Labyrinth pattern of bushy vegetation in Niger (© Google Earth). C:
480 Banded patterns in seagrasses in Australia (Picture : Marjolijn Christianen), D: Small-scale self-
481 organization in mussel bed in the Netherlands (Picture: H el ene de Paoli). Mussels organize in strings
482 (5-10cm wide). E: Large-scale self-organisation in mussel beds in the Netherlands (Picture: H el ene de
483 Paoli). Mussels organize in bands (5-7m wide).

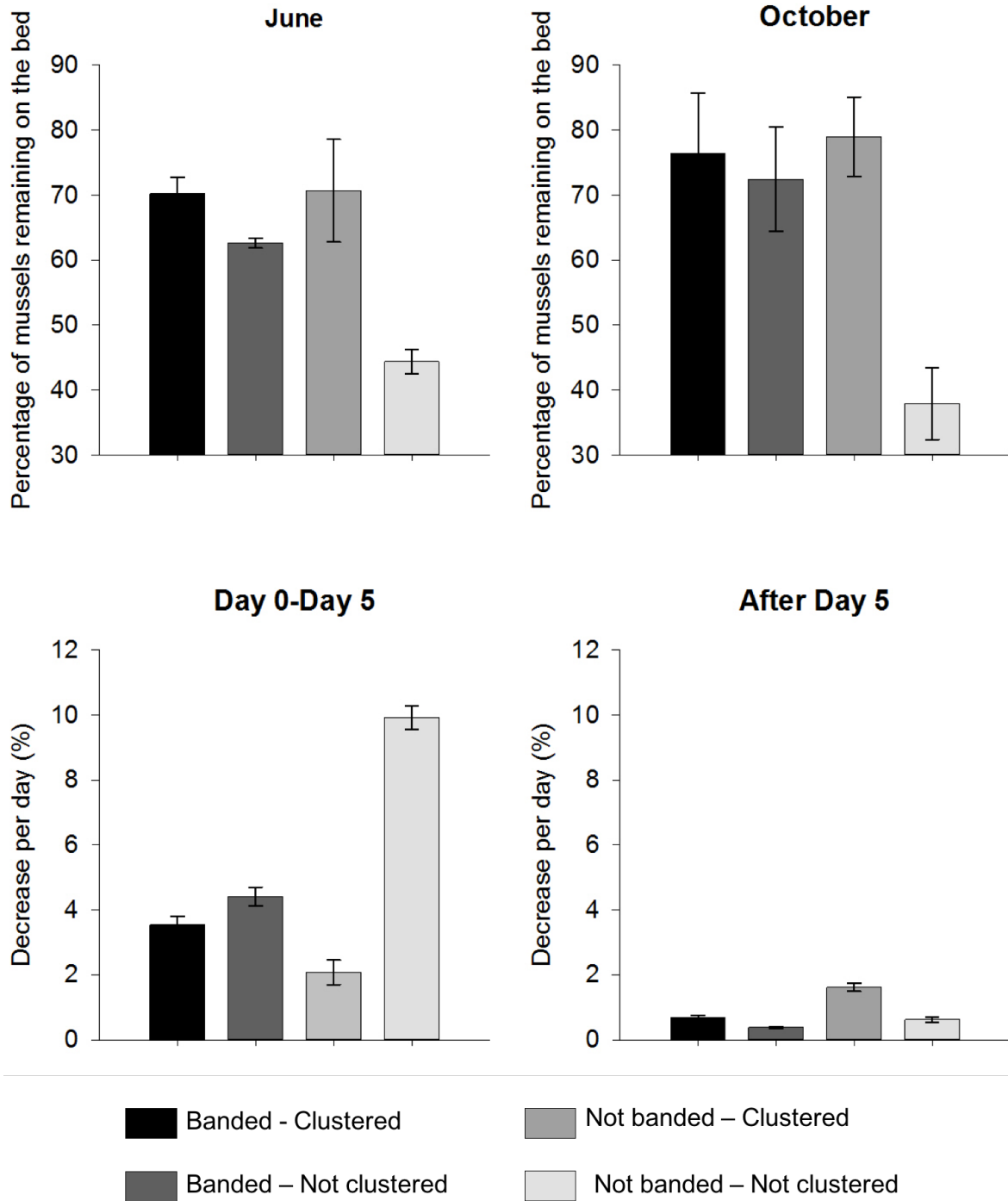
484



485

486 Figure 2: Experimental set up to study the effect of spatial self-organization on persistence of mussel
 487 beds. Artificial beds were set up using a full factorial design, using four treatments: A: Both bands and
 488 clusters, B: Clusters but no bands, C: Bands but no clusters, D: Mussels fully dispersed (control). Note
 489 that for each experimental plot, each treatment was repeated, making a 3 by 5 plot.

490



491

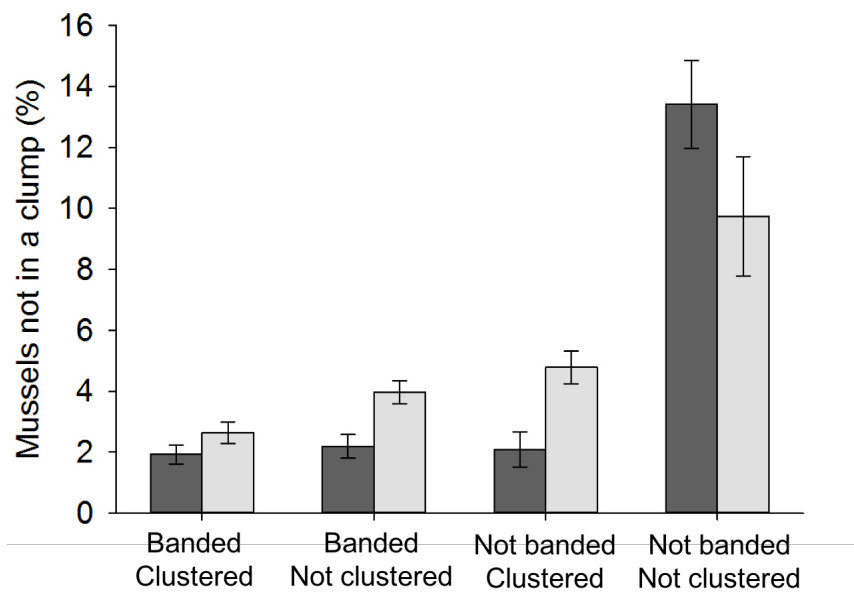
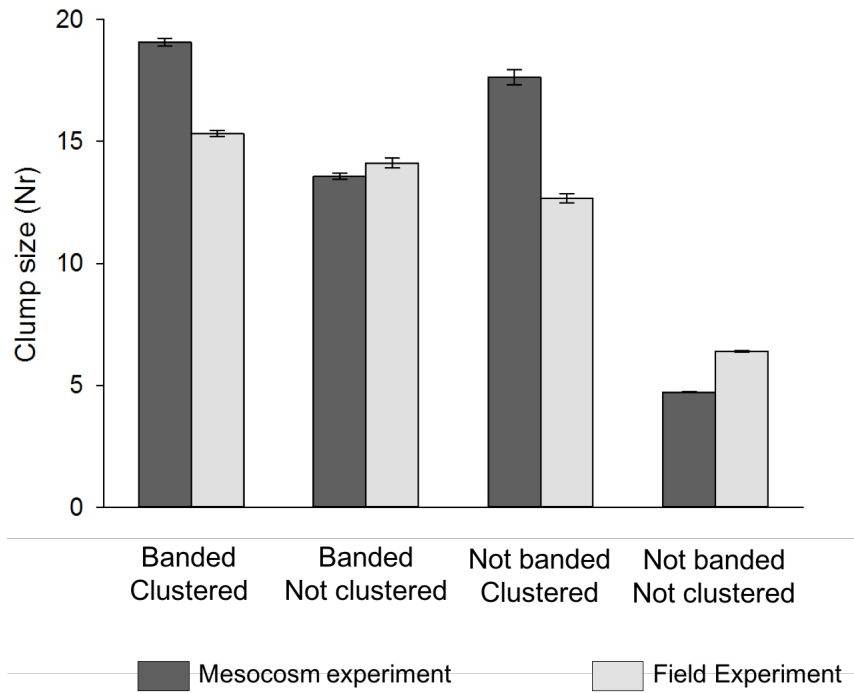
492

493

494

495

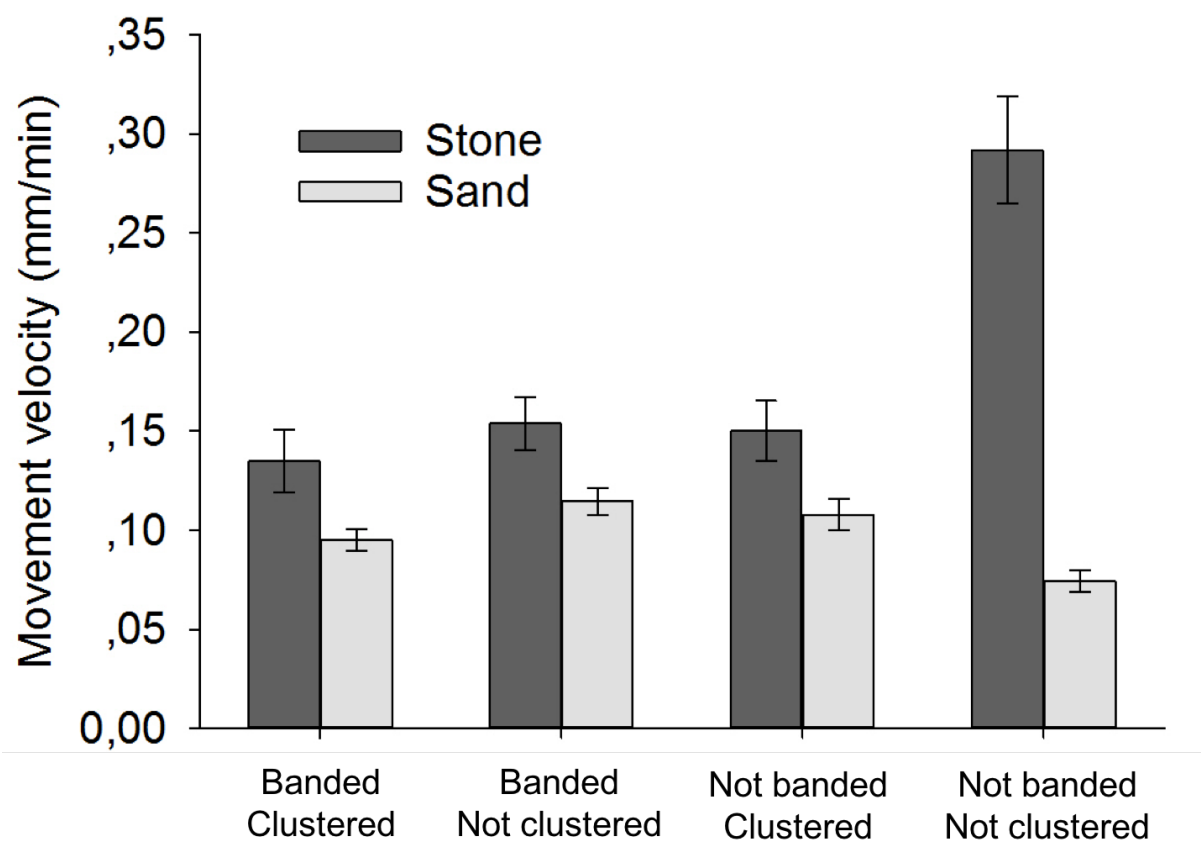
Figure 3: Persistence of experimental mussel beds in the field over time. A and B: Average cover decrease (% per day) over the course of the experiment for June and October. C: Decrease in cover (% per day) over the first 6 days, and D: in the remaining experimental period. N=28, Mean +/- S.E.



496

497 Figure 4: Effect of experimental self-organization treatments on clump formation in laboratory and
 498 field conditions. A: Average number of mussels per clump (Mean +/- SE). B: Average number of
 499 loose, individual mussels (Mean +/-SE).

500



501

502 Figure 5: Average movement velocity of a individual mussels under laboratory conditions (Mean +/-
 503 SE). Isolated individual mussle on a rocky surface increase their velocity, whereas movement on sand
 504 under these consitions is hampered.