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Published in:
 Science

DOI:
[10.1126/science.1163952](https://doi.org/10.1126/science.1163952)

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Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2008

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van de Koppel, J., Gascoigne, J. C., Theraulaz, G., Rietkerk, M., Mooij, W. M., & Herman, P. M. J. (2008). Experimental evidence for spatial self-organization and Its emergent effects in mussel bed ecosystems. *Science*, 322(5902), 739-742. <https://doi.org/10.1126/science.1163952>

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Supporting Online Material for

Experimental Evidence for Spatial Self-Organization and Its Emergent Effects in Mussel Bed Ecosystems

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Published 31 October 2008, *Science* **322**, 739 (2008)
DOI: 10.1126/science.1163952

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Materials and Methods
SOM Text
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Movies S1 and S2

Supporting Online Material

Materials and methods

Detailed site description

Mussel bed patterning was studied on the tidal flats of the Menai Strait, Wales, UK (N53.245649, W4.105625) in July 2006. The tidal flats are used by mussel fisherman that seed them with young mussels (+- 1.5 cm size) and harvest the mussels after one to two years. On the older mussel beds, mussel density generally tracks the elevation, with high-density, near-homogenous stands on the hummocks, and low-density beds forming isolated clusters in the depressions, differing approximately 30 cm in elevation. On recently seeded mussel beds, densities reflect variation in seeding intensity and are unrelated to bed elevation.

Laboratory setup

Pattern formation by mussels was studied in the laboratory within a 130x90x27 cm polyester container filled with seawater. Mussels were obtained from wooden wave-breaker poles on the beaches near Vlissingen, the Netherlands (51.458713N, 3.531643E). They were kept in containers and fed live cultures of *Phaeodactylum tricornutum* daily. In the experiments, mussels were laid-out on an 80x60 cm surface of either concrete tiles (initial aggregation experiments) or a red PVC sheet (later cluster-size experiments). The red PVC sheet was used to provide a contrast-rich surface for later analysis. The container was illuminated using fluorescent lamps. The movement of the mussels was recorded by taking an image every minute using a Logitech QuickCam 9000 Pro webcam (www.logitech.com), which was positioned about 60cm above the water surface, and attached to a laptop computer. Fresh, unfiltered seawater was supplied to the container at a rate of approximately one litre per minute.

Aggregation experiments

We tested the hypothesis that pattern formation would occur in the absence of underlying heterogeneity in substrate of environmental conditions, for four mussel densities of 6.0, 3.8, 2.5 and 1.5 kg/m² (fresh weight), being approximately 1850, 1200, 750 and 450 individuals, respectively. Mussels were evenly distributed at the start of the experiments, after which movement was recorded over 24 hours at one minute intervals. Mussel movement was determined from the images by tracking the position of the mussels during the first 5 hours of the experiment.

Cluster size experiments

To test for the effects of cluster size on mussel movement, 8 clusters of 2, 8, 32, and 128 individuals were positioned in a 2x4 grid on the PVC sheet. Clusters were compacted as much as physically possible. The effect of supply of algae within high density clusters was tested by pumping a culture of *Phaeodactylum tricornutum* (1.5×10^6 cells/l) into the centre of the cluster with a rate of about 50 ml/minute from a hole in the PVC sheet. Movement rate of mussels was compared to clusters that received filtered seawater at the same rate, as a procedural control, and with clusters that received nothing.

Analysing movement trajectories

The trajectories of individual mussels were recorded manually using a custom-made MatLab program. The density of mussels in the neighborhood of a tracked mussel was estimated by measuring the fractional cover of mussels within at distances of 1.87, 2.50, 3.75, 5.00, 6.25, 7.5, 8.75, and 10 cm radius. Images were converted to binary bitmaps indicating the presence or absence of mussels. Circles were extracted from these bitmaps, having the tracked mussel at the centre. The centre circle of 1.25 cm radius was excluded as it contained the tracked mussel itself. To convert the cover estimates to density (as used in the model), we precisely located each mussel on 3 test images and related mussel densities within the above radii to mussel cover. Regression of density to cover yielded a conversion factor of 1.89 ($R^2=0.94$, $N=6128$). We adopted 2 for our simulations.

Statistical analysis

Distances covered by the mussels in one minute followed an exponential distribution: i.e. the frequency f of occurrence decreased with movement distance x ; $f(x, \beta) = 1/\beta \cdot \exp(-x/\beta)$, where the scale parameter β is a function of the densities of mussels in the neighborhood. We analyzed the relation between local mussel cover and movement speed with a generalized linear model (GLM) with an exponential distribution. The best single-scale model, as well as the best two-scale multiple model were selected from all possible sets using Akaike's information criterion ($S1$). Mean movement speed per cluster-size treatment was tested using analysis of variance, with Tukey's Honestly Significant Difference to detect significant differences between specific treatments ($S2$), or Mann-Whitney U-test with Bonferroni correction if the variance remained inhomogeneous after log-transformation.

Model development

We developed a simple individual-based model that describes the movement of individual mussels and concurrent pattern formation within a 50x50 cm arena with periodic boundary conditions and an even initial distribution of the mussels. The movement rate of any individual mussels depended on the density of mussels in its direct neighborhood, at either a scale of 1.87 cm (first simulation, presented in Fig. 4B) or at a scale of 1.87cm and 7.5 cm (second simulation,

presented in Fig. 4D). The movement rate was described as a random process that followed an exponential distribution (as in the statistical analysis). The β parameter for this distribution was a linear function of the neighborhood densities at the above-described scales, with parameters derived directly from the laboratory experiments.

The sensitivity of the model for parameter settings and the movement distribution type, being exponential, power-law, or normal, was investigated extensively using numerical simulation. The analysis revealed that our results were very robust, and qualitatively similar results were obtained with alternative movement distributions.

Field experiments

We selected two beds in the Menai Strait for our observations and experiments, one seeded with new mussels (approximately 2 cm length) 3 weeks prior to our field period in July 2006, and another with older mussels of approximately 3 cm in length that had been seeded the year before. We determined biomass per square meter, mean individual weight, and proportional space coverage by mussels in beds that had 1) dense homogeneous cover, 2) clear spatial patterns, and 3) isolated clumps of mussels, by sampling all mussels within a 31x31cm frame (0.1m²). Seven replicates were obtained per bed type. To estimate growth differences between mussels we obtained subsamples of 20 mussels per treatment in the younger bed. Mussels were weighted fresh (without shells) and then dried in an oven at 90 degrees centigrade to obtain dry weight. Cover was determined by photographing the frames before sampling, and coloring all mussels digitally on the image. From these measurements, we determined mussel fresh biomass per square meter, mussel fresh biomass within the area covered by the clumps, and individual dry weight.

The effect of bed type on mussel persistence was determined by inserting 10 painted mussels within the beds, and following their persistence within a square meter around the insertion points during one week. To distinguish between the effects of active attachment by the mussels and physical protection against dislodgement, we repeated this experiment using mussel mimics, which were two mussel shells partially filled with Blu-tac paste and glued together with superglue. This provided mimics with the same shape and a similar weight and density to live mussels. All treatments were replicated 12 times. Field experiments were analyzed using analysis of variance with Tukey's HSD comparisons. Data were log-transformed if this improved the homogeneity of variances.

Pattern analysis

Photographs of mussel patterns were analyzed for clustering and regularity in relation to spatial scale using Ripley's $K(S3)$. Ripley's K tests whether the number of objects that fall within a distance d from a particular object differs significantly from that expected from a random distribution. The relative positions of the mussels were obtained from orthogonal photographs.

The spatial pattern of mussel locations within each photograph was analyzed using the linearized L -function: $L(d) = \sqrt{(K(d)/\pi)} - d$, where d is the distance class, and $K(d)$ is Ripley's K function (S4). If the distribution of mussels follows complete spatial randomness, $L(d) = 0$ for all d . $L(d)$ values above zero indicate that the mussels are clumped at a particular scale d , while $L(d)$ values below zero indicate that the mussels are regularly dispersed at scale d . The significance of any observed value $L(d)$ is assessed by comparing it to the 95% confidence envelope for completely random patterns, which is obtained by Monte Carlo permutation (S5). Spatial analysis was performed with R (<http://cran.r-project.org>).

Additional experiments

We tested the possibility that the aggregation resulted from directed movement of mussels towards clusters, for instance triggered by excreted chemical substances. We put a small cluster of about 25 mussels in the centre of our experimental tank, and allowed it to settle for 2 hours to allow for the build-up of possible chemical gradients. We then placed 8 mussels in a circle around the cluster at 7 cm distance from the edge of the central cluster. We recorded the initial movement of the mussels using our web-cam system. No relation was found between the initial movement direction of the mussel and its position relative to the central cluster. From this we conclude that, in our experiments, the movement direction of mussels is not influenced by chemical clues excreted by conspecifics.

Supporting text - Experimental studies on self-organization in literature

The theoretical possibility for spatial self-organization has sparked a great deal of interest among theoretical ecologists in the past two decades (S6). Theoretical models predict that local, non-linear interactions between organisms or between organisms and the environment can cause the formation of coherent large-scale spatial patterns, even in completely homogeneous conditions. These patterns can take the form of regular spots, labyrinth structures, spiral waves, or scale-free patch distributions. Despite of their popularity among theoretical ecologists, however, many ecologists have expressed doubt about their relevance to ecological dynamics in the real world (S6-8). In this section, we review experimental evidence for self organization in ecological systems. We distinguish between experimental evidence for the mechanisms that underlie observed spatial patterns, and experimental demonstration of the formation of spatial patterns under (controlled) homogeneous conditions.

A wide range of studies exists that has investigated the mechanisms behind observed spatial patterns in various ecosystems. A strong experimental tradition exists in studying the mechanisms of spatial pattern formation in intertidal systems. Early studies recognized that successional dynamics in combination with physical disturbance such as strong waves or biological disturbances such as limpet grazing could generate clear spatial patterns in rocky shores, independent of the prevailing intertidal gradient (S9). Later studies recognized that

aggregation by organisms, rather than random disturbance, was an important cause of spatial structure. Aggregation has often been related to anti-predator defense (*S10-13*), reduced wave exposure and reduction of thermal stress (*S14*). Aggregation can generate intricate scale-free spatial patterns in combination with wave-induced disturbance (*S15*). Recent studies provide evidence that biological interaction can be scale-dependent, as for example in the outbreaks of the tussock moth (*S16*), which can induce self-organized heterogeneity in ecosystems. Similar experimental evidence for scale-dependent pattern-forming mechanisms has been obtained for intertidal wetlands (*S17*), mussel beds (*S18*), arid ecosystems (*S19*), salt marshes (*S20*), and patterned peat lands (*S21*).

Pattern formation in ecosystems typically occurs on large spatial and temporal scales (*S22*). For this reason, it is difficult to demonstrate the formation of spatial patterns under controlled experimental conditions, as has been done in studies of pattern formation in microbial (*S23*) or socio-biological (*S24*) systems. Hence, for most ecosystems, it is not possible to test unambiguously whether the proposed mechanism is the ultimate cause of observed spatial patterns, for instance by demonstrating that patterns change in response to alteration of the underlying process in a manipulative experiment. A nice exception, although not discussed in this context, comes from a study of hummocking in acorn barnacles in the rocky intertidal by Bertness et al (*S25*). Dense stands of barnacles were found to develop regularly-spaced hummocks of large barnacles as a consequence of the interaction of facilitation and competition among the barnacles. The authors demonstrate that patterns develop, in field conditions, on a flat artificial surface. Although scale-dependence is not mentioned by the authors, their data suggests that barnacles have a positive effect on barnacle feeding closeby (i.e., within the hummocks), but a negative effect at a somewhat larger distance (i.e., in between the hummocks), compared to a solitary barnacle, emphasizing the localized non-linear nature of barnacle interactions. This strengthens the view that barnacle hummocking is a form of self-organization.

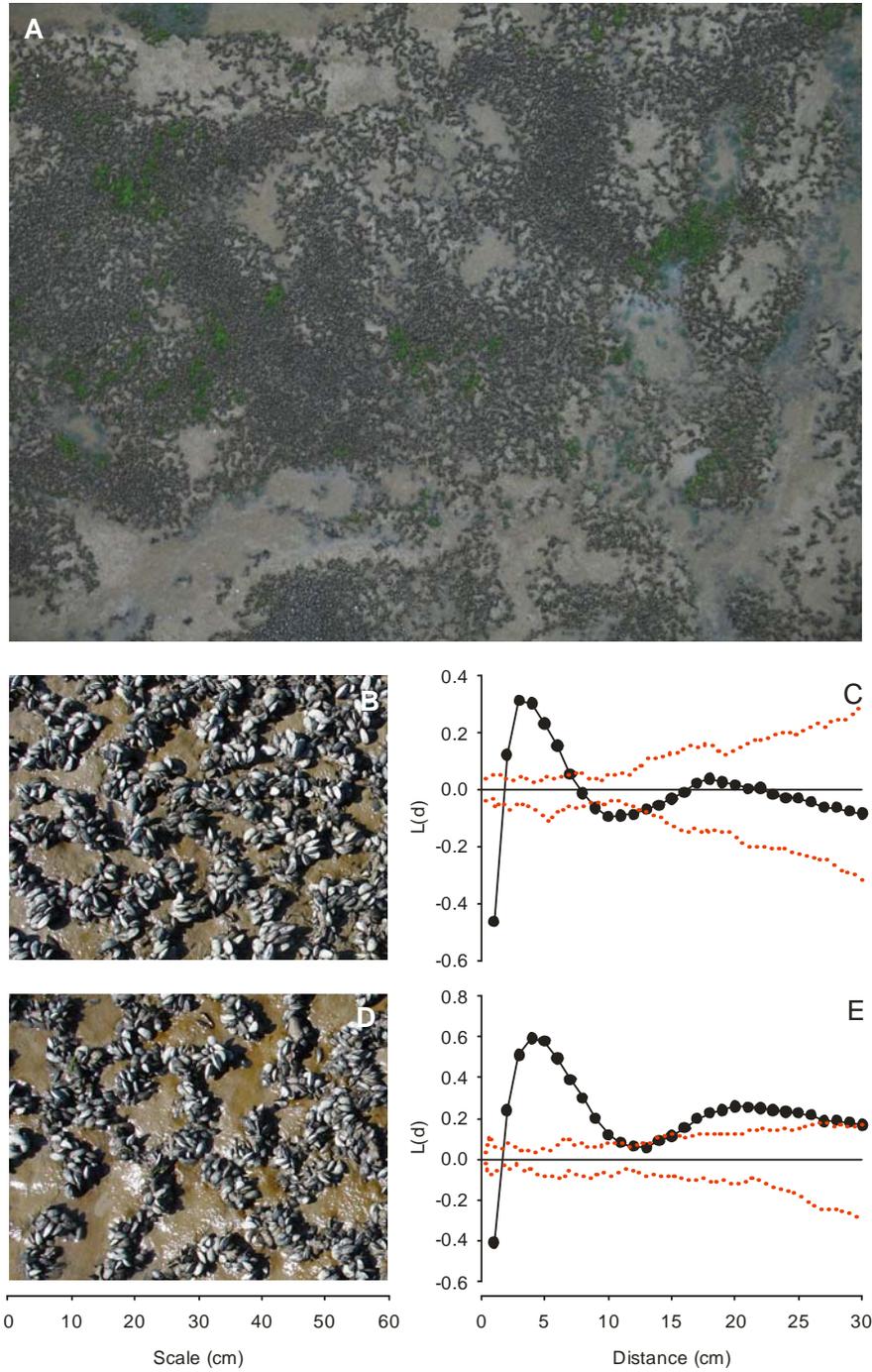


Fig. S1. An aerial photograph and two out-of-hand photographs of patterned mussel beds in the Menai strait near Bangor. The aerial photograph was shot using a remotely operated camera suspended from a blimp at approximately 30 meters height, providing an overview of an area of approximately 25 meters wide. **(B,D)** small-scale photographs represent various forms of spatial patterning that can be observed, loosely following the local micro-relief. **(C,E)** Point pattern analysis using the linearized Ripley's K : $L(d)$, indicating strong clumping at 3-5 cm scale ($L(d) > 0$), and regularity at 10 cm scale ($L(d) < 0$). This can be interpreted by the occurrence of clusters of about 5 cm across that sit at 10 cm distance from each other. The red dotted line represents the 95 % confidence interval, beyond which the observations deviate significantly from randomness.

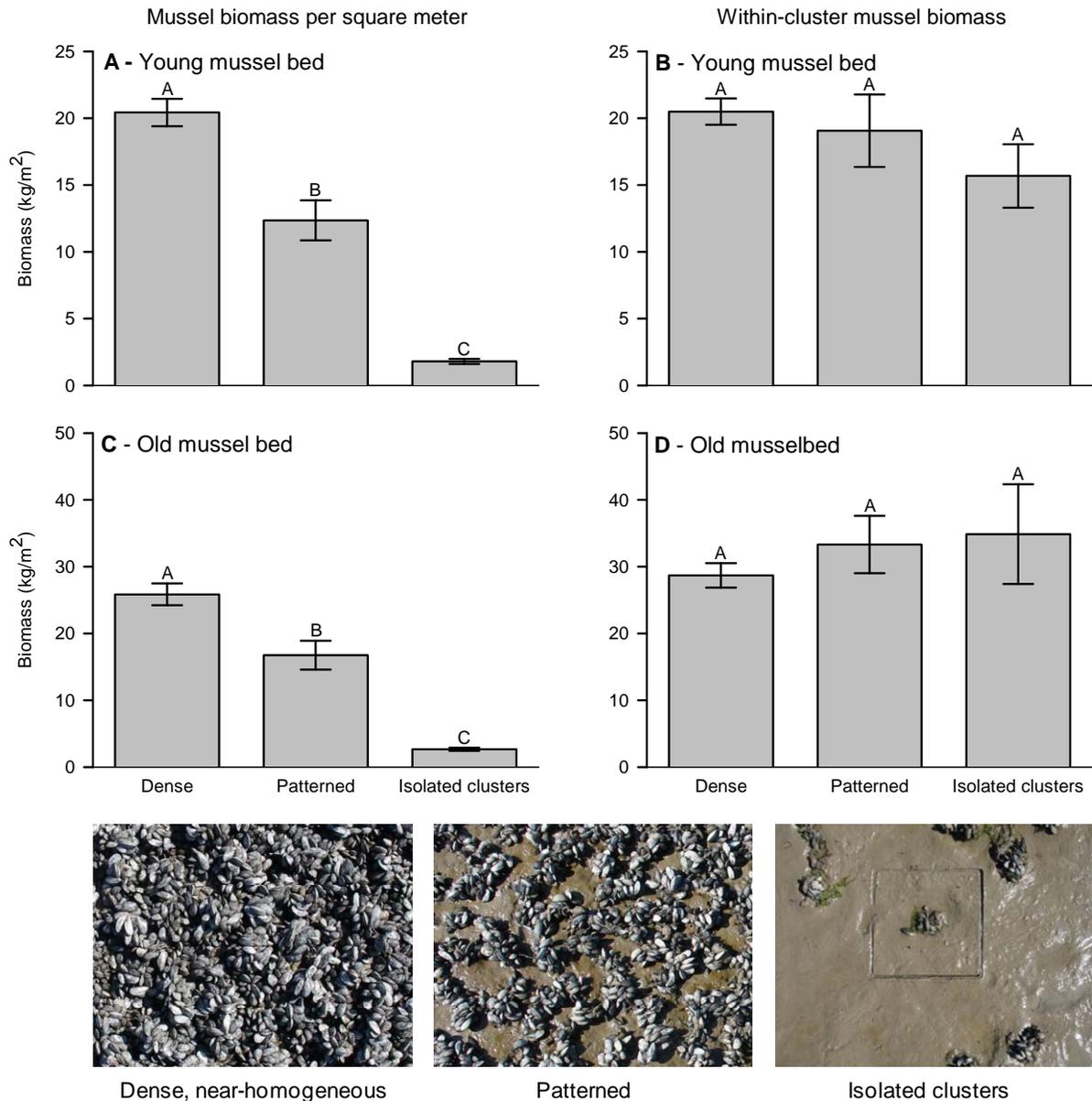


Fig. S2. Average biomass at a square meter scale and within-cluster biomass for dense homogeneous stands of mussels, patterned beds, and isolated clusters of mussels, for a young mussel bed that was seeded with mussels by fisherman 3 weeks prior to sampling, and an old mussel bed that was 3 years old. Whereas there was a clear difference in overall biomass per square meter in both the young (**A**: Oneway ANOVA, $F_{2,21} = 78.74$, $N = 21$, $P < 0.001$) and the old mussel bed (**C**: Oneway ANOVA, $F_{2,21} = 78.74$, $N = 21$, $P < 0.001$), no differences were found in the within-cluster biomass levels (Oneway ANOVA, young bed (**B**): $F_{2,21} = 1.3127$, $N = 21$, $P = 0.29$; old bed (**D**): $F_{2,21} = 0.4398$, $N = 21$, $P = 0.65$). Error bars represent the standard error of the mean, whilst the characters on top of the bars denote significant differences based on Tukey's Honest Significant Difference.

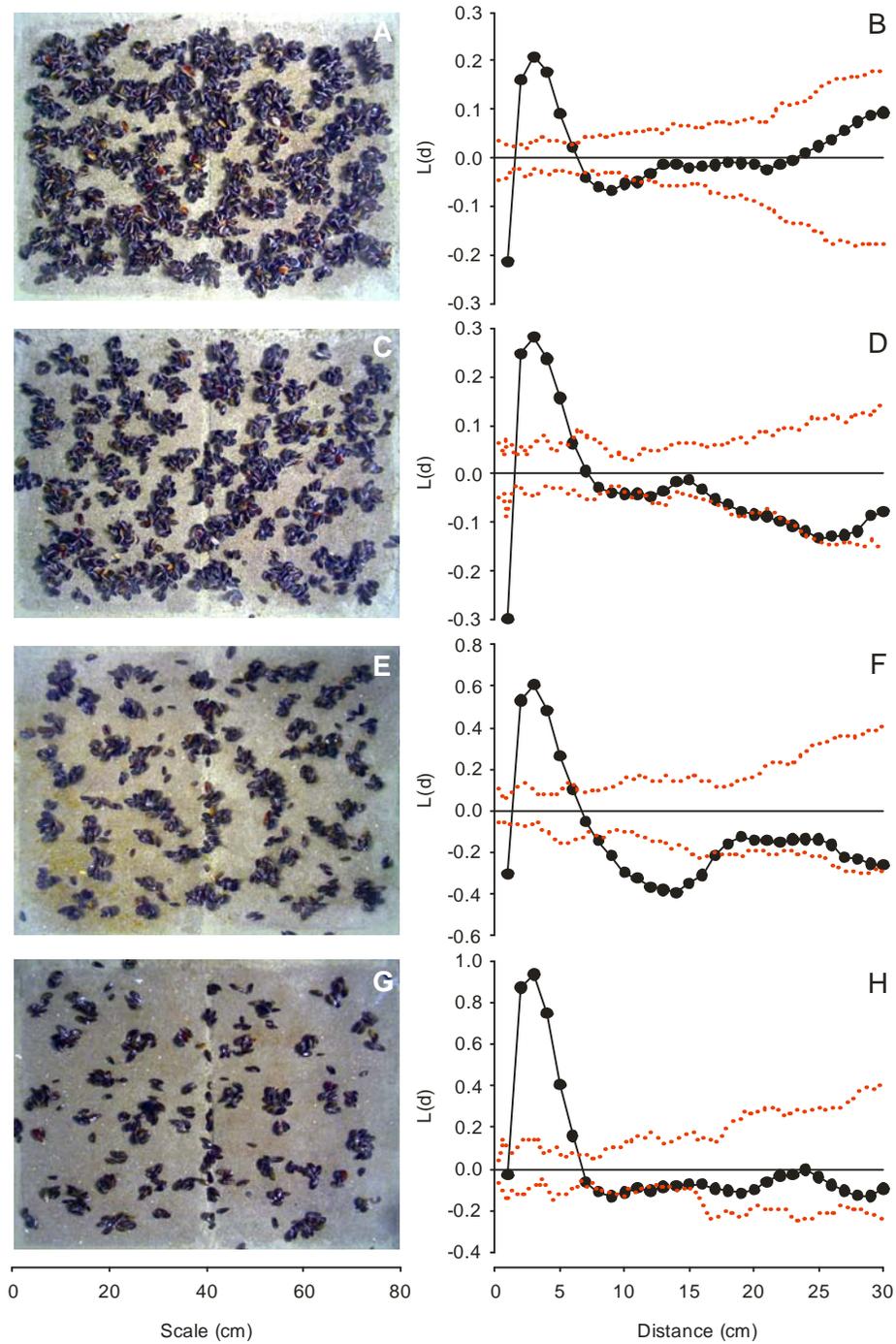


Fig. S3. Effects of mussel density on the formation of spatial patterns. Images **A**, **C**, **E**, and **G**, represent a density of approximately 1850, 1200, 750, and 450 mussels per 80x60 cm, weighing in total 2.5, 1.6, 1, and 0.63 kg, respectively. Panels **B**, **D**, **F**, **H** represent the respective point pattern analyses using linearized Ripley's K ($L(d)$). The analyses consistently reveal strong clustering at 3-5 cm scale ($L(d) > 0$), and regular spacing at 7-15 cm scale, which can be interpreted as clusters of 3-5 cm across at regular distance of 7-15 cm from each other. The red dotted line represents the 95 % confidence interval, beyond which the observations deviate significantly from randomness. Note that the degree of isolation of clusters increases with decreasing density.

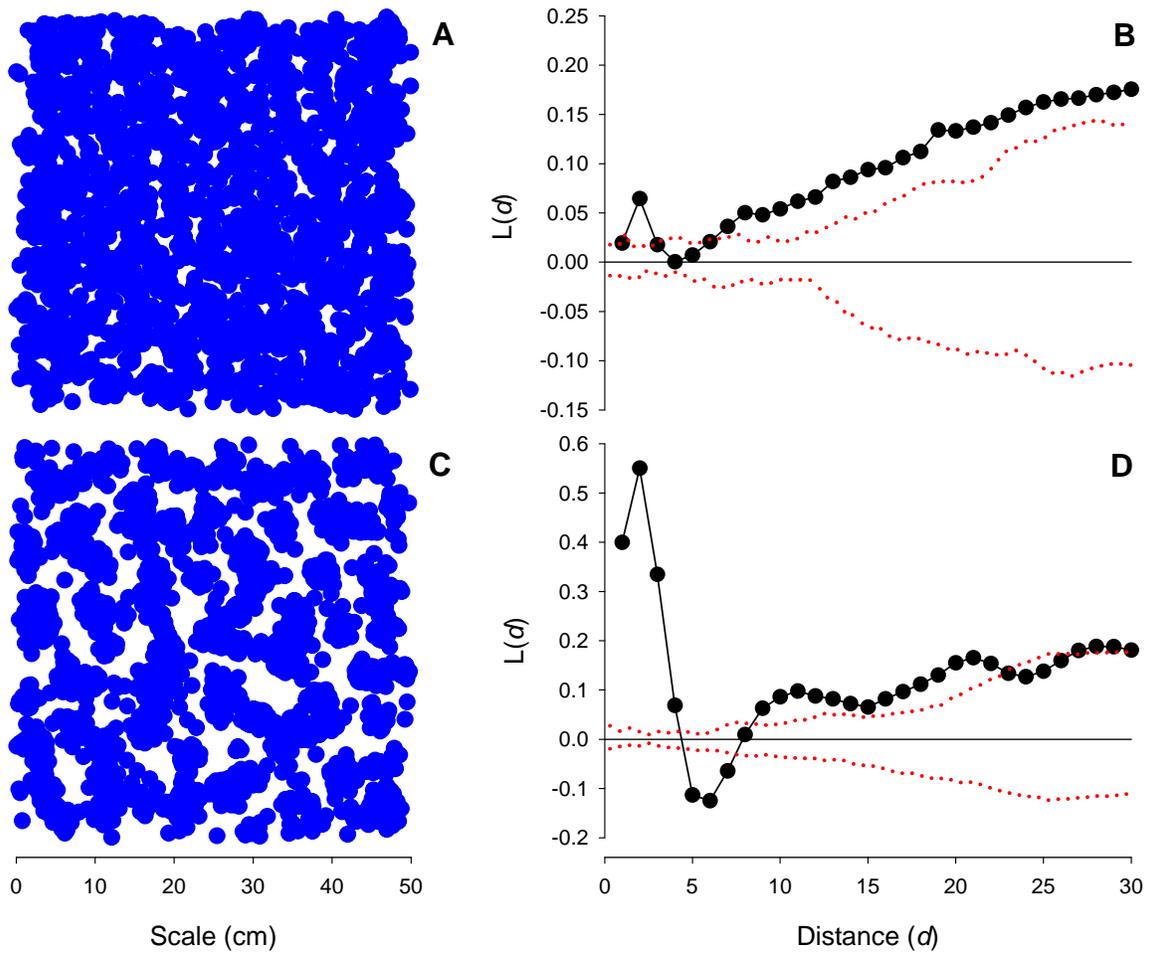


Fig S4. Point pattern analysis of the simulated patterns of Fig. 2, using the linearized Ripley's K ($L(d)$). The simulation with the single-scale model shows no signs of regularity, while the simulation with the two-scale model indicated strong clumping at 5 cm scale ($L(d) > 0$), and regularity at 10 cm scale ($L(d) < 0$), similar to those observed in both the Menai-strait field sites (Figure S1) and our laboratory experiments (Figure S3). The red dotted line represents the 95% confidence interval, beyond which the observations deviate significantly from randomness.

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Movies S1 and S2

1163952s1.mov: Time-laps movie showing the formation of spatial patterns by approximately 1850 mussels on an 80x60 cm concrete surface. The video covers a 10 hour time period (QuickTime movie, 9.0 MB).

1163952s1.mov: Time-laps movie showing the formation of spatial patterns by approximately 1200 mussels on an 80x60 cm concrete surface. The video covers a 10 hour time period (QuickTime movie, 7.8 MB).