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Eco-evolutionary feedbacks in self-organized ecosystems

de Jager, Monique

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Why mussels stick together:
self-organization affects the evolution of
cooperation

Monique de Jager, Franz J. Weissing & Johan van de Koppel

Abstract

Cooperation is an important driver for the persistence of populations in stressful environments. Yet, when neighbouring individuals provide sufficient help, less cooperative individuals may profit from their behavior and invade in the population. Using self-organizing mussels as our model template, we show that active aggregation into spatially structured populations can affect the evolution of cooperativeness. Using an individual-based model of mussel bed pattern formation, we demonstrate that active movement into the labyrinth-like patterns that we observe in natural mussel beds results in populations where individuals have an intermediate number of neighbours within cooperation distance. With an evolutionary model we then show that this intermediate number of neighbours can maximize the investment in between-mussel attachments in the population. Our results suggest that active movement of organisms into spatially structured populations can affect the evolution of cooperativeness.

Introduction

Cooperation between neighbouring individuals is often essential for survival in stressful environments (Bertness & Callaway, 1994; Callaway & Walker 1997; Holmgren et al., 1997; Stachowicz, 2001). Organisms ameliorate their environment locally, for instance by providing shade or by drawing moisture and nutrients towards themselves and close neighbours (Schlesinger et al., 1996; Aguiar & Sala, 1999), which allows others to survive in an otherwise hostile world. To what extent cooperation evolves in a population seems to depend on the nature and intensity of interactions between individuals (Doebeli & Hauert, 2005; West, Griffin, & Gardner, 2007; Van Dyken & Wade, 2012). When cooperation is costly and the recipients can reap the benefits of cooperation without helping others in return, cooperation by neighbouring organisms can be exploited by less cooperative individuals; an individual that profits from its neighbours' cooperative behaviour can afford to invest less in cooperation itself. The number of cooperating neighbours an individual has likely determines the effectiveness of its cooperation strategy and may affect the degree of cooperativeness that evolves within a population (Vainstein & Arenzon, 2001; Zhang et al., 2005; Ohtsuki et al., 2006; Hui & McGeoch, 2007).

Systems as diverse as mussel beds, coral reefs, marsh tussocks, tidal wetlands, peat lands, arid ecosystems, and ribbon forests are highly structured in space due to the interplay between local facilitation and long-range inhibition, for instance by depletion of nutrients (Klausmeier, 1999; Mistr & Bercovici, 2003; Rietkerk et al., 2004a; Rietkerk et al., 2004b; Van de Koppel et al., 2005; Van de Koppel & Crain, 2006; Rietkerk & Van de Koppel, 2008; Van de Koppel et al., 2008; Eppinga et al., 2009). In these systems, the number of potentially cooperating neighbours depends on the spatial scale and distribution pattern of the population. In many systems, the spatial pattern results from the active movement of organisms (Theraulaz et al., 2003; Jeanson et al., 2005; Hemelrijk & Hildenbrandt, 2012; Van de Koppel et al., 2008; De Jager et al., 2011). Accordingly, the movement strategies of these organisms can indirectly affect the number of neighbours an individual will encounter. In situations where costs and benefits of facilitation depend on the availability and density of local neighbours, the movement strategy

therefore affects the evolution of facilitation. It is, however, unknown under what circumstances movement promotes or hampers the evolution of cooperation.

An example of active pattern formation can be found in intertidal mussel beds. Mussels self-organize into large-scale labyrinth-like patterns (Van de Koppel *et al.*, 2005; Van de Koppel *et al.*, 2008). They use their foot to aggregate into a group of conspecifics after wide dispersion by the currents during the larval stage (Maas Geesteranus, 1942). When aggregated, mussels facilitate each other by attaching byssus threads (a glue-like substance) to the shells of conspecifics that are within reach. These attachments decrease dislodgement chance and predation risk for both the attaching mussel and the one receiving the byssus thread (Hunt & Scheibling 2001; Hunt & Scheibling 2002). Mussels that are sufficiently affixed by neighbours do not need to create attachments themselves and can therefore profit from having a lower level of cooperativeness. Through active aggregation into mussel clumps with various densities, mussels can modify the number of neighbours within their attachment range. By self-organizing into the labyrinth-like patterns that are characteristic for intertidal mussel beds, mussels attain an intermediate number of neighbours, which lies between the few neighbours within attachment distance in scattered distributions and many neighbours in dense mussel clumps.

In this paper, three questions regarding cooperation in mussel beds will be addressed. First, we investigate how the aggregation strategy of mussels affects the spatial pattern and, in particular, the number of neighbours available for cooperation. Aggregation in mussels typically leads to the formation of a spatial pattern consisting of regularly spaced strings and clumps (Van de Koppel *et al.*, 2005; Van de Koppel *et al.*, 2008). This self-organized pattern is likely related to the number of neighbours that mussels experience, ranging from few neighbours in scattered distributions to many neighbours in dense clumps. We tested this hypothesis using an individual-based model (IBM; de Jager *et al.*, 2011; de Jager *et al.*, 2014). Second, we examine how the number of neighbours affects the evolutionarily stable degree of cooperativeness with an adaptive dynamics approach (Geritz *et al.*, 1998). Here, cooperativeness corresponds to the tendency of attaching byssus threads to neighbours (e.g. the 'attachment tendency'). Building

on the fundamental assumption that the spatial pattern relates to the average number of neighbours that a mussel can attach its byssus threads to, investigating how the number of neighbours affects the evolution of the attachment tendency of mussels gives us insight into whether and how aggregation strategies promote or hamper cooperation. Third, we study the effect of harshness of the environment, which is likely to influence the results of our evolutionary model. How well a mussel is attached to its neighbours influences its survival under stressful conditions. We examine the evolution of between-mussel cooperation over a range of environmental conditions. Furthermore, we take into account that environmental stress likely differs substantially between generations, which may further affect evolutionary processes.

Methods

An individual-based model of self-organized patterning

We modelled the effect of individual aggregation strategies (the ‘settlement threshold’) on the formation of mussel beds with an individual-based model (IBM). The self-organized pattern in mussel beds is a compromise between reducing wave stress and predation risk (requiring dense aggregations) on the one hand and minimizing food competition (requiring low densities on a larger spatial scale) on the other (Van de Koppel *et al.*, 2005; Van de Koppel *et al.*, 2008). Hence, mussels move around until they find a location where the number of neighbours within attachment distance is high enough to decrease dislodgement risk while the mussel density over a longer range is sufficiently low to decrease competition for algae. We developed an individual based model that describes pattern formation in mussels by relating the chance of movement to the short- and long-range densities of mussels, following De Jager *et al.* (2011). We consider 1600 circular individuals with a diameter of 1 cm that are initially spread homogeneously on a 25 x 25 cm surface. In each of the 500 time steps within a simulation, all individuals get a chance to move in random order. Whether a mussel moves or not depends on the density of mussels within the local attachment range of 1.1 cm \emptyset (i.e. the ‘local density’) and the density of mussels within the larger, 3.3 cm \emptyset competition range (i.e. the ‘long-range density’); a mussel moves when the local density is lower than a certain settlement threshold (which we will vary below) and/or when the long-

range density is higher than 0.7 individuals/cm². These parameter values were estimated using a regression analysis of experimental data (Van de Koppel *et al.*, 2008; De Jager *et al.*, 2011). We modelled movement of individuals to correspond to natural mussel movements, using a heavy-tailed step length distribution (a Lévy walk with $\mu = 2$; De Jager *et al.*, 2011), where steps are made in random directions and their lengths are drawn from a power law distribution. A mussel ends its step prematurely when it encounters a conspecific (De Jager *et al.*, 2014). In our model, mussels cooperate after pattern formation (and not during); therefore the attachment of byssus threads does not impair mussel movement. To examine the relation between the number of neighbours within the facilitation range and the spatial structure that emerges in the self-organized mussel bed, we vary the settlement threshold, e.g. the minimum mussel density required for local aggregation. We simulated mussel bed formation for a range of settlement thresholds and plotted the emerged spatial patterns. We calculated the average number of neighbours \pm SE within attachment range for each simulation.

A model of the evolution of between-mussel cooperation

To investigate the evolution of cooperation, we make two plausible assumptions on how the survival probability and the fecundity of a mussel is affected by its attachment tendency A and on the number n of neighbours within attachment distance. The attachment tendency A ($0 \leq A \leq 1$) corresponds to the probability of attaching a byssus thread to any given neighbour. Hence, a mussel with attachment tendency A and n neighbors attaches itself on average to $n \cdot A$ of its neighbours. Mussels, however, do not only make attachments themselves, but also receive attachments from other mussels. Hence, the total number of attached neighbours N depends on both a mussel's own production of byssus threads ($n \cdot A$) and on the number of attachments produced by its neighbours. A mussel can be attached to a neighbour by its own byssus thread, by the byssal attachment of its neighbour, or by both; it stays disconnected from the neighbour if both do not attach to one another. Thus, we can calculate the probability that two mussels are attached as 1 minus the probability that they remain disconnected. Given that a mussel has n neighbours, an attachment tendency A , and neighbours with an attachment tendency A' , the expected total number of attached neighbours is given by:

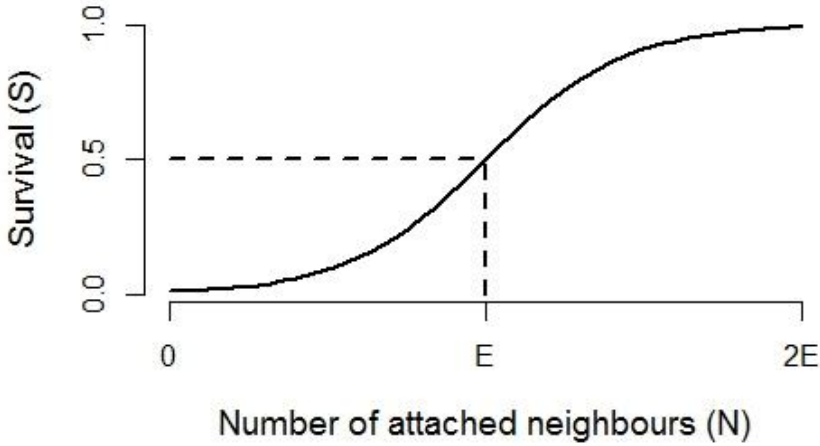


Figure 5.1: We assume that survival is a sigmoid function of the number of attached neighbours. The parameter E corresponds to that value of N for which the survival probability is 0.5. Intuitively, E may be viewed as a measure of the harshness of the environment: under mild conditions (small E), survival is already high for small values of N , while under harsh conditions (large E) survival is low unless mussels are attached to a large number of neighbours.

$$N(A, A') = n * [1 - (1 - A') \cdot (1 - A)]. \quad (5.1)$$

We consider this total number of attached neighbours to be an important determinant of an individual's survival probability. We assume that survival is high when a mussel is attached to many neighbours and is much lower when a mussel has only few attached neighbours:

$$S(A, A') = [1 + e^{-\lambda(N(A, A') - E)}]^{-1}. \quad (5.2)$$

Here, E is the number of attached neighbours needed for the survival chance to be 50 percent and λ determines the steepness of the logistic, S-shaped function (Fig. 5.1). Throughout, we will assume that survival for mussels attached to zero

neighbours is 1% ($S_0(0) = 0.01$). This imposes a constraint on the parameters λ and E , essentially reducing the number of parameters to one.

We further assume that the production and attachment of byssus threads has fecundity costs and consider a linear relation between fecundity and the average number of byssus threads produced:

$$F(A) = 1 - c \cdot n \cdot A. \quad (5.3)$$

Here, c denotes the costs per cooperation with a neighbour (Nicastro et al., 2009).

To study the evolution of the attachment tendency, we use an adaptive dynamics approach (Geritz *et al.*, 1998). To this end, consider a monomorphic resident population with attachment tendency A' , in which a mutant with strategy A arises. Whether this mutant invades the resident population depends on its relative fitness (W). For simplicity, individuals in the model are semelparous. We assume that fitness relates to the expected lifetime reproductive success, which corresponds to the product of the probability to survive (S) until reproduction and expected fecundity (F). Hence, the relative fitness of a mutant with attachment tendency A is given by:

$$W(A, A') = \frac{S(A, A') \cdot F(A, A')}{S(A', A') \cdot F(A', A')}. \quad (5.4)$$

If $W(A, A') > 1$, the mutant genotype has larger fitness than the resident genotype and can increase in relative frequency. Assuming asexual reproduction and mutations of small effect, the invasion of a mutant when rare typically guarantees that the mutant will spread to fixation, hence replacing the former resident (Geritz *et al.*, 1998). Through a series of consecutive gene-substitution events, the attachment tendency will evolve to an Evolutionarily Singular Strategy A^* (Dercole & Rinaldi, 2008). Such a strategy is evolutionarily stable if no mutant strategy can invade a population of individuals using strategy A^* . An Evolutionarily Singular Strategy A^* is convergence stable if those mutants successfully invade a given resident strategy A' that is closer to A^* (Geritz *et al.*, 1998).

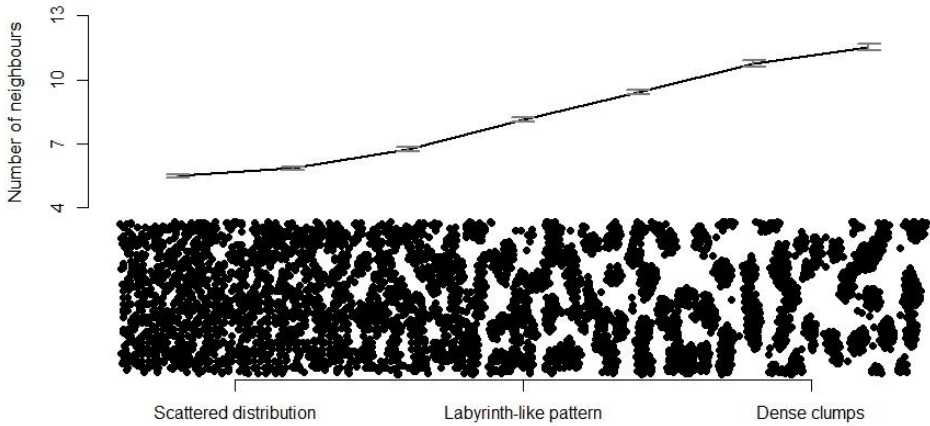


Figure 5.2: Spatial patterns and neighborhood sizes generated by the individual-based simulation model. (Bottom) By increasing the settlement threshold in the model from low (left) to high (right) values, the spatial distribution of mussels changes gradually from scattered to labyrinth-like to clumped. (Top) In line with pattern formation, the average number of neighbors in the attachment range increases as well (bars indicate SE).

The parameter E in eq. 5.3 represents environmental conditions, such as wave stress and predation risk. In harsh environments, E will take on a larger value than in benign environments. We will examine the evolution of attachment for a range of environmental conditions. Furthermore, environmental conditions are likely to vary between generations. Hence, we will also investigate the effect of alternating environments on the evolution of cooperation.

Results

Spatial patterning relates to number of neighbours

As a first step, we demonstrate that the aggregation strategy of mussels strongly affects their spatial distribution as well as the number of neighbours a mussel can interact with. To this end, we systematically changed the settlement threshold of the mussels in a population. Our individual-based simulations reveal that a scattered distribution results when the settlement threshold is low, that a labyrinth-like pattern emerges when the settlement threshold is intermediate, and that dense clumps are formed when the settlement threshold is high (Fig. 5.2 Bottom). The

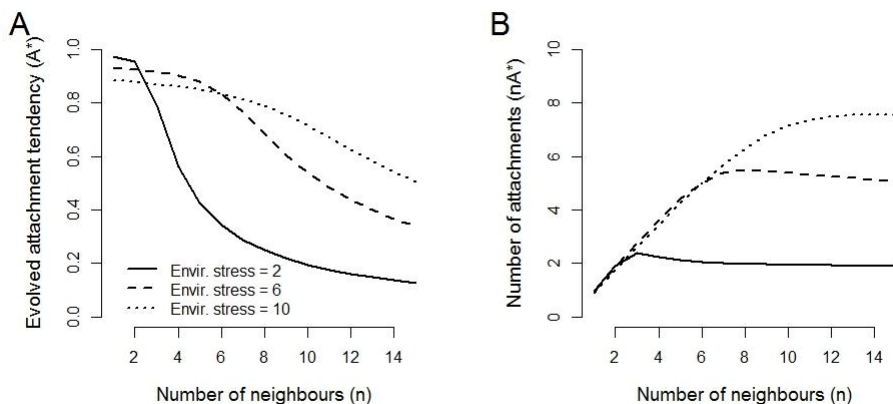


Figure 5.3: (A) Evolution of the attachment tendency is influenced by the number of neighbours within attachment distance and the level of environmental stress. (B) Investment in the number of attachments created to neighbouring individuals is hump-shaped and is for moderate stress levels maximized in the labyrinth-like patterns that we observe in nature ($n = 8$).

average number of neighbours increases with the degree of aggregation (Fig. 5.2 Top). For the remainder of this paper, we will use the following neighbourhood sizes (n) to represent the different spatial structures: $n = 6$ for scattered distributions, $n = 8$ for labyrinth-like patterns, and $n = 12$ for dense mussel clumps. Because natural mussel beds are often labyrinth-like, we specifically concentrate on how an intermediate number of neighbours ($n = 8$) affects the evolution of the attachment tendency A .

Evolution of the attachment tendency A

By actively aggregating into spatially structured mussel beds, mussels are able to modify the number of neighbours they can cooperate with and may thereby also affect the level of cooperativeness that evolves in the population. For three different environmental conditions (benign ($E = 2$), moderate ($E = 6$), and stressful ($E = 10$)), Figure 5.3A shows how the evolutionarily stable attachment strategy A^* depends on the neighbourhood size n . In all three cases, the evolved level of attachment tendency decreases when increasing the number of neighbours. The differences in how the number of neighbours affects the evolution of the

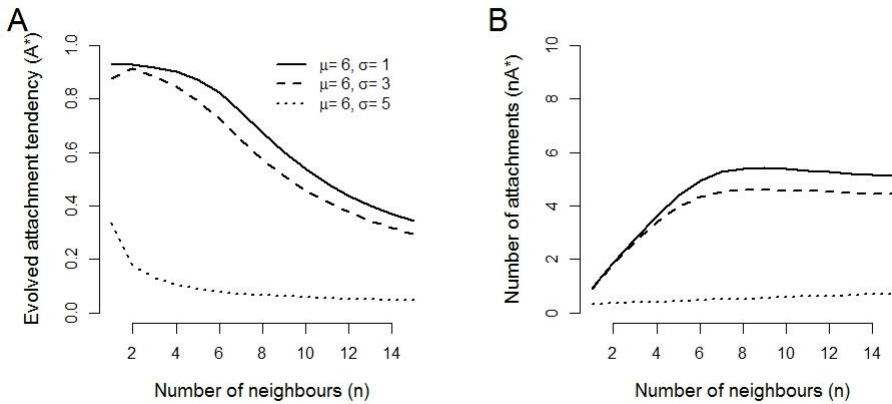


Figure 5.4: Evolution of attachment tendency when environmental conditions differ between generations and vary according to a normal distribution. **(A)** The evolved attachment tendency and **(B)** the number of attachments created per individual for a range of numbers of neighbours, given three different variances of the stress level distribution. The solid line indicates the case where environmental stress is normally distributed with little variance ($\mu = 6, \sigma = 1$); variance is increased for the two dashed lines ($\sigma = 3$ and $\sigma = 5$, respectively).

attachment tendency in Figure 5.3A illustrates that environmental conditions are of key importance in this evolutionary process. Especially in benign environments, active aggregation into spatially structured populations can have substantial effects on the attachment tendency that evolves.

Interestingly, the number of attachments created when cooperating at the evolved level A^* is maximized at intermediate numbers of neighbours ($n = 8$) for intermediate levels of environmental stress (Figure 5.3B). Though the attachment tendency provides us with a measure of cooperativeness, the costs and benefits of cooperation are better represented by the average number of attachments made to neighbouring individuals ($n \cdot A^*$). Investment in attachment peaks at different numbers of neighbours for different levels of environmental stress. In moderate environments, self-organization into a labyrinth-like pattern, which is characterized by intermediate numbers of neighbours ($n = 8$), can yield an evolved attachment tendency that maximizes the number of attachments made. Note that the number of attachments created can never be larger than n . Interestingly, $A \cdot n$ in Figure 5.3B

first increases more or less linearly with n before levelling off. Given the constraints of the system, the maximal number of attachments is realized for low numbers of neighbours. In that sense, cooperativeness is maximized at low values of n . Nevertheless, investment in attachments is maximized in labyrinth-like patterns or dense mussel clumps, depending on environmental conditions.

Changing environmental stress levels

Because mussels disperse over a wide range as larvae before settling on a mussel bed, environmental conditions are most likely different between generations. Adaptation of between-mussel cooperation to a particular stress level is therefore difficult and evolution of cooperation becomes more challenging than described above. In Figure 5.4, we considered the three situations where the environmental stress level a generation encounters is drawn from a random distribution ($\mu = 6$) with low ($\sigma = 1$), intermediate ($\sigma = 3$), and high ($\sigma = 5$) variation in stress, but the results below are also valid for stress level distributions with higher or lower μ . When variation in E is high, the evolutionarily stable attachment tendency is very low for all n (Fig. 5.4A), as is the number of attachments created (Fig. 5.4B). Highest levels of between-mussel cooperation evolve when mussels have few neighbours and variation in environmental stress is low. With a mean stress level $\mu = 6$, little variation in environmental stress gives rise to a hump-shaped relation between the number of neighbours and the average number of attachments a mussel produces, which is quite similar to the situation without variation in environmental conditions between generations (Figure 5.3). Increased variation in environmental stress between generations causes lower attachment tendencies to evolve than when conditions are more stable.

Inter-generational variation in environmental stress implies that the attachment tendency that evolves when environmental stress differs between generations is either lower or higher than the attachment tendency that would evolve when conditions throughout all generations remains constant. For instance, when stress follows a normal distribution with $\mu = 6$ and $\sigma = 1$, the evolved attachment tendency is approximately 0.82, 0.69, and 0.43 in scattered distributions ($n = 6$), labyrinth-like patterns ($n = 8$), and dense clumps ($n = 12$), respectively, regardless of the environment met by the current generation. When a mussel bed

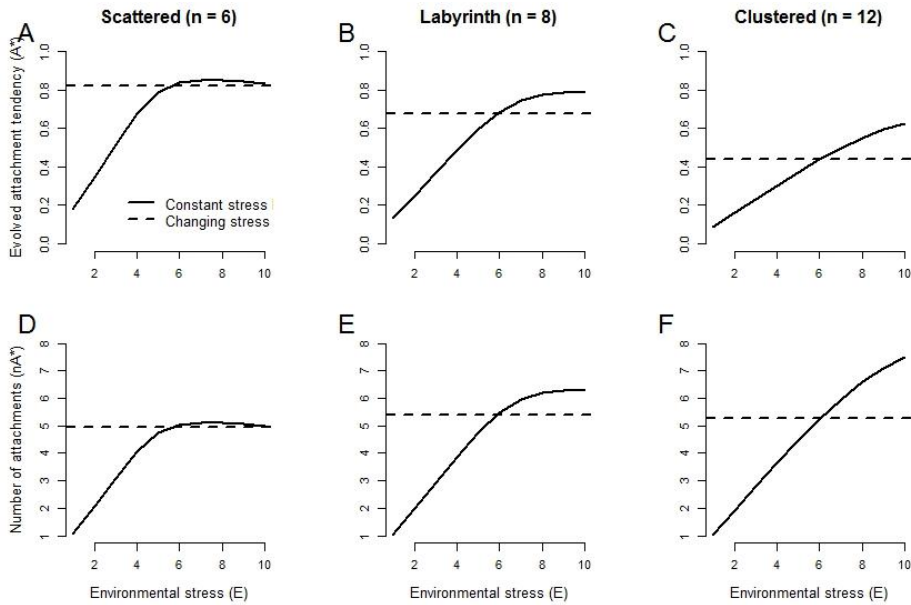


Figure 5.5: Evolution of between-mussel cooperation for three spatial population distributions and a range of environments, when environmental stress differs between generations (dashed lines) or remains constant (solid lines). The attachment tendencies that evolved in both constant and changing environments in scattered beds (A), labyrinth-like patterns (B), and dense clumps (C). (D-F) The average number of attachments created by an individual per spatial pattern and stress level. Here, we used the normally distributed stress levels ($\mu = 6$, $\sigma = 1$) to model evolution of between-mussel cooperation in inter-generational variation in environmental stress.

emerges in a benign environment, the mussels are attached to more neighbours than minimally needed for survival (Fig. 5.5D-F). However, mussel beds in harsh environments can easily get dislodged, as the evolved attachment tendency results in too few attachments than required for adequate mussel survival. Especially in dense clumps, the attachment tendency that would have evolved if all generations had experienced high environmental stress is substantially higher than the attachment tendency that evolves when generations experience different stress levels (Fig. 5.5C). In this sense, dense clumps are more risk-prone than scattered distributions. Overall, the level of cooperativeness that evolves in self-organized mussel beds appears to depend on the range and frequency of occurrence of environmental conditions and on the spatial pattern that is generated within the mussel bed.

Discussion

Cooperation is often a necessity for survival in harsh environments and is therefore found in many species. Organisms utilize a multitude of supporting traits and behaviours, such as local dispersal, reciprocity, and punishment, to maintain high levels of cooperation (West *et al.*, 2007). Here, we demonstrate a new behaviour that can promote the evolution of cooperation: active movement into spatial patterns. Though earlier studies have highlighted the importance of spatial structure in locally dispersing populations to improve relatedness amongst cooperating individuals (Ohtsuki *et al.*, 2006; Santos *et al.*, 2006; Masuda 2007), we demonstrate that spatial patterning can also promote cooperation in the absence of kinship between neighbours. Our theoretical analysis reveals that in intertidal mussels – where individuals disperse over a wide range – aggregation into spatial patterns stimulates the evolution of cooperation, despite of a complete absence of relatedness among the cooperating conspecifics. Yet, because mussels benefit from any attachment of byssus threads with neighbouring individuals, some degree of between-mussel cooperation evolves in any type of mussel bed, irrespective of the spatial pattern. Our analysis, however, shows that cooperative interactions by formation of byssal attachments can be maximized when the mussels form a self-organized, labyrinth-shaped pattern, where they interact with an intermediate number of neighbours. From this study and others (Ohtsuki *et al.*, 2006; Santos *et al.*, 2006; Masuda 2007), we can conclude that spatial patterning can substantially influence the degree of cooperativeness that evolves in a population, both in species with local and long-range dispersal.

From a game-theoretical point of view, spatial population structure is generally thought of as the consequence of local dispersal of offspring (Nowak & May, 1992). As local dispersal initiates spatial heterogeneity in a population, related individuals cooperate more amongst themselves than in mixed populations. Because of the advantages of cooperating with kin (i.e. inclusive fitness), cooperativeness can readily evolve in viscous populations where offspring remains local. Spatial population structure, however, is not necessarily the consequence of local dispersal; other factors, such as habitat suitability, predation, and food availability, might affect spatial population structure, also in populations with wide-ranging offspring dispersal. Recent studies have let go of the assumed link between

local dispersal and spatial structuring, but yet maintain using local dispersal in their models of cooperation in network-structured populations (Santos & Pacheco, 2005; Ohtsuki et al., 2006; Santos et al., 2006; Masuda 2007). Our work suggests that this assumption is not essential. We demonstrate that, despite of offspring dispersing over a wide range, spatial population structure can substantially increase the amount of cooperativeness that evolves in a population, depending on environmental conditions. Our work corroborates with a number of studies stressing that cooperative species exist that have spatially structured populations, but are genetically well-mixed (Godfrey & Kerr, 2009) and which act out of an innate cooperative strategy. Hence, our study highlights the importance of spatial structure and active aggregation for the evolution of cooperation even in populations where dispersal is not localized.

Self-organized ecosystems are known for their characteristic large-scale spatial patterns, including spots, stripes, labyrinths, and gaps, which are partly caused by local cooperation (Rietkerk & Van de Koppel, 2008). Kéfi *et al.* (2008) showed that cooperation in self-organized arid ecosystems can only be sustained when plants disperse locally. If these plants would disperse over a wide range, uncooperative individuals could invade in the population, causing the entire system to collapse. In our paper, we show that this conclusion may not be general for all self-organizing populations. In mussel beds, local dispersal is not necessary for the evolution of cooperation. Although cooperation in self-organized arid systems and mussel beds show similarities – for instance, cooperation in both systems resembles a Snowdrift Game (Doebeli & Hauert, 2005) – the main difference lies in the mobility of the individuals. In arid systems, plants cannot move around, and hence have to accept the neighbourhood they encounter, as they are dependent on the location to which their seeds disperse. When plant density drops because of a decrease in cooperativeness, plants have fewer neighbours to cooperate with. As life with less neighbours is even tougher, less individuals produce offspring, causing the eventual collapse of the system. In mussel beds, a similar number of neighbours can be maintained throughout generations, despite fluctuations in mussel density. Hence, because of their mobility, mussel populations can be maintained at low levels of cooperation, which would cause evolutionary suicide in arid systems. This suggests that cooperation can more easily

be sustained in ecosystems with actively aggregating organisms, where local neighbourhood size is to a certain extent independent from population density.

Variability in environmental conditions can have substantial consequences for how well a population is adapted to its environment. The level of cooperativeness that evolves when environmental conditions are continually changing between generations can be too little in highly stressful environments, resulting in the dislodgement of entire mussel beds after settlement in the wrong locations. In most intertidal ecosystems, an extensive range of environmental conditions can be encountered at any time, from very benign habitats that also provide little food, to very harsh conditions where food is often abundant. Moreover, mussel offspring is likely to reach all of these habitats, as is witnessed by the high availability of mussel spat on artificial settlement structures. This implies that the offspring of any mussels can spread itself over different habitats where a harsher environment implies a better food supply. For simplicity, we did not take this correlation between environmental stress and food availability into account; further research may show whether the inclusion of this relationship will give different results. It is likely that the levels of cooperation that are found in real-world mussels reflects an adaptation to the habitat where they can generate the highest number of offspring, taking into account the availability of the habitat in the overall area.

For the sake of simplicity, we adopted a number of simplifying assumptions that do not agree with the conditions that mussels, or any real-world organism, would encounter. In our model, we used semelparous individuals, whereas real mussels can survive for many years and reproduce at least once a year. In mussels, reproductive output per unit of biomass increases with age, as growth takes an ever smaller part of energy. Under most circumstances, our simplification has little consequences, yet it might become important in temporally variable environments. We assumed a fixed self-organizing behavior within each and throughout generations; in each simulation of our IBM, all individuals used the same set of rules, including the settlement threshold, to move into a spatial pattern. This is an unrealistic assumption for several reasons. For example, generations are likely to differ in initial overall density; a scattered population in a

dense mussel bed will result in a higher number of neighbours within attachment distance than in less dense but patterned beds. Especially for small and large settlement thresholds, a stable population structure may not be reached due to too high or too low overall mortality rates, respectively, hence creating differences in mussel densities. Furthermore, individuals might differ in their self-organizing strategy; though some are aggregating in dense clumps, others may be strategically moving away from dense mussel clusters. The settlement threshold used in our IBM may be a trait that is under evolutionary selection itself and might even jointly evolve with cooperation. Because we were interested in how spatial patterning affects the evolution of cooperation, we stayed with our assumption of a fixed aggregation behavior within and between generations.

Our study demonstrates that active self-organization can have substantial consequences for the degree of cooperation that evolves in a population. Inversely, self-organized spatial patterns have been described in a wide range of ecosystems, and many of these studies highlight the importance of cooperative interactions for the formation of these spatial patterns. In patterned arid bush lands, for instance, plants promote the infiltration of water into the soil, facilitating other plants (Klausmeier, 1999). This highlights the potential importance of feedback interaction between pattern formation processes on the one hand, and cooperation on the other. Yet, so far, the evolution of cooperation and the pattern forming characteristics of organisms, such as their aggregative behavior, have been studied in isolation. The joint evolution of pattern forming properties and cooperative behavior is, for this reason, an interesting subject for further investigation.

