

ARE MUSSEL BEDS SELFISH HERDS? MUSSELS SELF-ORGANIZE INTO FRACTAL AGGREGATIONS

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Abstract

Soft-bottom mussel *Mytilus edulis* L. beds have tremendous ecological and economic importance, yet little is known about the mechanisms that create their fractal power-law spatial distributions. I propose that the presence of light warns mussels of thermal stress and predation by visual predators. The response of mussels follows “the selfish herd” phenomenon, where animals self-organize into tight groups to lower their per capita mortality risks. Self-organization is known to create fractal power-law distributions in nature, so aggregation may be the underlying reason for mussel bed spatial structure. I tested the hypotheses that:

1. Juvenile and adult mussels move into aggregations at higher rates in the light than in the dark.
2. P:A ratio, A/mussel, and P/mussel decrease as aggregation size increases.
3. Mussel aggregation causes fractal power-law clustering and fractal assemblages.

In the laboratory on July 2007 at Great Wass Island, Maine, USA, intertidal mussels from identical size-class distributions (10-40mm) were placed in a uniform pattern on the bottom of 25cm-diameter, water-filled arenas in a paired design of light (natural light-dark cycle) and dark (foil-wrapped) treatments (N=8 arenas/treatment, 20 mussels/arena). After 24h, arenas were digitally photographed, and mussels were scored *in situ* for number of individuals per aggregation. Arena images were converted with ArcGIS into polygon shapefiles. For each arena

and each aggregation size, perimeter (P , relative length units), area (A , relative area units), $P:A$ ratio (relative length and area units), and fractal dimension D were calculated.

Mussels began to move immediately and formed aggregations of up to 6 individuals. The proportion of mussels that aggregated was significantly higher in the light than in the dark, with significantly different frequency distributions of aggregation sizes/arena. Aggregations had fractal outlines ($D \sim 1.10$) and singletons (single mussels) did not ($D=1.0$). Experimental arenas had fractal assemblages ($D \sim 1.15$) and initial conditions did not ($D=1.02$). $P:A$ and P/mussel were significantly lower for aggregated mussels than for singletons. A/mussel was significantly higher for aggregated mussels than for singletons. Moreover, mussels pulled themselves up onto each other, resulting in lower total A/arena and P/arena compared to uniformly distributed mussels.

These results are the first to demonstrate a self-organization behavior mechanism that produces fractal patterns in mussels. Such post-larval aggregation may contribute to the spatially complex power-law distributions of soft-bottom mussel beds in Maine.

Keywords: *Mytilus edulis*, fractal geometry, self-organization, facilitation, selfish herd, thermal stress

Introduction

Mussel beds are common features of marine intertidal and subtidal zones. They exhibit high densities, biomass, and respiratory flows (reviewed by Commito and Dankers 2001, Commito et al. 2005). *Mytilus edulis*, the blue mussel, is an economically important species that is found in both soft sediment and rocky habitats, where it is often a dominant spaceholder (Bertness and Leonard 1997, Gascoigne et al. 2005) and represents the largest proportion of the

biomass (Asmus 1987). In these areas, *M. edulis* acts as an ecosystem engineer by altering bottom surface topography and flow regimes (Fréchete et al. 1989) and producing copious amounts of organic waste (Commito et al. 2005). Such impacts lead to different fauna densities in areas of high mussel cover or mussel culturing sites compared to bare sediment (Commito 1987, Commito and Boncavage 1989, Dittmann 1990, Asmus and Asmus 1991, Grant et al. 1995, Ragnarsson and Raffaelli 1999, Dolmer et al. 2001, Hartstein and Rowden 2004, Smith and Shackley 2004, Commito et al. 2005). Thus, mussels are an important foundation species in hard-and soft-bottom habitats. Consequently, knowledge of mussel bed spatial organization is central to understanding the abundances and diversity of species within the community.

Numerous studies on mussel bed organization have shown that mussel beds have a fractal spatial pattern in rocky and soft-bottom systems (Snover and Commito 1998, Commito and Rusignuolo 2000, Kostylev and Erlandsson 2001, Erlandsson and McQuaid 2004, Crawford et al. 2006). However, the mechanisms underlying this organization pattern are largely unknown. One possible explanation for fractal organization is the “template hypothesis,” in which the distribution of species is fractal due only to the fractal nature of their suitable habitat (Halley et al. 2004). Power-law scaling can result from local positive interactions without an environmental power-law template (Pascual et al. 2002). Mussels need hard substrate for recruitment. But variability of terrestrial gravel and mussels occurs at different spatial scales, indicating that mussel spatial patterns are not simply the result of responding to a gravel template (Commito et al. 2005). Small mussels are positively correlated with adult mussels (Platt et al. 2008, Commito et al. 2008), and recent field experiments show greater mussel recruitment to live mussels than to gravel (Commito et al. 2008). It is instead probable that mussel spatial pattern is

the result of self-organization into fractal aggregations that lead to an overall patchy habitat (Snover and Commito 1998, Halley et al. 2004, Crawford et al. 2006, Commito et al. 2008).

In mussel beds, self-organization is likely the result of larval settlement and post-larval movement. Almost half of all mussels in the field are attached to live mussels (Commito et al. 2008). Other bivalve larvae, such as oysters, respond rapidly to chemical cues of conspecifics by moving downward to settle (Tamburri 1996). Gregarious behavior is also seen in adult zebra mussels, which will attach to sites with high mussel densities more often than to those with low mussel densities (Kobak 2001). Adult mussels placed downstream of mussel aggregations move significantly greater distances upstream than in control seawater without mussels (de Vooy 2003). Communication between mussels is caused by peptide cues, which are water soluble and can be produced by all living organisms (de Vooy 2003).

Living in an aggregation is costly for animals, as intraspecific competition often leads to reduced growth size, especially for mussels living at the center (Bertness and Grosholz 1985, Okamura 1986, Svane and Ompi 1993). However, mortality rates are still higher for solitary mussels than for those within an aggregation (Bertness and Grosholz 1985). This is because of the “selfish herd” phenomenon, in which aggregations lead to a decrease in the mortality risk of an individual (Hamilton 1971). Certain environmental factors and their associated risks can therefore lead to an increase in the aggregation response. For example, mussels in predator effluent or the effluent of injured conspecifics form more clumps, at a faster rate, than those that are placed in control seawater (Côté and Jelnikar 1999, Nicastro et al. 2007). This response makes evolutionary sense, as living in aggregations decreases the exposed perimeter (P) and area (A) of each mussel and therefore decreases per mussel predation risk. Mussels in aggregations are also less susceptible to extreme heat, so thermal stress may also increase the tendency of

mussels to aggregate (Helmuth 1998). Because the risks of both visual predators and high heat are usually accompanied by light, we propose that the presence of light “warns” mussels and causes them to aggregate. I propose that for *M. edulis*:

1. Juvenile and adult mussels move into aggregations at higher rates in the light than in the dark.
2. P:A ratio, A/mussel, and P/mussel decrease as aggregation size increases.
3. Mussel aggregation causes fractal power-law clustering and fractal assemblages.

Methods

I collected mussels at low tide 16 July 2007, from a natural mussel bed at Black Duck Cove, Great Wass Island, in Washington County, Maine. I removed mussel clumps from the substrate using scissors to cut the byssal threads, so as not to damage the foot. I conducted all laboratory work in the Downeast Institute for Applied Marine Research and Education. I placed mussels in flowing seawater in the laboratory for a 24 h acclimation period. The water was pumped from offshore (temperature=11°C, salinity=33ppt) through 750 µm mesh. Test arenas consisted of sixteen 18.93 L (5 U.S. gallon), white, semi-opaque plastic buckets that were chosen specifically for having smooth bottoms. Each arena had an inside diameter of 25cm and a height of 36cm. I filled all test arenas with seawater, conditioned them for 24 h, and emptied them before use.

After an acclimation period, I measured mussels using vernier calipers and temporarily placed them into small seawater-filled holding containers based on the following size classes: 5.0-19.9mm, 20.0-29.9mm, 30.0-39.9mm, 40.0-49.9mm, and 50.0-59.9mm. I filled each of the 16 arenas with 2L of water. I wrapped eight of the arenas with aluminum foil to ensure the

blockage of light. I placed the arenas in 2 rows, 8 arenas per row, in a paired design, with each pair consisting of a covered “dark” and a non-covered “light” arena. On 17 July at 1400 hrs, I set mussels up in the arenas in a radically symmetrical pattern, equidistant (3.5cm) from each other in concentric circles with their umbos facing the center. I used mixed age-classes, following the procedures of Côté and Jelnikar (1999) and Nicastro et al. (2007). In each arena 5 mussels were from the 5.0-19.9mm size class, 10 were from the 20.0-29.9mm size class, and 5 were from the 30.0-39.9mm size class. I determined mussel positions with a random number table. Previous experiments have found that mussels in this size range are optimal for movement experiments because they are not too small to monitor visually, but are small enough to move readily (de Vooy 2003).

I left the arenas undisturbed for 24 h, until 1400 hrs on 16 July. The temperature of the arena water was 17°C, the same as the air temperature in the laboratory and slightly below the typical low tide summer water temperatures that I recorded at Black Duck Cove (air: 21.0°C; rocky intertidal pools: 24.5-28.0°C (sun) and 18.0-21.5°C (shade); 10-50cm deep in water at low tide line: 18.0-24.5°C; mussel clumps at low tide: 21.0-22.5°C (sun) and 18.0:22.0°C (shade); exposed sand 3cm deep: 28.5-29°C). During the experiment, the laboratory’s fluorescent lights were turned on at 0730 hrs and turned off at 1600 hrs. Natural light entered the room through numerous windows. Sunset on 17 July occurred at 2011 hrs and sunrise on 17 July occurred at 0501 hrs, and the lunar cycle was at a new moon. A small amount of ambient light was discernible at night from plankton grow-lights 10m away.

At the end of the experiment, I categorized mussel aggregations in 2 ways: shells physically touching (ST) and individuals connected by byssal thread attachment (BTA). For each of these two categories within each arena, I recorded the number of aggregations and the

number of mussels in each aggregation. I defined an aggregation as containing 2 or more mussels (following Côté and Jelnikar 1999). I used a heterogeneity chi-square test to ensure that the arena data could be pooled. I ran chi-square tests to compare aggregation in light vs. dark conditions.

I took a digital photograph of the bottom of each arena to later determine fractal dimension and perimeter:area (P:A) ratios. I could not use initial photographs of the experimental arenas as a baseline because mussel movement was so rapid that it occurred before the setup of each pair of arenas was complete. For comparison with 24h arena results, I set up 3 “initial condition arenas” as described above. I took digital photographs of the bottom of these arenas immediately upon emplacement of the mussels.

I transformed arena photographs for analysis using ArcGIS 9.2 software (Environmental Systems Research Institute 2006). With ArcGIS 9.2 Modelbuilder, I classified the image into 10 classes using a Maximum Likelihood Classification method (Environmental Systems Research Institute 2006). I combined the darkest two classes into a “mussel” class, leaving the other eight classes to be combined into a “non-mussel class.” I converted the resulting raster into a polygon shapefile, and deleted all of the polygons that were not classified as mussel. I simplified the mussel polygons with an ArcGIS 9.2 Bend-Simplify algorithm to remove noise in the polygon outline, and removed any remaining noise manually using the ArcEditor toolbar (Environmental Systems Research Institute 2006). I signified mussel polygons with a 1 pixel white boundary on a black background.

To measure perimeter (P) and area (A), I selected for white polygons and exported them as a layer. I calculated P and A using the geometry calculator of ArcGIS 9.2 (Environmental Systems Research Institute 2006). I compared arena-wide perimeter, area and perimeter:area

values, respectively, across all groups using the non-parametric Kruskal-Wallis test. I then used an a posteriori test to determine where significant differences existed between groups. I used the Mann-Whitney U test to compare perimeter, area and perimeter:area values, respectively, of aggregated mussels to singletons.

I calculated fractal dimension in two ways, one for the outlines of individual clumps and one for the arena-wide spatial distribution of clumps. I calculated fractal dimension (D value) for the outlines of individual clumps using the box-dimension method available on Benoit 1.31 (TruSoft International Incorporated 2000). This program used 19 box sizes with a side-length of 120 pixels for the largest box size, a coefficient of box size decrease of 1.3, and an increment of grid rotation of 15.0° (TruSoft International Incorporated 2000). In this method, various sized squares are imposed upon an image of the system of interest and $N=kn^{-D}$, where n=the size of the square, k=a constant, and N=the number of squares intercepted by the image's outline (see Figure 1 for example). To determine arena-wide fractal dimension, I plotted perimeter and area on a scatterplot with a log-log axis for each arena. For this technique, the fractal dimension value is equal to double the slope of the resulting trendline (Slope=D/2; see Figure 2 for example). I compared arena-wide fractal dimension values across all groups using the non-parametric Kruskal-Wallis test. I then used an a posteriori test to determine where significant differences existed between groups. I used the Mann-Whitney U test to compare fractal dimension values of aggregated mussels to singletons.

Results

The Influence of Light on Aggregation Intensity

The presence of light increased the intensity of aggregation in mussels. At the start of the experiment, mussels began to move immediately. After 24 h, they had formed aggregations of up to 6 individuals by ST (shells touching; Figure 3 and Table 1) and 5 individuals by BTA (byssal thread attachment; Figure 4 and Table 2). All chi-square heterogeneity tests were not significant, so arenas could be pooled within each treatment (Table 3). Using ST, a mean (± 1 S.E) of 8.00 ± 0.87 mussels aggregated in the dark arenas and a mean of 10.63 ± 1.12 mussels aggregated in the light arenas. Using BTA (byssal thread attachment), a mean of 5.38 ± 0.918 mussels aggregated in the dark arenas and a mean of 8.75 ± 0.94 mussels aggregated in the light arenas. The proportion of mussels in ST aggregations was significantly different from the proportion in BTA aggregations in the light, but not in the dark (Table 3). For both ST and BTA aggregations, the ratio of aggregated to non-aggregated mussels was significantly different between the light and dark arenas (Table 3). The frequency distribution of the number of mussels in different aggregation sizes was significantly different between the light and dark treatments for BTA aggregations but not for ST aggregations (Table 3).

Perimeter, Area, and Perimeter:Area

Laboratory observations showed that aggregated mussels had pulled themselves up on top of each other, thereby decreasing arena-wide P as well as A. When comparing the light and dark treatments with the initial conditions, light arenas had the lowest mean P and A values and the highest mean P:A values, and the initial condition arenas had the highest mean P and A values and the lowest mean P:A values (Table 4). The Kruskal-Wallis test showed there to be a significant difference between P and A of the L, D and initial condition arenas (Table 5). The a posteriori test showed that this significant difference existed between the L and initial condition

arenas for both P and A (Figure 5). There was no significant difference between the P:A values of the arenas (Table 5).

P:A and P/mussel were significantly lower for aggregated mussels than for singletons according to the Mann-Whitney U test ($p < 5.29E-32$ for P:A and $p < 2.25E-04$ for P, Figures 6 and 8). A/mussel was significantly higher for aggregated mussels than for singletons according to the Mann-Whitney U test ($p < 0.0448$, Figure 7). P/mussel and A/mussel were highly correlated (Figure 9). P and A both showed a negative relationship with P:A (Figures 10 and 11).

Fractal Geometry

Mussels showed self-organizing behavior and aggregated into fractal power-law distributions. Both the light and dark arenas had fractal assemblages but the initial condition arenas did not (Table 7). The Kruskal-Wallis test showed no significant difference between the fractal dimension values of the arenas (Table 5 and Figure 12).

Single mussels had smooth Euclidean outlines and were not fractal ($N=20$, mean fractal dimension = 1.01 ± 0.02). However, mussel aggregations from both light and dark arenas had irregular, fractal outlines with higher fractal dimensions than single mussels (Table 8). Fractal dimension was higher for aggregated mussels than for singletons according to the Mann-Whitney U test ($p < 2.05E-05$, Figure 13).

Discussion

My experiments demonstrated that light is an environmental cue that causes significantly increased rates of aggregation in mussels. Furthermore, my experiments showed that when uniform mussels aggregate, their perimeter:area and exposed perimeter significantly decrease and that the fractal dimension of their habitat significantly increases. The arenas in this study had smooth bottoms, and aggregation was therefore the result of self-organization and not the result of an environmental template.

Aggregation behavior is crucial to our understanding of mussel bed dynamics and may be important in a wide variety of hard- and soft-bottom benthic systems. This behavior impacts the survivorship of mussels themselves as well as the physical structure of their habitat, which, in turn, affects the abundance and diversity of other species. Mussels are successful in rocky and soft bottom systems in both intertidal and subtidal habitats, which may in part be due to their gregarious behaviors (reviewed by Commito and Dankers 2001). For mussels, aggregation is an example of the “selfish herd” phenomenon and the recent emphasis on facilitation. In the past, much emphasis has focused solely on negative interactions in communities, such as competition (e.g. Dayton 1971, reviewed by Sih et al. 1985, Wilson 1990). For mussels, the presence of conspecifics creates a broader “realized niche” for an aggregated individual relative to the “fundamental niche” of a solitary individual (Bruno et al. 2002, Shouse 2003). The “selfish herd” phenomenon, which states that aggregation decreases per individual mortality risks, aids in creating this broader niche (Hamilton 1971). For example, fiddler crabs spatial pattern changes from dispersed to aggregated when there is the threat of predation (Viscido and Wethey 2002). Furthermore, fiddler crabs tend to run towards the center of the aggregation, as this is the area of least risk according to the “selfish herd” hypothesis (Hamilton 1971, Viscido and Wethey 2002). For mussels, risk factors include predation, thermal stress, and dislodgement by ice scour or

currents (e.g. Suchanek 1978, Worrall and Widdows 1984, reviewed by Commito and Dankers 2001).

The Influence of Light on Aggregation Intensity

The results supported my hypothesis that aggregation rates are higher in the light than in the dark. *M. edulis* veligers concentrate away from the light, regardless of the direction that light is coming from, whereas veligers in the dark distribute themselves randomly (Bayne 1964). Adult zebra mussels show strong negative phototaxis under laboratory conditions, where light significantly affects their direction of movement (Toomey et al. 2002) and their rate of site attachment (Kobak 2001). Small and large mussels also show negative phototaxis through a preference for shaded areas and a preference of re-settlement on black substratum over white substratum (*Limnoperna fortunei*- Uryu et al. 1996; *Dreissena polymorpha*- Marsden and Lansky 2000, Kobak 2001, Kobak and Nowacki 2007). From an evolutionary prospective, the aversion to light is probably due to the fact that its presence is a good indicator of thermal stress and visual predation. Both predation (Worrall and Widdows 1984) and thermal stress (Tsuchiya et al. 1983) are substantial mortality factors for populations of *M. edulis*. As a result, thermal stress and predation often set the upper and lower tidal height limits of bivalves, respectively (Suchanek 1978, Connell 1961).

Light acts as a way for mussels to perceive higher risks of mortality that may be reduced by gregarious behaviors. Research has shown that the threat of predation leads to an increase in aggregation, which decreases the prey mortality risk. For example, mussels aggregate significantly more in the both the presence of predator effluent and the presence of crushed

conspecific effluent, a predation risk cue, than they do in control seawater (Côté and Jelnikar 1999, Nicastro et al. 2007). For *M. edulis* and *Mercenaria mercenaria*, the per individual probability of being eaten by crabs drops as bivalve density increases (Walne and Dean 1972). The threat of per individual predation also decreases with aggregation in marine gastropods, for which mortality shows a strong negative correlation with density (Ray and Stoner 1994). At least three possible explanations for this decreased risk exist. First, per capita predation may drop simply as a density-dependent functional response. For example, wolf predation on moose increases up to an asymptotic value, after which further an increase in moose density will no longer impact predation rates (Messier 1994). This phenomenon is also seen in aphids, where ladybird predation intensity increases slightly with aphid aggregation, but per aphid predation mortality rate decreases (Turchin and Kareiva 1989). Second, conspecifics create a surface irregularity, which allow mussels to attach to two surfaces with their byssal threads instead of flat sediment, enhancing stability and protection (Marsden and Lansky 2000). Third, aggregated mussels present less surface area per mussel for predators to attack, especially for mussels at the center of aggregations. Aggregations can also decrease predation rates because the closing of one mussel in response to a predator may prompt other mussels in that aggregation to close (de Vooy 2003).

To my knowledge, no studies have shown that thermal stress directly causes aggregation. Aggregating has, however, been shown to reduce thermal stress. Aggregating helps to decrease heat stress and control water loss in neritid gastropods (Garrity 1984). In acorn barnacles, crowding decreases the temperature of the habitat surface and of the barnacles themselves (Bertness 1989). Crowding of barnacles increases barnacle survivorship (Bertness 1999) and also increases mussel recruitment (Lively and Raimondi 1987). Cordgrass and ribbed mussels

increase blue mussel recruitment by reducing solar stress on New England cobblestone beaches (Altieri et al. 2007). Similarly, goose barnacles increase survivorship rates of mussels during thermal stress by protecting the substrate surface from irradiation and increasing rates of evaporative cooling (Kawai and Tokeshi 2004).

Mussels living in aggregations during extreme heat conditions can be up 4-5°C cooler than solitary mussels and are able to maintain their temperatures better (Helmuth 1998). Aggregation reduces thermal stressors for a number of reasons. Aggregation lowers the area of mussel subject to solar radiation (Helmuth 1998) and the retention of water in beds absorbs heat from mussels and aids in evaporative cooling (Etter 1988). In addition, mussels bind cobbles and sediment together with their byssal threads, therefore decreasing substrate surface area and heat uptake (Stephens and Bertness 1991). Re-radiation of heat between mussels helps to even out temperature between mussels of different sizes (Helmuth 1998).

Although mussels aggregate under either light or dark conditions, varying their rates of aggregation is beneficial because aggregated living bestows costs as well as benefits on the mussels. In the absence of severe environmental pressures, for example when shade is added to a high heat area, the advantages of aggregated living are often lowered or absent (Bertness 1989). Acorn barnacles living in crowded areas show altered morphologies that can lead to lowered survivorship with up to 40% decreases in population size within one month (Bertness 1989). Aggregated mussels have low growth rates relative to unaggregated mussels due to density dependent pressures (Okamura 1986). Mussels living at the center of an aggregation tend to be the most susceptible to lowered growth rates (Bertness and Grosholz 1985, Okamura 1986, Svane and Ompi 1993). Live mussels alter conspecific growth rate more than inanimate mussel models, and negative impacts are therefore based on live mussel interactions (Okamura

1986). For example, competition for phytoplankton and other food items in the water column often leads to reduced growth rates (Bertness and Grosholz 1985, Okamura 1986, Svane and Ompi 1993, Fréchette et al. 1989). In addition, crowding by mussels may lead to decreases valve gaping and a subsequent decrease in potential feeding rates independent of phytoplankton concentration (Fréchette et al. 1989). The decrease in per mussel food availability also leads to decreased levels of reproduction rates (Okamura 1986, Starr et al. 1990).

There is often little movement of mussel positions within an aggregation once the aggregation has formed (Okamura 1986). Movement would not necessarily benefit mussels, as each position within an aggregation (edge and center, respectively) has both costs and benefits. For mussels living at the center of an aggregation, mortality risks are based on density dependence and but there is protection from predators (Hamilton 1971). For those living at the edge of an aggregation, external factors are the highest mortality risks but growth rates are not lowered relative to singletons (Okamura 1986).

Despite the costs, rates of density independent mortality are substantially lowered and recruitment rates are higher for mussels living in an aggregation (Bertness and Grosholz 1985). In fact, in their study of *Guekensia demissa*, Bertness and Grosholz (1985) projected that if there were no aggregations, within 5 years the mussel population would be reduced by 90% and juvenile survival over 2 years would drop to zero. *M. edulis*, *G. demissa*, and the brown seaweed *Ascophyllum nodosum* all show increased survivorship at high densities, especially in the presence of high physical stressors (Bertness and Leonard 1997). Goose barnacles and mussels show a similar relationship where, as measured by survivorship, the benefits of nonconspecific aggregation are greater than the costs (Kawai and Tokeshi 2004). The overall benefit of aggregation is also seen in marine gastropods, where survivorship is strongly correlated with

density, despite the influence of competition on the gastropod aggregations (Ray and Stoner 1994). Even being close to an aggregation increases survivorship of marine gastropods, as compared to those that are isolated (Ray and Stoner 1994).

Perimeter, Area and, Perimeter:Area

As aforementioned, one possible reason that aggregation decreases the risk of predator or heat related mortalities is that perimeter:area ratios decrease as mussels aggregate. My results supported this explanation. P/mussel and P:A were both significantly lower for aggregated mussels than for singletons. This phenomenon leads to decreased contact/mussel with the surrounding environment and its possible risks. However, my hypothesis was not completely supported, as A/mussel was larger for aggregated mussels than for singletons. This may be due to the fact that we used mixed size classes. Therefore, if large mussels were more likely to aggregate there would be a larger average area/mussel for aggregated mussels. Large mussels could be more likely to aggregate either because they release more aggregation cues or they are able to move around the arena easier.

For arena-wide values, only P and A differed significantly. Because my study arenas were a three-dimensional system, mussels could cover each other and therefore decrease not only their resulting P but also their resulting A. In fact, these two parameters were highly correlated across all aggregation sizes ($R^2=.764$). Because both arena-wide P and A values decreased when mussels aggregated, no significant difference in P:A between initial and experimental arenas resulted.

Fractal Geometry and Spatial Dispersion

Previous studies have shown that *M. edulis* beds are fractal when looked at from all scales (Snover and Commito 1998, Commito and Rusignuolo 2000, Crawford et al. 2006). The results of this study supported my hypothesis that aggregation causes fractal power-law clustering and fractal assemblages. Aggregated mussels had a significantly higher fractal dimension than did singletons. Experimental arenas (light and dark) had fractal geometry ($D \sim 1.5$) whereas initial condition arenas did not ($D \sim 1.0$). Arena-wide fractal dimension comparisons were almost significant ($P=0.0526$).

Cellular-automaton models have shown that positive interactions, such as local facilitation and seed dispersal, also lead to patch size distributions that follow a power-law for vegetation in arid Mediterranean ecosystems (Kefi et al. 2007). Young mussel aggregations in the Wadden Sea show banded spatial patterns that are locally the result of facilitative interactions, such as protection from waves (van de Koppel et al. 2005). At larger scales, negative interactions such as phytoplankton depletion may begin to play a substantial role in spatial pattern formation (van de Koppel et al. 2005).

The density of mussels in a given habitat has substantial impact on other species, many of which are ecologically and commercially valuable (Commito 1987, Commito and Boncavage 1989, Dittmann 1990, Asmus and Asmus 1991, Ragnarsson and Raffaelli 1999, Commito et al. 2005). For example, the loss of *M. edulis* after extreme heat conditions has a negative impact on species richness (Tsuchiya 1983). In these habitats, there is an immediate decrease in the small fauna that usually live within the mussel aggregations and infaunal species completely disappear once the dead mussel shells are gone (Tsuchiya 1983). The impact on small species is probably due to that fact that fractal environments have disproportionately more space for small animals (Halley et al. 2004).

Mussel aggregation is important to other organisms because an increase in fractal dimension is intimately associated with an increase in habitat complexity (Suighara and May 1990). The more complex and convoluted the outline of an object is, the higher its perimeter will be relative to area. Because the light and dark arenas had a higher fractal dimension than initial condition arenas, they also had an overall greater shape complexity.

Habitat complexity impacts the structure of communities (e.g. MacArthur and MacArthur 1961, Gorman and Karr 1978, Diehl 1992, Beck 2000, Lassau and Hochuli 2004) so fractal objects, such as mussel beds, have a similar impact. In marine habitats, fractal dimension of macroalgae has been found to impact faunal species richness (Gee and Warwick 1994) and in terrestrial environments, plant types with higher fractal dimensions support a greater number of arthropod species (Gunnarsson 1992). Jeffries (1993) found that even when weed size was kept constant, the total number of taxa and the number of individuals within each taxa was directly related to the weed's shape complexity. Furthermore, simulations have shown that, in general, the fractal dimension of an environment is positively correlated the number of coexisting species at that site (Palmer 1992).

Conclusion

Where there is the energy of life, dynamic self-assembly can occur in a liquid medium on a smooth surface (Whitesides and Grzybowski 2002). The arenas in my study fit these criteria. Mussel spatial pattern in my study could not have been the result of a template, but was instead caused by dynamic self-assembly. My results are the first to demonstrate a self-organization behavior mechanism that produces fractal patterns in mussels. Studying the factors that

influence the aggregation behaviors of *M. edulis* and other species is necessary to increase the knowledge of spatial distribution and its impact on habitats. My study also serves as a part of the recent focus on facilitation. Mussel aggregation increases the survivorship of mussels as well as other species in their habitat. Studies pertaining to the impact of environmental factors on distribution and thus habitat structure will become even more important as new invasive species are introduced into habitats and as global warming leads to increased thermal stressors as well as shifts in important species' ranges.

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