

Separation anxiety: mussels self-organize into similar power-law clusters regardless of predation threat cues

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ABSTRACT: Mussels have myriad effects on population, community, and ecosystem processes. Their aggregation behavior is an inducible defense that links non-consumptive effects of predators to benthic spatial pattern formation. Aggregation increases intraspecific competition but can be beneficial due to lower perimeter-related predation and other risks. *Mytilus edulis* aggregation responses to predation threats have not been investigated outside of Europe. We studied the effects of chemical cues from heterospecifics (predators *Carcinus maenas*, *Nucella lapillus*; herbivore *Littorina littorea*) and conspecifics (injured and intact *M. edulis*) on *M. edulis* aggregation behavior in Maine, USA. Mussels self-organized into fractal power-law spatial patterns like those in the field. Aggregations had lower perimeter:area (P:A) ratios than singletons, despite having more complex, irregular shapes with higher fractal dimensions (*D*). However, with one exception, no significant differences in aggregation rate, P:A ratio, and *D* were observed for any chemical cue treatment when compared to no-cue controls. Our experiment revealed higher aggregation rates than reported from similar experiments, leaving little scope for additional aggregation when exposed to chemical cues. We suggest that increased aggregation in response to predation threat is context-dependent: costs outweigh benefits beyond some optimal aggregation size, and mussels in our experiment were at the upper aggregation limit beyond which more aggregation could have negative consequences. Bet-hedging with a power-law distribution of aggregation shapes and sizes may be the optimal spatial strategy, especially if predation and other risks are variable in space and time.

KEY WORDS: Chemical cue · Fractal power-law · Inducible defense · Maine · Mussel aggregation · *Mytilus edulis* · Non-consumptive effect · Predation threat

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INTRODUCTION

The spatial patterns of seafloor organisms have myriad effects on population, community, and ecosystem processes (Thrush et al. 2006, Zajac 2008, Gutiérrez et al. 2011). Yet we know little about the

factors that control benthic spatial structure. Marine and freshwater mussels provide many ecosystem services and play important ecological roles in hard- and soft-bottom systems (Gutiérrez et al. 2011). Their spatial patterns are important because mussels are often superior competitors for primary substrate

space and can have positive and negative effects on the settlement and survivorship of other organisms, thus regulating species composition and distribution in a spatio-temporal mosaic that has been particularly well studied in rocky intertidal systems (Benedetti-Cecchi & Trussell 2014).

In laboratory and field experiments, mussels actively crawl towards each other to form aggregations (i.e. 2 or more individuals in contact; *Dreissena polymorpha*: Kobak et al. 2010; *Limnoperna fortunei*: Uryu et al. 1996; *Mytilus edulis*: Côté & Jelnikar 1999, van de Koppel et al. 2008, Commito et al. 2014; *M. galloprovincialis*: Nicastro et al. 2007; *M. trossulus*: Liu et al. 2011; *Perna perna*: Nicastro et al. 2007). This behavior may be advantageous because mussels in large aggregations are less vulnerable to predator attack than are isolated mussels and small aggregations with high perimeter:area ratios (Bertness & Grosholz 1985, Okamura 1986, van de Koppel et al. 2008, 2012, Liu et al. 2012, 2013). Aggregation may also increase fertilization rates (Liu et al. 2011), decrease thermal stress (Helmuth 1998), and provide protection from dislodgement (van de Koppel et al. 2008). However, aggregation has disadvantages, too. It can lead to increased local competition for food and other resources (Bertness & Grosholz 1985, Okamura 1986, McGrorty et al. 1993, Svane & Ompi 1993, van de Koppel et al. 2008, 2012, Liu et al. 2012, 2013, Orrock et al. 2013). Thus, aggregation may be a form of bet-hedging that balances benefits and costs.

Aggregations of mussels are not simple, compact formations spaced evenly over the seafloor. On hard and soft bottoms in Maine, USA, and elsewhere, *M. edulis* typically exhibit a hierarchical spatial structure of irregularly shaped patches nested within larger patches, producing a complex network of mussels and open gaps (McGrorty et al. 1993, Stillman et al. 2000, Wootton 2001, Guichard et al. 2003, Commito et al. 2006, 2014). This spatial pattern has power-law characteristics described with fractal analysis (Commito et al. 2014), a well-established tool in landscape ecology (Hastings & Sugihara 1993), where fractal dimension (D) is the power-law exponent. Power-law patterning occurs in Maine over scales from millimeters to hundreds of meters (Crawford et al. 2006).

Aggregation behavior plays a role in creating power-law patterns because mussels of all sizes preferentially attach to live mussels rather than to soft sediment or hard substrate (Commito et al. 2014). In the laboratory, they self-organize by crawling towards each other to create aggregations with power-law structure and fractal dimensions similar to those

observed in nature (Commito et al. 2014). Power-law structure is found in self-organizing systems where growth occurs by the attachment of individuals to existing ones, often when 2 processes are working in opposition to each other (Bak 1996, Barabási & Albert 1999, Guichard et al. 2003, Kéfi et al. 2007, Scanlon et al. 2007). For example, power-law structure may result from the interplay between behaviors that cause mussels to move towards each other for safety, yet avoid close contact to reduce intraspecific competition and other risks.

Some laboratory studies have reported increased aggregation rates when mussels were exposed to chemical cues from predators and injured conspecifics, the latter simulating individuals attacked by predators (Reimer & Tedengren 1997, Côté & Jelnikar 1999, Nicastro et al. 2007, Kobak & Kakareko 2009, Kobak et al. 2010). Mussel aggregation may be a relatively rapid and inexpensive defense compared to inducible morphological changes such as building thicker shells, stronger adductor muscles, and more massive byssal thread structures (Reimer & Tedengren 1997, Leonard et al. 1999, Cheung et al. 2004, Shin et al. 2008, Freeman et al. 2009, Christensen et al. 2012). Thus, mussel aggregation behavior is an interesting example of a flexible, inducible defense that links the non-consumptive effects of predators to spatial pattern formation.

However, the case for inducible mussel aggregation as a universal response to the threat of predation has not been firmly established. Cues from predators or injured conspecifics often fail to produce a significant mussel aggregation response (Nicastro et al. 2007, Kobak & Kakareko 2009, Kobak et al. 2010, Christensen et al. 2012). Only a small number of mussel species from a few geographic locations have been studied. Despite the ubiquity of *M. edulis* at intertidal and subtidal locations throughout the northern hemisphere, few papers have been published on the impact of predation threat cues on *M. edulis* aggregation (Reimer & Tedengren 1997, Côté & Jelnikar 1999). No such studies have been conducted outside of Europe. Given the ecological importance of *M. edulis* in the northwest Atlantic region, the aggregated power-law spatial patterns observed in Maine, and the wide variety of mussel responses to predation threat cues observed elsewhere, the lack of such studies represents a major gap in our understanding of benthic systems in North America.

The purpose of this study was to investigate the aggregation responses of *M. edulis* to chemical cues in Maine. We attempted to answer these questions:

(1) How do spatial metrics (perimeter, area, perimeter:area ratio, fractal dimension) differ between mussel aggregations and isolated mussels (i.e. singletons)?

(2) How do aggregation rates (proportion of mussels forming aggregations) and spatial metrics differ for mussels exposed to heterospecific (predator and non-predator) and conspecific (intact and injured mussel) chemical cues when compared to no-cue controls?

MATERIALS AND METHODS

The experiment was conducted 13–24 July 2009 at the Downeast Institute for Applied Marine Research and Education, Black Duck Cove, Great Wass Island, Maine, USA (44.4805°N, 67.5971°W; Fig. 1). The experimental design exposed *Mytilus edulis* in test arenas to a no-cue (i.e. seawater-only) control and 5 heterospecific and conspecific chemical cue treatments.

Animal collection

Organisms were collected at low tide from the rocky intertidal zone of a narrow embayment within Black Duck Cove (Fig. 1). This location is generally protected from strong winds. High abundances there of the snails *Nucella lapillus*, *Littorina littorea*, and *L. obtusata* and high cover of the alga *Ascophyllum nodosum* are indicators of low to moderate wave exposure (Menge 1976, Bertness et al. 2002). Animals used in the experiment included mussels (*M. edulis*), a shell-crushing predator (the crab *Carcinus maenas*), a shell-drilling predator (the snail *N. lapillus*), and an herbivore (the snail *L. littorea*). All of these species are commonly found together in the intertidal zone on both sides of the Atlantic Ocean, although *C. maenas* invaded eastern Maine only in the middle of the 20th century (Scattergood 1952). The history of *L. littorea* in the region is contested, but it may have arrived from Canada sometime after its introduction there in the mid-1800s (Chapman et al. 2007). *M. edulis*, *M. trossulus*, and their hybrids can be found together in Maine, but the vast majority of individuals at sites like ours in eastern Maine are *M. edulis* (Hayhurst & Rawson 2009). Mussels at the

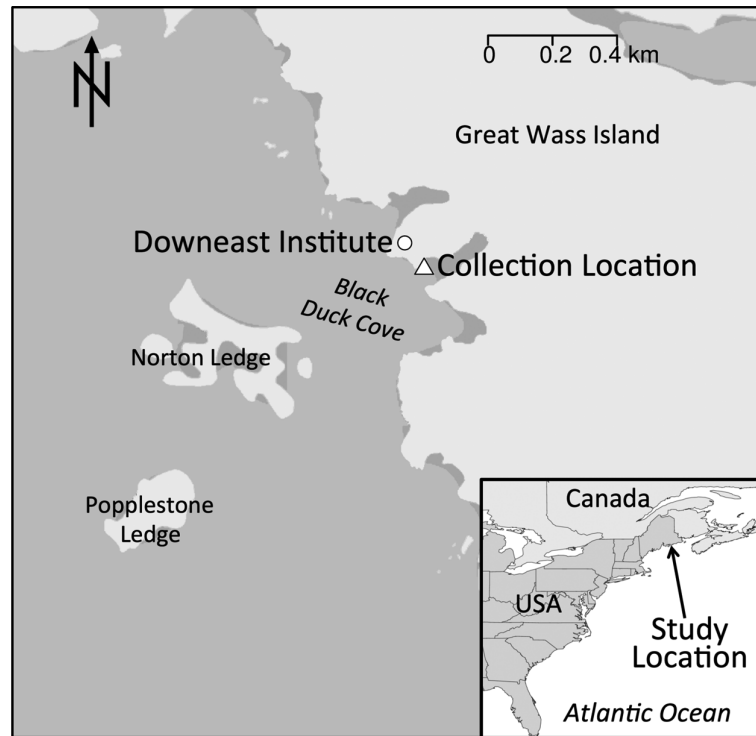


Fig. 1. Research location at the Downeast Institute for Applied Marine Research and Education on Black Duck Cove, in eastern Maine, USA, 44.4805°N, 67.5971°W (inset: east coast of USA). Map data copyright 2015 Google

collection site lived in small clumps (generally 5–15 cm in diameter) near the mean low tide line. They were carefully detached from the substrate and each other by cutting their byssal threads with scissors to prevent tissue damage. Individuals were immediately put into species-specific mesh containers and held in the laboratory in a long channel with running seawater to acclimate for 24 h. Mussel containers were placed well upstream of the containers holding other organisms in order to avoid exposure to their chemical cues. All seawater used in the investigation was pumped from 2 m above the bottom at a subtidal site approximately 25 m offshore, 100 m from the animal collection site, and filtered through 750 μ m mesh. Because of space constraints in the laboratory, the experiment was conducted on 4 dates, and new organisms were collected for each date. Each organism was used only once.

Chemical cue treatments

Chemical cue water was created using animal mass, immersion time, and water volume values similar to those from comparable mussel behavior experi-

ments, following their methods where enough details were provided (Côté & Jelnikar 1999, Cheung et al. 2004, Nicastro et al. 2007, Shin et al. 2008, Kobak & Kakareko 2009). For each experiment date, 300 g allotments of *C. maenas* (carapace widths: 30–40 mm), *N. lapillus* (shell lengths: 25–35 mm), *L. littorea* (20–30 mm), intact *M. edulis* (30–40 mm), and injured *M. edulis* (30–40 mm) were created to produce chemical cue water. Mussels were injured by striking them with a hammer (wrapped in tape to prevent metal ions from touching mussel tissue) to crack the shell and expose damaged tissue. Each allotment of organisms was held for 24 h in its own plastic tub containing 30 l of seawater with an airstone, as were the seawater-only controls. The tubs were placed into a single, large flowing seawater bath to maintain water temperature at ambient 13°C. The flowing water did not enter the tubs (or the test arenas; see next subsection). All tubs and experimental arenas had been filled with seawater for 24 h to condition them before use and then emptied. Pre-testing showed that some *L. littorea* crawled above the water line, which meant that they might not have been releasing chemical cues into the water. To avoid this problem, the allotment of organisms for each species treatment was placed into a conditioned plastic mesh bag weighted to stay submerged within its respective tub. Each seawater-only control tub was established in exactly the same way, including an empty mesh bag.

Experimental design

Test arenas were 25 cm diameter, 18.93 l (5 US gallons), white, plastic buckets with smooth, featureless

interiors. Each arena held 2 l of water from one of the 5 chemical cue treatments or the no-cue control. The focus of our investigation was active mussel movement, so to avoid passive animal movement by water currents, the experiment was run under static conditions following Côté & Jelnikar (1999), Nicastro et al. (2007), and Commito et al. (2014). Arenas were deployed in the seawater bath to maintain water temperature at 13°C, and no mussels died or exhibited stress behavior such as gaping valves or absence of crawling during the experiment. On each experiment date, mussels were divided into 10–19.9, 20–29.9, and 30–39.9 mm size classes. Twenty mussels were placed on the bottom of each arena, with mussel centers 3.5 cm equidistant from each other in concentric circles and their narrow ends facing the center (Fig. 2a,b). Five small, 10 medium, and 5 large mussels were used to simulate the frequency distribution in the field. Mussel positions within arenas were randomized across size classes.

In our randomized complete block design (see next subsection), a block consisted of 6 arenas, one from each of the 5 chemical cue treatments and no-cue controls. Three blocks were established within the seawater bath on each of the 4 experiment dates, creating $3 \times 4 = 12$ replicate arenas per treatment. The laboratory's fluorescent lights were turned on at 07:30 h and turned off at 16:00 h, and natural light entered the room through numerous windows. Sunrise and sunset occurred at approximately 05:00 h and 20:00 h during the experiment. Based on previous studies (Côté & Jelnikar 1999, Nicastro et al. 2007, Commito et al. 2014) and our preliminary observations of aggregation formation, arenas were deployed for 24 h, long after mussels had stopped crawling. A

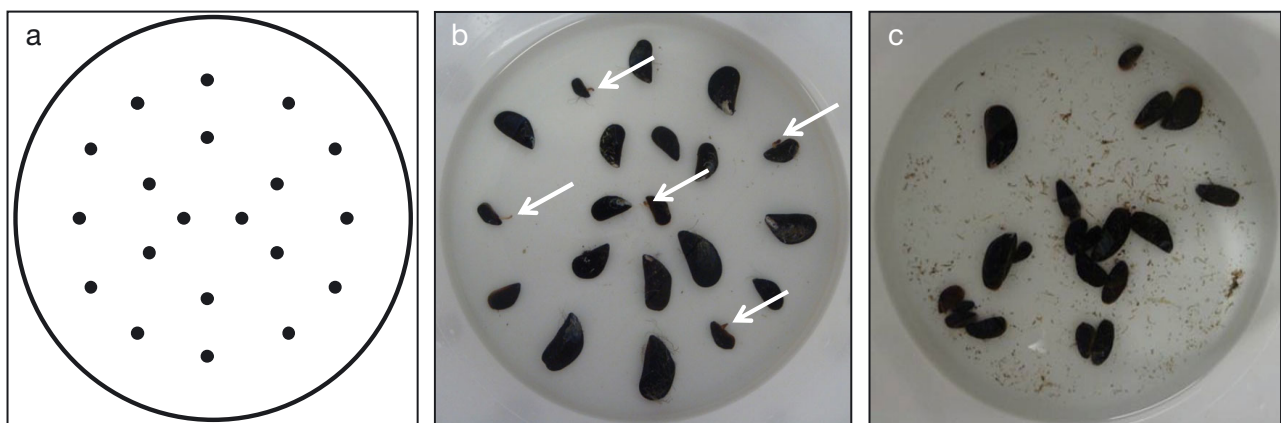


Fig. 2. Mussel positions in arenas, diameter = 25 cm. (a) Initial mussel placement with dots signifying centers of the 20 individuals. (b) Mussels several seconds after placement. Numerous mussels have already begun to move from initial positions. Arrows indicate extended foot visible in 5 individuals. (c) Mussels in aggregations after 24 h

digital (JPEG) image was then taken of each one, and mussel aggregation was assessed *in situ*.

Data collection and analysis

Mussels were classified as either singletons (isolated individual that did not become part of an aggregation) or aggregations (group of 2 or more mussels), following Côté & Jelnikar (1999), Nicastro et al. (2007), and Commito et al. (2014). Mussel aggregation was determined visually and with a slender probe using 2 scoring methods: physical contact of shells or byssal thread attachment to each other. Both methods yielded similar results, so only the shell contact results are presented. The JPEG images were imported into ESRI ArcGIS 9.3.1 and manually digitized to create a polygon for each singleton and aggregation.

For each singleton and aggregation, the perimeter (P), area (A), and P:A ratio were determined with the geometry calculator of ArcGIS 9.3.1, following Commito et al. (2014). The fractal dimension (D) was determined with the boundary-grid method (Hastings & Sugihara 1993), following Snover & Commito (1998), Crawford et al. (2006), and Commito et al. (2014), utilizing TruSoft Benoit 1.3 software. Data were pooled across treatments to determine how experiment-wide aggregations differed from experiment-wide singletons, irrespective of treatment. Differences between aggregations and singletons were analyzed using Wilcoxon rank sum tests in the R statistical environment.

For each arena, the proportion of mussels that aggregated and arena-wide P, A, and P:A ratio were determined, following Commito et al. (2014). Other aggregation parameters (number of aggregations, number of singletons, and total number of aggregations plus singletons) yielded results similar to those for the proportion of mussels that aggregated, so only the latter are presented. The area-perimeter exponent technique (Hastings & Sugihara 1993) was used to calculate D , following Commito et al. (2014), where P and A values for all the singletons and aggregations in an arena were plotted on log-log axes, and fractal dimension $D = 2 \times \text{slope}$. This method was chosen because it was developed specifically for clusters of patches (as opposed to the shape of an individual patch) and is appropriate for arena-wide power-law clustering.

A randomized complete block design was used to examine Treatment effects (fixed factor) and added variation due to Date and Block (random factors).

Data were transformed for the proportion of mussels that aggregated (arcsine) and fractal dimension (square root) to meet the ANOVA assumptions of normality and homoscedasticity. Analyses were performed using SAS 9.4 TS Level 1M3, following the procedure for expected mean square estimates outlined in Underwood (1997). All factors and interactions were tested, except Date \times Block and Date \times Block \times Treatment, because neither source of variation in these 2 interactions had an appropriate error term after examining the mean square estimates using the Cornfield-Tukey rules (Underwood 1997). Power analysis was performed when Treatment revealed no significant differences.

Because Date and Block were random factors, no *a posteriori* test was performed in the one case where a significant difference was detected for these factors (Date for P:A ratio, see 'Results' below). For Treatment, a particular mass value of one species may not produce the same cue dose as the equivalent mass of another species. Therefore, rather than comparing treatments with each other, we took the somewhat more conservative approach of comparing each chemical cue treatment to the no-cue control. For this reason, and as prescribed by Underwood (1997) and Zar (1999) to control experiment-wise error rate and increase power relative to comparing all treatments to each other, significant Treatment results were followed by Dunnett's tests (2-tailed; $\alpha = 0.05$) to compare each treatment to the no-cue control.

RESULTS

Moments after deployment, mussels began to crawl by extending the foot and pulling themselves along the bottom (Fig. 2b). Within the first minute, mussels began to make contact and form byssal thread attachments with each other. After a few minutes, aggregations were common. Mussels moved alone and also pushed and pulled other individuals in mobile clumps. Aggregations were highly dynamic at first. Mussels often separated from aggregations and then rejoined them, formed new aggregations, or stayed isolated. Aggregations (Fig. 2c) became stable after the first few hours, after which time virtually no movement was detected.

Aggregation metrics

The majority of mussels were in aggregations at the end of the experiment, $77.64 \pm 1.23\%$ (mean \pm

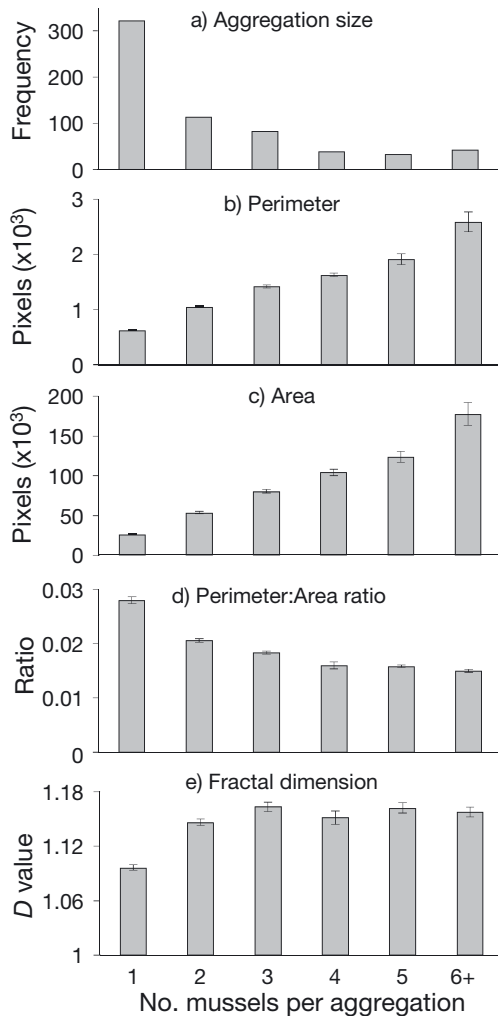


Fig. 3. Spatial metrics for mussel aggregations. (a) Frequency distribution of aggregation sizes. (b) Perimeter, (c) area, (d) perimeter:area ratio, (e) fractal dimension D , across aggregation sizes. Values are mean \pm 1 SE for (b–e)

1 SE) across all treatments. Summary data were pooled for presentation here because treatment results were so similar (see 'Arena-wide comparisons across treatments'). Aggregations ranged in size from 2 to 13 individuals. Aggregations containing ≥ 6 mussels were rare and thus grouped into one aggregation class (Fig. 3a). As aggregation size (i.e. number of mussels per aggregation) increased, the parameters P and A increased, $P:A$ ratio decreased, and D increased before leveling off (Fig. 3b–e).

Comparison of aggregations to singletons

Aggregations had significantly longer P values, larger A values, and lower $P:A$ ratios than singletons

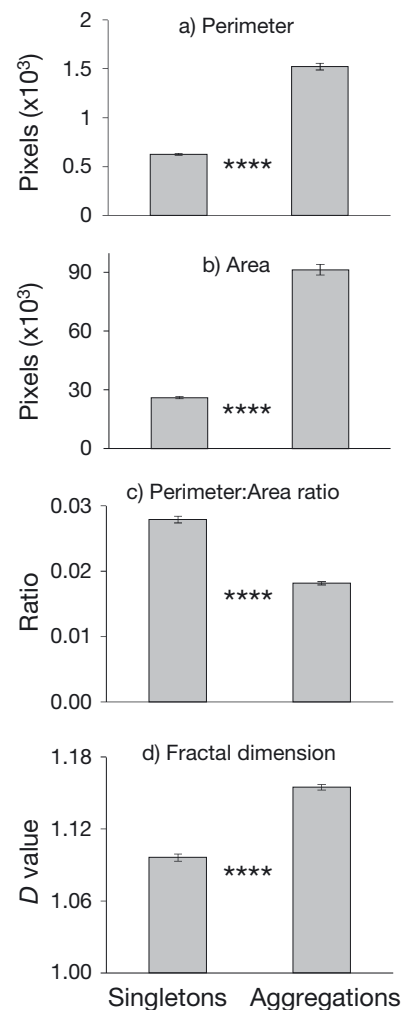


Fig. 4. Spatial metrics comparing single mussels and mussel aggregations. (a) Perimeter, (b) area, (c) perimeter:area ratio, (d) fractal dimension D . Values are mean \pm 1 SE. Results of Wilcoxon rank sum tests shown for comparisons of singletons and aggregations; **** $p < 0.0001$

(Fig. 4a–c). Two factors in addition to overall aggregation size were involved in the lower $P:A$ ratios for aggregations than singletons. First, P per capita was significantly shorter for aggregations than for singletons (Wilcoxon rank sum test, $p < 0.0001$), indicating that adjacent mussels within aggregations were in contact along a substantial length of their shared shell boundaries. Second, A per capita was not significantly different for aggregations than for singletons (Wilcoxon rank sum test, $p = 0.5133$), indicating that mussels did not aggregate selectively based on body size.

Aggregation shapes were not as simple and compact as singletons, even though they had lower $P:A$ values. Their complexity was revealed by the fractal

Table 1. ANOVA tables for aggregation experiment. Randomized complete block design, with Date and Block as random factors and Treatment as fixed factor. Significant treatment results ($\alpha = 0.05$) were followed by Dunnett's tests for differences between each chemical cue treatment and no-cue control. See 'Data collection and analysis' for details

Source	df	SS	MS	F	p
(a) Proportion of mussels that aggregated					
Date	3	0.06720	0.02240	2.12	0.1991
Block	2	0.05146	0.02573	2.43	0.1682
Date × Block	6	0.06342	0.01057	–	no test
Treatment	5	0.32460	0.06492	5.17	0.0015
Date × Treatment	15	0.18806	0.01254	0.71	0.7345
Block × Treatment	10	0.17668	0.01767	1.41	0.2252
Date × Block × Treatment	30	0.37698	0.01257	–	no test
Total	71	1.24840			
(b) Perimeter:area ratio (P:A)					
Date	3	4.551×10^{-5}	1.516×10^{-5}	15.87	0.0029
Block	2	1.334×10^{-6}	6.672×10^{-7}	0.70	0.5339
Date × Block	6	5.736×10^{-6}	9.559×10^{-7}	–	no test
Treatment	5	1.512×10^{-5}	3.024×10^{-6}	1.72	0.1601
Date × Treatment	15	3.792×10^{-5}	2.528×10^{-6}	0.87	0.6093
Block × Treatment	10	2.907×10^{-5}	2.907×10^{-6}	1.65	0.1387
Date × Block × Treatment	30	5.270×10^{-5}	1.757×10^{-6}	–	no test
Total	71	1.874×10^{-4}			
(c) Fractal dimension, D					
Date	3	0.00276	0.00092	0.40	0.7596
Block	2	0.01101	0.00551	2.38	0.1733
Date × Block	6	0.01387	0.00231	–	no test
Treatment	5	0.01779	0.00356	2.68	0.0408
Date × Treatment	15	0.03424	0.00228	1.51	0.2598
Block × Treatment	10	0.01516	0.00152	1.14	0.3669
Date × Block × Treatment	30	0.03989	0.00133	–	no test
Total	71	0.13472			

dimension, D , which can range from 1 for a simple Euclidian shape to 2 for a shape so complicated that a trace of its outline fills the entire plane. D values ranged from 0.99 (a singleton) to 1.25 (the most complex aggregation). Every singleton had a lower D value than did even the simplest aggregation, resulting in a significant difference between aggregations and singletons (Fig. 4d).

Arena-wide comparisons across treatments

Proportion of aggregated mussels. A significant Treatment effect was detected (Table 1a, Fig. 5a), but the Dunnett's test found no treatments significantly different from the no-cue control. Date, Block, and their interactions with Treatment showed no significant differences (Table 1a).

P:A ratio. No significant Treatment effect was detected (Table 1b, Fig. 5b). The power was 0.068, and to detect a difference as small as the difference be-

tween the minimum and maximum mean P:A ratio (i.e. effect size of 0.0010) would have required 366 replicates for each treatment rather than the 12 that we used. This result strongly supports the conclusion that differences in P:A ratio between treatments did not exist. Date showed significant differences, but Block and the interactions of Date and Block with Treatment did not (Table 1b).

Fractal dimension. A significant Treatment effect was detected (Table 1c, Fig. 5c), and the Dunnett's test found that the *Littorina littorea* treatment had a significantly higher D value than did the no-cue control. Date, Block, and their interactions with Treatment showed no significant differences (Table 1c).

DISCUSSION

Comparison of aggregations to singletons

Investigations on several mussel species found that predation rates were higher on singletons than on individuals in aggregations and higher along aggregation edges than in more protected centers (Bertness & Grosholz 1985, Okamura 1986, McGrorty et al. 1990, Lin 1991, Stiven & Gardner 1992, Reusch & Chapman 1997). The logical explanation is that because P:A ratio declines as the size of an aggregation increases, the edge-related risk is reduced. But the P:A ratio relationship with size holds true only for objects whose shapes are the same, and aggregations in our experiment had significantly more complex fractal shapes than singletons. Complex, irregular shapes with bumps, projections, and invaginations have longer perimeters than do simple shapes with the same area. So an aggregation could have a higher P:A ratio than a singleton, even though the aggregation is larger. However, our results demonstrate clearly that size took precedence over shape as a determinant of P:A ratio. The P:A ratio decreased with increasing aggregation size and was significantly lower for aggregations than for singletons.

At the scale of the individual aggregation, the relationship between shape complexity and size may

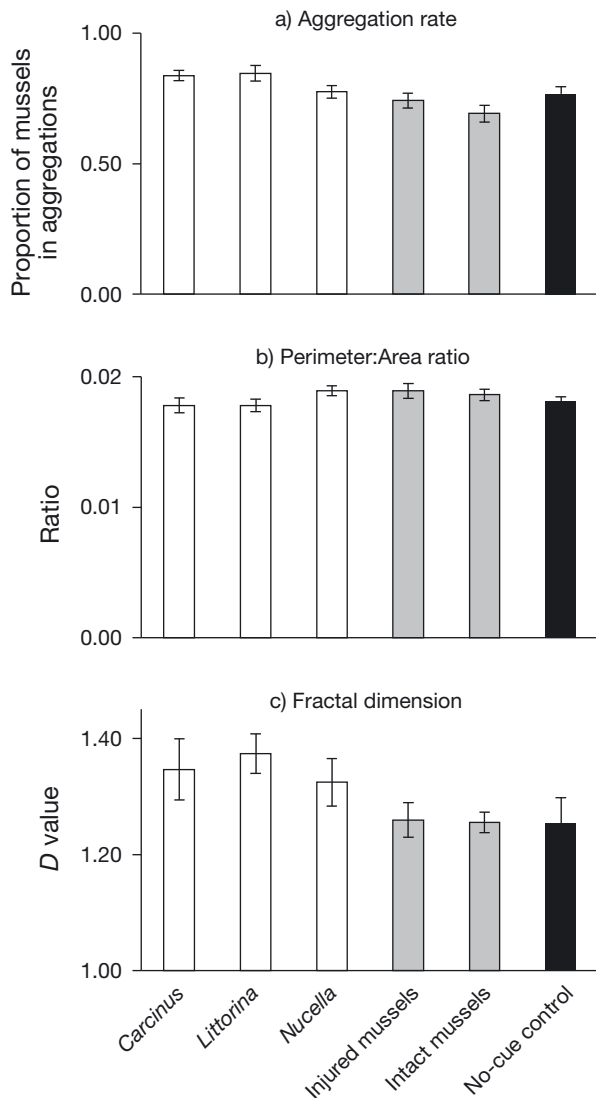


Fig. 5. Spatial metrics across treatments. (a) Aggregation rate, (b) perimeter:area ratio, (c) fractal dimension D . Values are mean ± 1 SE. *Carcinus* = *Carcinus maenas*, *Littorina* = *Littorina littorea*, *Nucella* = *Nucella lapillus*, white bars = heterospecific cues, gray bars = conspecific cues, black bars = no-cue controls

represent a behavioral optimization that confers upon mussels the benefits of protection from edge-related predation, dislodgement, thermal stress, and other risks, while keeping the costs of interior-related intraspecific competition at reasonable levels (Bertness & Grosholz 1985, Okamura 1986, Gascoigne et al. 2005, van de Koppel et al. 2008, 2012, Liu et al. 2012, 2013, Commito et al. 2014). However, beyond a certain size, an aggregation may have such a low P:A ratio that benefits decline compared to a cluster of smaller aggregations. For example, in the laboratory, *Mytilus edulis* individuals crawled more rapidly

under high-density conditions than low-density conditions, facilitating escape from large aggregations (Liu et al. 2013). In the field, *M. edulis* individuals actively moved to the exterior of aggregations containing a second mussel species, despite much higher rates of dislodgement there (Schneider et al. 2005). Thus, *M. edulis* may be particularly averse to the crowded conditions within aggregations. In our experiment, mussels in the arenas never coalesced into one large aggregation or even several medium-sized aggregations. They always formed power-law clusters of aggregations of different sizes.

Bet-hedging and aggregation clusters

Extending the argument about individual aggregations to the scale of clusters of aggregations, group living for mussels can have high costs in terms of resource-limited growth, fecundity, and survivorship (Bertness & Grosholz 1985, Okamura 1986, McGrorty et al. 1993, Svane & Ompi 1993, Liu et al. 2012, van de Koppel et al. 2012, Orrock et al. 2013). Aggregation may even increase, rather than reduce, the risk of predation (Lipcius & Hines 1986, Dolmer 1998, Seitz et al. 2001, Frandsen & Dolmer 2002, Whitton et al. 2012) and dislodgement (Cole & Denny 2014). Thus, the costs of group living may outweigh the benefits beyond some optimal aggregation rate, even when predation threat cues are present. At the arena-wide scale in the laboratory and the landscape scale in the field, bet-hedging with a cluster of many aggregations of different sizes may be more beneficial for mussels than one large aggregation.

Moreover, environmental conditions for mussels vary over space and time, including predator abundance and consumption rates, as well as factors like phytoplankton availability that contribute to intraspecific competition (Carrington et al. 2009, Trussell et al. 2011, Miller et al. 2014, Weissburg et al. 2014). One aggregation size with one particular P:A ratio would almost certainly be maladaptive for mussels in a heterogeneous and fluctuating environment like the Maine intertidal zone. Rapidly and repeatedly altering this aggregation size in response to minute-by-minute changes in threat level may be possible, but it would be energetically costly and expose crawling mussels to predators and dislodgement. Bet-hedging with an array of aggregation shapes and sizes is most likely a better strategy.

Spatial patterns in the field are consistent with the bet-hedging strategy. At the landscape scale in Maine and elsewhere, *M. edulis* individuals live in

fractal power-law clusters with a wide range of sizes and complex shapes (Snover & Commito 1998, Azovsky et al. 2000, Kostylev & Erlandsson 2001, Wootton 2001, Guichard et al. 2003, Crawford et al. 2006, Commito et al. 2014). Our investigation showed that mussels quickly self-organized into that kind of power-law pattern, as did a recent lattice model and laboratory experiment (Commito et al. 2014). A large field experiment yielded similar results (Capelle et al. 2014), where *M. edulis* placed uniformly over the substrate aggregated into arrays of patches of many sizes and shapes, similar to what we observe in natural mussel beds in Maine.

Arena-wide comparisons across treatments

For aggregation rate and D , some weak patterns were observed. The heterospecific treatments, especially the herbivore *Littorina littorea*, produced somewhat stronger responses than did the conspecific treatments, and the injured mussels produced slightly stronger responses than did intact mussels. For P:A ratio, no clear pattern emerged at all. Overall, the results did not demonstrate significant treatment effects. Despite what has become almost conventional wisdom regarding the importance of predation threat cues, exposure often fails to induce significant mussel aggregation (Nicastro et al. 2007, Kobak & Kakareko 2009, Kobak et al. 2010) or other behavioral or morphological responses in marine organisms (Freeman & Hamer 2009, Freeman et al. 2009, 2014, Johnson & Smee 2012, Large & Smee 2013, Hill & Weissburg 2014, Schwab & Allen 2014, Harding & Scheibling 2015, Wilkinson et al. 2015). Specifically with respect to *M. edulis*, to our knowledge, only 2 studies have demonstrated that this species increases its aggregation rate in the presence of predation threat cues (Reimer & Tedengren 1997, Côté & Jelnikar 1999). The only other studies on *M. edulis* aggregation in response to predator cues failed to show a significant aggregation response: our experiment, and one that measured *M. edulis* aggregation when mussels were in direct physical contact with feeding *Carcinus maenas* (Christensen et al. 2012). Experimental results taken as a whole suggest that predation risk may not always be the most important driver of aggregation behavior. However, the distinguishing feature of our results was not that predation cue treatments had low aggregation rates. On the contrary, they had high aggregation rates. But so did the no-cue controls. What can explain these results?

High aggregation rates across treatments

Predation risk varies spatially, with greater risk at protected locations, where predators are abundant because they are not carried away by waves (Menge 1976, Menge & Sutherland 1987, Freeman & Hamer 2009). Our animals were taken from a site with low to medium wave exposure. We did not quantitatively measure snail and crab population densities in the field, but qualitatively they were so abundant that it took only a few minutes to collect enough for use in our experiments on each of the 4 days. The mussels may have already allocated resources to morphological defenses, so that additional expenditures on aggregation were unwarranted when exposed to threat cues in our experiment. Similarly, the mussels may have had an inherently strong propensity for aggregation because they came from a high-risk location, so they aggregated at high rates even in our no-cue control arenas. Both mechanisms may have worked together to cause aggregation rates that were similar and high across treatments and no-cue controls.

Our results are consistent with this explanation. The mussels in our experiment had very high aggregation rates regardless of exposure to a chemical cue treatment, leaving little scope for additional aggregation when exposed to chemical cues. Consistently high aggregation across treatments and no-cue controls resulted in little variation in P:A ratio and D across treatments as well.

In our no-cue controls, $76.67 \pm 2.78\%$ of the mussels aggregated. This value is higher than the no-cue aggregation rates from similar experiments where rates were reported for 24 h exposures or could be extracted from the data presented (Uryu et al. 1996, Côté & Jelnikar 1999, Nicastro et al. 2007, Kobak et al. 2010, Commito et al. 2014). In fact, our no-cue control aggregation rate was higher than even the predator and injured conspecific treatment aggregation rates in studies where those treatments were tested (Côté & Jelnikar 1999, Nicastro et al. 2007, Kobak et al. 2010). In the one investigation where aggregation rates in some trials were higher than ours (Nicastro et al. 2007), the rate was higher only when mussels were initially placed closer together than in our and other experiments, or when injured conspecifics were placed directly into the experimental arenas, introducing tactile cues together with the chemical cue.

It is unclear why aggregation rates were low in these other studies compared to ours. Mussels in other experiments may have been stressed due to

low oxygen levels, high concentrations of metabolites, or some other factor. For example, Côté & Jelnikar (1999) stated that 6% of the mussels in their experiments showed no movement, which the authors interpreted as abnormal behavior. Another possibility is that other studies used animals taken from locations with a low risk of predation, so that mussels had an inherently weak propensity for aggregation. This possibility could explain why no-cue controls in other studies had low aggregation rates, allowing scope for increased rates when exposed to predation threat cues, but still lower overall than in our study. Predation risk levels at mussel source locations are difficult to determine and were not reported in any studies. Regardless of the reasons behind the aggregation rates we observed in our experiment, we suggest that the mussels had a no-cue control aggregation rate high enough to render unnecessary an additional response to threat cues, and that further aggregation would have been detrimental.

Alternative explanations

Another possible explanation for our results is that naïve prey may not respond to novel predators (Nicastro et al. 2007, Freeman et al. 2014). Although *C. maenas* is a relative newcomer to the Gulf of Maine and did not produce an aggregation response in our study, neither did the native predator, *Nucella lapillus*, or the injured conspecifics. Both predators induced significant morphological responses in *M. edulis* at another location in the Gulf of Maine (Freeman 2007).

We focused on aggregation because we were specifically interested in possible links between predation and *M. edulis* spatial pattern formation in Maine (Commito et al. 2014). But it is possible that mussels in a given situation may rely on morphological defenses rather than aggregation. For example, in a laboratory experiment that exposed *M. edulis* to *C. maenas*, the mussels exhibited increased byssal attachment strength, but no significant aggregation response (Christensen et al. 2012).

It is possible that the mussels in our experiment were stressed, or that chemical cue concentrations were too low to induce an aggregation response, did not reach the mussels, or did not serve as an accurate indicator of predation threat (Weissburg et al. 2014). These explanations seem unlikely because the lack of significant differences stemmed from high aggregation rates even in the absence of cues, not from low aggregation rates even in the presence of cues. We

established cues using animal mass, water volume, and immersion time values similar to those in the literature where significant aggregation responses were observed. No study, including our own, has included a positive control that guarantees cue delivery to mussels, although it might be possible to use a dye or some other tracer. We used 3 predation threat cues that induced defense responses in other experiments, plus 2 other cues not known to represent a threat. We followed the protocols of other studies, the mussels were literally bathed in chemical cue, and 100% of the mussels opened their valves, pumped the cue-laden water, and crawled.

Implications

Mussel beds on hard and soft bottoms are highly dynamic, with changing densities, age-class structures, and spatial patterns over time (Nehls & Thiel 1993, Reusch & Chapman 1997, Hunt & Scheibling 2001, Dolmer & Frandsen 2002, Guichard et al. 2003, Petrović & Guichard 2008, Folmer et al. 2014). Yet beds persist by rebounding after declines. Storms and commercial dredging and raking cause bed fragmentation and change their P:A ratios and fractal dimensions, most likely by reducing the number of large patches and increasing the number of small ones. Our results provide strong evidence that disrupted mussel distributions have the potential to self-organize into power-law distributions, contributing to the reestablishment of pre-disturbance spatial patterns. The role of predation risk in this spatial response remains poorly understood. We suggest that risks are strongly context-dependent and often lead to power-law patterns as mussels balance the costs and benefits of aggregation and hedge their bets in an uncertain world.

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