1 Substratum type and conspecific density as drivers of mussel patch formation
2 Camilla Bertolini^{1, 2*}, Nathan R. Geraldini^{1,2,3}, W. I. Montgomery¹, Nessa E. O'Connor¹,
3 ²

4

5 **Addresses:** ¹School of Biological Sciences, Queen's University Belfast, 97 Lisburn
6 Road, Belfast, BT9 7BL, Northern Ireland, UK; ²Queen's University Marine
7 Laboratory, 12-13 the Strand, Portaferry, BT22 1PF, Northern Ireland, UK; ³ Present
8 address: Red Sea Research Center, King Abdullah University of Science and
9 Technology, Thuwal, Saudi Arabia

10

11 *Corresponding author:

12 email: cbertolini01@qub.ac.uk , phone +44 (0) 2890972030

13

14 Abstract

15 Biogenic reefs are an important component of aquatic ecosystems where they enhance
16 biodiversity. These reefs are often established by dense aggregations of a single taxa
17 and understanding the fundamental principles of biogenic reef formation is needed for
18 their conservation and restoration. We tested whether substratum type and density
19 affected the aggregation behaviour of two important biogenic-reef forming species,
20 the horse mussel, *Modiolus modiolus* (Linnaeus, 1758), and the blue mussel, *Mytilus*
21 *edulis* (Linnaeus, 1758). First, we tested for effects of substratum type on mussel
22 movement and aggregation behaviour by manipulating substrata available to mussels
23 in mesocosms (three treatments: no sediment added, sediment added, sediment and
24 shells added). Both mussel species moved less in treatments with sediment and with
25 both sediment and shells present than when no sediment or shells were added and the
26 percentage of these mussels that aggregated (clumps of two or more individuals) was
27 lower when shells were present compared to treatments without shells, however,
28 fewer *M. modiolus* attached to shells than *M. edulis*. There was no effect of different
29 substratum type on patch complexity of either mussel species. In addition, motivated
30 by our interest in the restoration of *M. modiolus*, we also tested experimentally
31 whether the aggregation behaviour of *M. modiolus* was density-dependent. *M.*
32 *modiolus* moved a similar distance in three density treatments (100, 200 and 300
33 mussels m⁻²), however, their aggregation rate appeared to be greater when mussel
34 density was higher, suggesting that the encounter rate of individuals is an important
35 factor for aggregation. *M. modiolus* also formed aggregations with a higher fractal
36 dimension in the high and medium density treatments compared to lower density,
37 suggesting that at higher density this increased patch complexity could further
38 facilitate increased recruitment with the enhanced habitat available for settlement.

These findings add to the growing evidence showing that adding dead shells to substratum to encourage *M. modiolus* restoration is not likely to be effective. Our findings suggest that mussel density is a more important driver for patch and subsequently reef formation. Moreover, two seemingly functionally similar mussel species showed some differences in their behaviour (e.g. attachment to shells). This highlights the importance of considering the specific ecology of a target species, such as *M. modiolus*, when designing restoration methods because information garnered from experimentation on an ostensibly similar species (e.g. *M. edulis*) may not be appropriate.

Keywords: Biogenic reefs, Bivalve reefs, Ecosystem engineers, *Modiolus modiolus*, *Mytilus edulis*, Restoration

1. INTRODUCTION

Aggregating species can play an important role as autogenic ecosystem engineers, modifying the physical structure of their environment (Jones et al., 1997, 1994). Molluscs are particularly important in this context because their shells provide additional habitat for other species (Gutierrez et al., 2003a), which can be extremely important in soft-sediment dominated areas, where suitable habitat for sessile species can be scarce (Buschbaum et al., 2008; De Smet et al., 2015; Thrush et al., 2001; van der Zee et al., 2015). The horse mussel *Modiolus modiolus* is a relatively slow growing, long-lived species, known to form large biogenic reefs (Lindenbaum et al., 2008; Rees et al., 2008; Seed and Brown, 1978, 1977) and is considered an important ecosystem engineer facilitating biodiversity hotspots and playing an important role in terms of ecosystem functioning contributing to nutrient cycling, potentially including

64 carbon storage in the form of shell deposits (Brown and Seed, 1976; Burrows et al.,
65 2014; Cook et al., 2013; Fariñas-Franco et al., 2013; Geraldi et al., in press; Navarro
66 and Thompson, 1997; Ragnarsson and Burgos, 2012; Rees et al., 2008).

67 Biogenic reefs are affected heavily by anthropogenic activities (Green et al., 2016;
68 Firth et al., 2015) and populations of reef-forming bivalves, such as oysters and
69 mussels, have declined significantly in recent decades (Lotze et al., 2006). The
70 intense use of bottom-towed fishing gear has caused fragmentation of many mussel
71 reefs, including those of *M. modiolus* (Collie et al., 2000; Cook et al., 2013; Cranfield
72 et al., 2003; Roberts et al., 2011), and this species is also under threat from
73 anthropogenic climate change (Gormley et al., 2013). These reefs are listed as
74 threatened under Annex I of the EU Habitats Directive (Directive 93/43/EEC) and the
75 OSPAR convention (Rees, 2009). For example, the historically extensive beds of *M.*
76 *modiolus* at Strangford Lough, Northern Ireland have been subject to considerable
77 degradation following the use of bottom towed fishing gear and have not recovered
78 naturally even after the closure of two areas within the Lough to all fishery activity
79 (Brown, 1989; Magorrian and Service, 1998; Roberts et al., 2011; Service, 1998;
80 Service and Magorrian, 1997). The specific reasons for the lack of natural recovery in
81 Strangford Lough has not yet been identified. Possible factors hampering *M. modiolus*
82 recovery include the increased local abundance of predators, such as the starfish
83 *Asterias rubens*, the lack of available habitat for spat settlement, and increases in
84 sedimentation within the Lough (Roberts, 1975; Strong et al., 2016). Active
85 restoration of *M. modiolus* has, therefore, been recommended in this region (Fariñas-
86 Franco et al., 2013). Previous restoration efforts have identified that, unlike oyster
87 restoration, a shell cultch is not necessary to restore *M. modiolus* and the associated
88 community (Fariñas-Franco et al., 2013), indicating that optimal methods for bivalve

89 reef restoration should be identified on a species by species basis.

90 A better understanding of how reef-forming species aggregate to form these complex

91 reefs is essential to design more effective restoration practices, such as species

92 translocation, aimed at re-introducing eradicated populations to establish functioning

93 and stable reefs. Fast aggregation should result in a reef containing many small

94 interstitial spaces, which promotes further successful settlement (Comely, 1978;

95 Roberts, 1975) by providing refuge from predators (Dolmer, 1998; Okamura, 1986).

96 Few studies to our knowledge, however, have tested whether substratum type or

97 initial mussel density affects mussel aggregation behaviour (e.g. wa Kangeri et al.,

98 2014 for substratum type), and the complexity of their formations (aggregations). If

99 substratum type and density alter mussel aggregation behaviour, it is likely that their

100 fractal organisation will be affected. Understanding these mechanisms, therefore, is an

101 important prerequisite to improve restoration success (Beck et al., 2009).

102 While the relationships between bivalve aggregation density and survival, growth,

103 reproduction and predation rates have been studied widely (e.g. Okamura 1986,

104 Dolmer 1998, Nicastro et al. 2012), the environmental factors and conditions driving

105 aggregation of these reef-forming bivalves are not yet understood. Differences in

106 substratum type can affect mussel aggregation patterns, thus, affecting attachment

107 strength (Babarro and Comeau, 2014; Christensen et al., 2015; wa Kangeri et al.,

108 2014). Density is another important factor that alters how individuals aggregate

109 (Gascoigne et al., 2005). In general, a greater density of adult mussels stimulates

110 attachment of mussels to the substratum (Kobak 2001), which can be an important

111 predictor for spatial self-organisation (Koppel et al., 2005; van de Koppel et al., 2008)

112 and size of aggregations (Capelle et al., 2014), ultimately having the potential to

113 affect the stability of the whole reef (Bertness & Grosholz 1985, Capelle et al. 2014).

114 To date comparatively more research has been done on more common mussel species
115 (e.g. *M. edulis*) than less abundant species (e.g. *M. modiolus*; Dinesen and Morton,
116 2014; Ragnarsson and Burgos, 2012). Although mytilid mussels may be functionally
117 similar in many ways, it is also possible that their unique natural histories may
118 underpin different behavioural and physiological responses to environmental
119 conditions. While many studies have examined the aggregation behavior of *M. edulis*
120 (e.g. Maas Geesteranus, 1942), only one study, to our knowledge, has assessed the
121 aggregation of *M. modiolus*, however this did not manipulate substrata or include soft-
122 sediment representative of local field conditions (Roberts et al., 2004), thus
123 knowledge regarding initial patch and reef formation for this species is still lacking.
124 In response to the need to develop optimal restoration methods (Pérez et al., 2012),
125 the primary aim of this study was to test whether differences in substratum type and
126 mussel density affected the aggregation behaviour of *M. modiolus* and to identify the
127 mechanisms driving patch and subsequently reef formation in this species. We also
128 tested whether the behaviour of *M. modiolus* differed from that of the well-studied
129 mussel, *M. edulis*, which is taxonomically distinct but often considered functionally
130 similar. The comparison between species will allow us to determine whether it would
131 be prudent to include available data describing *M. edulis* movement to develop
132 restoration methods for *M. modiolus*. Further, we assessed how substratum type and
133 density can affect patch complexity of resulting aggregation to gain insights on the
134 availability and size range of interstitial spaces within the mussel habitat and can be
135 used as a proxy for refuge availability (Kostylev et al., 2005; Tokeshi and Arakaki,
136 2012), at the initial stages of patch formation before three dimensional reef accretion
137 occurs.

We designed two experiments to quantify individual mussel movement, aggregation formation and the complexity of mussel aggregations (patches) on different substratum types and with different mussel densities. Based on the physiology of both species (*M. edulis* epibyssate, *M. modiolus* endobyssate), we hypothesised that *M. modiolus* will move less where no hard substratum was present, while *M. edulis* movement will be similar across all sediment types. In a second experiment, we tested the density-dependence of *M. modiolus* aggregation behaviour based on their propensity to attach to conspecific shells in our first experiment. We hypothesised that: (i) clumping and the formation of more complex patches will be greater in both species, where substratum was enhanced with empty shells than in treatments without shells; and (ii) at greater initial density of *M. modiolus*, aggregation success will be greater (percentage of mussels attached to their conspecifics), and the patch complexity will be greater than at lower densities. Hence, based on key concepts in behavioural, fundamental and applied ecology, these results should provide essential data for the restoration of important bivalve reefs.

2. MATERIALS AND METHODS

Experiments were conducted in outdoor, flow-through mesocosms at Queen's University Marine Laboratory, Portaferry, Northern Ireland (described in Mrowicki & O'Connor 2015). Mesocosms were plastic cylindrical tanks (diameter = 24.5 cm, vol = 10 L) on shallow tables supplied with sand-filtered seawater from the adjacent Strangford Lough. The factorial design of the first experiment comprised two fixed factors: mussel species identity (two levels: *M. modiolus* and *M. edulis*); and substratum type (three levels: no sediment added, sediment present, sediment and shell present). This design allowed us to test for all possible interactions among terms

on individual mussel movement, percentage of aggregated mussels and the patch complexity of resulting aggregations (fractal dimension). A second experiment tested for effects of mussel (*M. modiolus*) density (three levels; low, medium and high) on individual mussel movement over time, percentage of aggregated mussels and fractal dimension of resulting aggregations (patch complexity).

M. modiolus were collected locally (54° 34' 51" N, 5° 27' 24" W) in October 2014, using a day grab (0.1 m²) and had mean shell length of 6.16 ± 0.32 cm ($\pm$ SE). *M. edulis* were collected from local shores (54° 29' 15.96" N, 5° 32' 24.74" W) and had a mean shell length of 5.86 ± 0.12 cm ($\pm$ SE). Prior to the experiment, mussels were held in flow-through tanks and supplied with unfiltered seawater from Strangford Lough (flow rate = 1.30 L min⁻¹). Mussels were fed every 48 hours with 150 ml *Tetraselmis suecica* (1.6×10^6 cells mL⁻¹) and 150 ml *Isochrysis galbana* (2.6×10^6 cells mL⁻¹) in each mesocosm because the water supplied to the system is sand filtered and this insured that mussels were replete. Water flow (400 mL min⁻¹) was halted for two hours when food was introduced in the mesocosms to give mussels time to feed. No mortalities were observed in either the acclimation or experimental periods.

2.1 The effect of substratum-type on M. modiolus and M. edulis movement, aggregation, attachment to shells and patch complexity

Mesocosms were assigned randomly to one of three treatments (substratum type): 'no sediment added', 'sediment added', 'sediment with shells added'. We included a 'no sediment added' treatment, which consisted of only the plastic tank substratum, although this is not necessarily representative of field conditions it allowed comparison with the findings of previous studies and allows a direct test for the effects of the presence of sediment and sediment with shells (e.g., Roberts et al.

2004). Ten mussels, either *M. modiolus* or *M. edulis*, were then added randomly to each mesocosm ensuring mussels were not in physical contact with each other. The average response (mean) of these mussels per mesocosm (replicate) was used for analyses to avoid confounding treatments and each treatment was replicated six times, thus, yielding 36 experimental units. The ‘sediment present’ and ‘sediment with shells present’ treatments comprised of 4.4 ($\pm$ 0.1 S.E) cm depth of locally collected mud in each mesocosm to create an even layer of soft substratum representative of field conditions. To simulate the availability of hard substratum for potential mussel attachment, six intact shell valves of adult *M. modiolus*, creating 25 ($\pm$ 1 S.E.) % cover were evenly added to 12 mesocosms to form the sediment with shell treatment. The experiment ran until mussel movement ceased, which was after 7 days.

2.2 *The effect of density on M. modiolus movement, aggregation and patch complexity*

Mesocosms were assigned randomly to one of three treatments: low mussel density (5 individuals per mesocosm; 100 m⁻²); medium mussel density (10 individuals per mesocosm; 200 m⁻²); and high mussel density (15 individuals per mesocosm; 300 m⁻²). Mean responses of all mussels per mesocosm (replicate) were used in analyses to avoid confounding treatments, which were each replicated five times, yielding 15 experimental units. Mussels were evenly distributed across the bottom of each mesocosm. The minimum distance between each individual was initially 0.5 cm in the high density treatment (Fig 1). Each mesocosm contained 5.5 ($\pm$ 0.1 S.E) cm (depth) of locally collected mud to create representative soft substratum. Mussel movement was recorded in this experiment until all movement ceased, which was after 14 days.

2.3 Quantifying movement, aggregation & patch complexity

In both experiments, individual mussel movement was estimated firstly following Jelnikar & Cote (1999). Photographs of each mesocosm were taken at multiple times throughout the experiments (substratum type and mussel species identity experiment after: 1 hr, 6 hrs, 24 hrs, 48 hrs, 96 hrs and 1 week; *M. modiolus* density experiment: every 48 hrs for two weeks). Images were viewed using ADOBE® Photoshop® CS3 for Mac (Adobe) and ImageJ using the grid overlay plug-in (Schneider et al. 2012) . At each time, the position of the umbo of each mussel under the grid was marked and the distance moved was estimated using ImageJ. Cumulative mussel movement over the experimental duration was then calculated and averaged over each mesocosm before using for data analysis.

At the end of both experiments, mussels were considered to be clumped when two or more mussels were attached together with byssal threads (Cote and Jelnikar, 1999). The abundance of clumps, and number of mussels in each clump, was counted and the percentage of mussels clumped in each mesocosm was recorded. The number of mussels attached to shells in the sediment with the shell treatment were also counted and recorded as a percentage of total mussels attached. No byssal threads were attached to the mesocosm surfaces during the experiment.

Patch complexity within each mesocosm was estimated from the final photos taken in both experiments. Patch complexity was described using fractal dimensions (D) because this metric distinguishes between habitats with few large irregularities from those with many small ones, and is related to the number of interstitial spaces provided by the habitat, allowing assessment of changes in habitat shape relevant to recruitment of conspecifics and biodiversity (Commito and Rusignuolo, 2000; Gutierrez et al., 2003; Kostylev et al., 2005; Tokeshi and Arakaki, 2012). D was

calculated using the grid method (Sugihara & May 1990) following Snover & Commito (1998). Seven different sized grids were overlaid on each image, using the grid overlay plug-in in ImageJ. The number of squares on the side of each grid was equal to $2^0, 2^1, 2^2, 2^3, 2^4, 2^5, 2^6$ (Appendix 1). The number of squares that had a mussel-substratum boundary was entered per each grid square size. D was estimated by performing a linear regression on a double log scale of the length of the side of the squares in the grids against the number of squares containing boundaries. All of the regressions were highly significant ($P < 0.001$). D was the negative value of this slope. A comparison of this top-down method versus the measurement of fractals from vertical profile (Commito and Rusignuolo, 2000; Snover and Commito, 1998) suggests that despite losing accuracy using top-down methods the loss ‘may be more than offset by the savings in time compared to making surface casts that are then cut into sections to produce true profiles’. This non-destructive technique would also be preferable for use in the field in subtidal areas where it is not possible to produce casts for vertical profiling, thus, our approach will be useful to monitor the aggregation of translocated mussels directly in the field (Commito and Rusignuolo, 2000).

2.4 Data analyses

Prior to analyses, all data were tested for heterogeneity of variances using Levene’s test (Quinn and Keough, 2002). A general linear model was used to test for differences in mean cumulative mussel movement, mussel aggregation rates and their fractal dimension (D) based on mussel species identity (fixed factor, two levels), substratum type (fixed factor, three levels) and their interaction for the first experiment and density (fixed factor, three levels) for the second experiment. The residuals were visually checked by plotting them against the fitted values and were

also tested for normality but visually using Q-Q plots and with the Shapiro-Wilk's test. After checking model fitness, type II ANOVA was run to obtain p-values and F-values. Tukey post-hoc was used when p-values were significant ($p < 0.05$).

3 RESULTS

3.1 The effect of substratum-type on M. modiolus and M. edulis movement, aggregation & patch complexity (D)

Mussel movement rate was similar between both species, *M. modiolus* and *M. edulis*, and both were affected similarly (as shown by the lack of a significant interaction term) by substratum type ($F_{2,30} = 8.31$, $p < 0.01$, Fig. 2a). Post-hoc tests show that both species moved more in the treatment without added sediment than in both treatments with sediment ($p < 0.01$, Fig. 2a) and with sediment and shells present ($p < 0.01$, Fig. 2a). The percentage of mussels aggregating was also similar between both species, which also differed similarly (as shown by the lack of a significant interaction term) among substratum types ($F_{2,30} = 4.73$, $p < 0.05$; Fig 2b). Post hoc tests showed that both species aggregated less in the treatment with sediment and shells than the other two treatments (without sediment added, with sediment but no shells; $p < 0.05$, Fig. 2b). Within the treatment with sediment and shells, more *M. edulis* (37%) than *M. modiolus* (18%) attached to empty shells (Fig. 2c). There was no significant difference in patch complexity (*D*) between the two species or among substratum types (Fig. 2d).

3.2 The effect of density on M. modiolus movement, aggregation & patch complexity (D)

There was no effect of density on the distance moved after one week (Fig. 3a) nor two weeks (Fig 3b), however, the percentage of individual *M. modiolus* aggregating differed with density ($F_{2,12} = 5.28$, $p < 0.05$; Fig. 1, 3c). Post hoc tests did not conclusively identify which treatments categorically differed from each other because a significant difference was identified between low and high density treatment ($p < 0.01$) but both treatments were statistically similar to the medium density treatment (Fig. 3c). Mean patch complexity (D) across all treatments was $1.3 (\pm 0.02 \text{ S.E.})$ and there was a significant effect of density on patch complexity D ($F_{2,12} = 13.85$, $p < 0.001$ Fig. 3d). Patch complexity was significantly greater in the high-density and medium-density treatments compared to the low-density treatment based on post-hoc tests ($p < 0.05$, Fig, 3d).

4 DISCUSSION

Our findings show that for both mussel species, *M. modiolus* and *M. edulis*, individual movement was dependent on the substratum type. Both species moved more in the absence of sediment compared to when sediment was present, however, they had different attachment rates to dead shells. When shells were present both species aggregated less, and *M. edulis* had tendency to aggregate less than *M. modiolus* when the shells were present, although this trend was not statistically significant. The greater movement of both species in the treatment with no sediment added compared to the other two treatments, however, did not lead to increased aggregation success, which contradicted our hypothesis that hard substratum is required for reef formation. The addition of shells did not affect movement in either species but seemed to limit aggregation with conspecifics. Moreover, our results suggest that encounter rates with conspecifics may be the main aggregation driver for *M. modiolus* because increased

312 density did not lead to increased movement but tended toward increase aggregation
 313 rates. The fractal dimension of the resulting aggregations was not affected by shell
 314 addition, contrarily to our initial hypothesis. The fractal dimension of these
 315 aggregations was, however, greatest at high and medium *M. modiolus* density as
 316 hypothesised.

317 The movement responses of both mussel species may reflect the habitat type in which
 318 these species are found most commonly (Dinesen and Morton, 2014). *M. edulis* forms
 319 reefs on a variety of substrata, from soft-sediments to rocky areas (Maas Geesteranus,
 320 1942), while *M. modiolus* reefs are generally limited to soft-sediment habitats
 321 (Ragnarsson and Burgos, 2012). The greater movement of *M. modiolus* in the
 322 treatment without sediment compared to other treatments could be a response to the
 323 reduced stability of this substratum, because it is known that this species searches
 324 within the sediment layer for substrata suitable for attachment (Meadows and Shand,
 325 1989). This may also explain why *M. modiolus* tends to be a more stationary species
 326 than *M. edulis* because it does not benefit from exploring the sediment surface for
 327 attachment, as it attaches its byssal threads to suitable substrates under the sediment
 328 surface. This inference was further supported by our findings that *M. modiolus* moved
 329 the shortest distance in the sediment treatment (3.95 ± 0.46 cm week⁻¹) and sediment
 330 with shells (4.67 ± 0.64 cm week⁻¹), while *M. edulis* moved a shorter distance when in
 331 sediment with shell (4.27 ± 0.72 cm week⁻¹). Alternatively, *M. modiolus* may find it
 332 easier to move on a hard substratum as suggested by Roberts et al. (2004). It should
 333 be noted that these findings are based on mesocosm experiments where current speeds
 334 were close to null, whereas *M. modiolus* reefs are found commonly in areas of
 335 moderate to high currents speeds (Rees et al., 2008), therefore, their behaviour in the
 336 field may differ and this should be tested further.

Differences in attachment to dead shells between both species could also be explained by their different modes of living. *M. edulis* used shells for attachment when they were available contrary to *M. modiolus*. *M. modiolus* has an initial fast growth phase until it is large enough to escape most predation (c. 40 mm length), after which growth rates slow considerably (Anwar et al., 1990), and reaches full maturity at 3-5 years (Seed and Brown, 1978). In contrast, in optimal conditions *M. edulis* may grow to 60-80 mm in length within two years (Seed and Suchanek, 1992) and reach full maturity after 1-2 years (O'Connor, 2010; Seed and Brown, 1977). *M. modiolus* larvae may also only settle within the adult matrix (Comely, 1978; Dinesen and Morton, 2014; Fariñas-Franco et al., 2013; Roberts, 1975). These different life-history mechanisms may signify a stronger intra-specific competition among *M. edulis* than *M. modiolus* individuals and, thus, the need for *M. edulis* to attach to other available hard substrata to avoid competition for food and space with conspecifics, while benefitting from the complex habitat as a refuge from predation, even though this may increase their risk of dislodgement (Frandsen and Dolmer, 2002; Okamura, 1986). Another possible explanation for the differences in attachment to non-living shells is that *M. modiolus* has stiffer and less extensible byssal threads than *M. edulis* (Pearce and Labarbera, 2009), suggesting that it is less likely to invest energy by attaching and detaching to identify suitable settlement substratum. In addition, *M. modiolus* has distinct phenotypic morphologies at different sites within Strangford Lough, which are thought to reflect adaption to different current regimes and substratum conditions (Fariñas-Franco et al., 2014). It is possible that because representative *M. modiolus* for this study were collected from a single location, only one phenotype was present, which may have limited their responsive capability.

361 Encounter rate with mussel conspecifics may be an important factor determining *M.*
362 *modiolus* aggregation. In other mussel species, such as *M. edulis* and *Limnoperna*
363 *fortune* (Dunker, 1857), aggregation has been shown to result from random walks (de
364 Jager et al., 2011; Uryu et al., 1996). A greater density of conspecifics has the
365 potential to enhance encounter rates and stimulate attachment during a random walk.
366 *M. modiolus* moved a similar distance in all three density treatments, and in the soft-
367 substratum treatment of the first experiment, which tested for effects of substratum
368 type on aggregation behaviour of this species, aggregation was dependent on initial
369 density with nearly 100% of mussels formed aggregations in the high-density
370 treatment compared to 50% in the low-density treatment. This supports our hypothesis
371 that, owing to the limited movement in soft-sediments environments, encounter rate is
372 an important factor determining aggregation in *M. modiolus*. The response of *M.*
373 *modiolus* to density treatments was similar to that of juvenile *M. edulis*, based on
374 previous studies which found that these mussels tended to aggregate in one patch
375 when relaid at high densities, compared to when they were relaid over a larger area at
376 lower densities (Capelle et al., 2014).

377 Density also affected the resulting patch complexity of the aggregation, with the
378 initial highest density producing aggregations with the highest value of fractal
379 dimension (D). This has some implications for bivalve restoration projects. In a
380 previous study an increase in fractal dimension for aggregation of two or more
381 mussels (D of most complex aggregation = 1.25) compared to single mussels (D =
382 0.99; Commito et al., 2016) was found, indicating that our results (mean value
383 ranging from 1.29 to 1.38 between low and high *M. modiolus* density) are realistic
384 and representative of complex aggregation. In the same study (Commito et al., 2016)
385 differences in fractal dimension (D) of 0.1-0.2 were found between aggregations of

mussels formed under different cue exposures further signify that small but significant differences are often found when using this metric.

Calculating fractal dimension using a down-from-above technique as proxy for habitat complexity may underestimate real three dimensional habitat complexity, which can be typical of long established beds with especially high densities (Snover and Commito, 1998) , however, fractals are a useful, efficient and established method to estimate ‘architectural’ complexity (Commito and Rusignuolo, 2000; Kovalenko et al., 2012), which could be particularly useful to describe initial aggregation of translocated mussels and their likelihood to develop into established reefs. Successful restoration should result in a persistent population with sufficient recruitment rates to replace individuals lost by mortality. If the creation of a habitat with a variation of sizes of interstitial spaces (high fractal dimension) increases recruitment rates, then enhancing the formation of aggregations with high fractal values should be a priority of biogenic reef restoration projects (Fariñas-Franco et al., 2013). Future studies should investigate whether endobyssate species, such as *M. modiolus*, increase in speed of movement and aggregation when exposed to predation risk, similarly to the epibyssate *M. edulis* (Cote and Jelnikar, 1999; Reimer and Tedengren, 1997). These processes should also be examined in field conditions where other environmental factors, such as currents and food availability, could also play an important role.

We, therefore, conclude that: (1) movement of mussels is affected by substratum type; (2) shell presence did not lead to enhanced clumping in either species; (3) aggregation success increased with density of *M. modiolus*; and (4) at greater densities *M. modiolus* aggregations had a higher patch complexity. Our findings suggest that where restoration via translocation of individuals is attempted as a management strategy (Pérez et al., 2012), there is no benefit in manipulating the elevation using

shell cultch as suggested by previous research (Fariñas-Franco et al., 2013), nor would we expect any benefit in substratum enhancement in sediment with shells for *M. modiolus*, contrarily to what is suggested for *M. edulis* (wa Kangeri et al., 2014). We also suggest that the initial density of translocated *M. modiolus* should be at least 200 mussels m⁻², which should allow for a high encounter rate of conspecifics during the first week. This should ensure that aggregations form quickly, and thus limit predation, in turn enhancing the success of the translocation efforts. Aggregations of individuals are common in many ecosystems suggesting that living in close proximity to other conspecifics could maximise survival. Our results also illustrate the importance of understanding the functional ecology of each species that form dense aggregations, with carefully designed experiments when developing restoration methodologies.

ACKNOWLEDGMENTS

We are thankful to the School of Biological Sciences at Queen's University Belfast and the Northern Ireland Environment Agency for funding. We are also thankful to Emma Gorman (QUB), Dr Henk van Rein (QUB) and Tim Mackie (DoE marine division) for boat and technical support. We are also thankful to two anonymous reviewers for helpful comments.

REFERENCES

Anwar, N.A., Richardson, C.A., Seed, R., 1990. Age determination, growth rate and population structure of the horse mussel, *Modiolus modiolus*. J. Mar. Biol. Assoc. UK 441–457.

436

437 Babarro, J.M.F., Comeau, L. a, 2014. Byssus attachment strength of two mytilids in
 438 mono-specific and mixed-species mussel beds. *Biofouling* 30, 975–85.
 439 doi:10.1080/08927014.2014.953941

440

441 Beck, M.W., Brumbaugh, R.D., Airoidi, L., Carranza, A., Coen, L.D., Crawford, C.,
 442 Defeo, O., Edgar, G.J., Hancock, B., Kay, M., Lenihan, H., Luckenbach, M.W.,
 443 Toropova, C.L., Zhang, G., 2009. Shellfish Reefs At Risk: A Global Analysis of
 444 Problems and Solutions, The nature conservancy. Arlington VA.

445

446 Bertness, M.D., Grosholz, E., 1985. Population dynamics of the ribbed mussel,
 447 *Geukensia demissa*: The costs and benefits of an aggregated distribution. *Oecologia*
 448 67, 192–204. doi:10.1007/BF00384283

449

450 Brown, R.A., Seed, R., 1976. *Modiolus modiolus* (L.) - an autoecological study, in:
 451 Keegan, B., Ceidigh, P., Boaden, P. (Eds.), Proceedings of the 11th European
 452 Symposium on Marine Biology, Galway, 5-11 October, 1976. Biology of Benthic
 453 Organisms. pp. 93–100.

454

455 Brown, R. a, 1989. Bottom trawling in Strangford Lough: problems and policies, in:
 456 Hallers, C., Bijlsma, A. (Eds.), Proceedings from the 3rd North Sea Seminar.

457

458 Burrows, M.T., Kamenos, N., Hughes, D.J., Stahl, H., Howe, J.A., Tett, P., 2014.
 459 Assessment of carbon budgets and potential blue carbon stores in Scotland ’ s coastal
 460 and marine environment. Scottish Natural Heritage Commissioned Report N.

461 Buschbaum, C., Dittmann, S., Hong, J.-S., Hwang, I.-S., Strasser, M., Thiel, M.,
 462 Valdivia, N., Yoon, S.-P., Reise, K., 2008. Mytilid mussels: global habitat engineers
 463 in coastal sediments. *Helgol. Mar. Res.* 63, 47–58. doi:10.1007/s10152-008-0139-2
 464
 465 Capelle, J.J., Wijsman, J.W.M., Schellekens, T., van Stralen, M.R., Herman, P.M.J.,
 466 Smaal, A.C., 2014. Spatial organisation and biomass development after relaying of
 467 mussel seed. *J. Sea Res.* 85, 395–403. doi:10.1016/j.seares.2013.07.011
 468
 469 Christensen, H.T., Dolmer, P., Hansen, B.W., Holmer, M., Kristensen, L.D., Poulsen,
 470 L.K., Stenberg, C., Albertsen, C.M., Støttrup, J.G., 2015. Aggregation and attachment
 471 responses of blue mussels, *Mytilus edulis* - impact of substrate composition, time
 472 scale and source of mussel seed. *Aquaculture* 435, 245–251.
 473 doi:10.1016/j.aquaculture.2014.09.043
 474
 475 Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of
 476 fishing impacts on shelf-sea benthos. *J. Anim. Ecol.* 69, 785–798. doi:10.1046/j.1365-
 477 2656.2000.00434.x
 478
 479 Comely, C.A., 1978. *Modiolus modiolus* (L.) from the Scottish west coast. I. Biology.
 480 *Ophelia* 17, 167–193. doi:10.1080/00785326.1978.10425481
 481
 482 Commito, J.A., Gownaris, N.J., Haulsee, D.E., Coleman, S.E., Beal, B.F., 2016.
 483 Separation anxiety: Mussels self-organize into similar power-law clusters regardless
 484 of predation threat cues. *Mar. Ecol. Prog. Ser.* 547, 107–119. doi:10.3354/meps11642
 485

486 Commito, J.A., Rusignuolo, B.R., 2000. Structural complexity in mussel beds : the
 487 fractal geometry of surface topography. J. Exp. Mar. Bio. Ecol. 255, 133–152.
 488
 489 Cook, R., Fariñas-Franco, J.M., Gell, F.R., Holt, R.H.F., Holt, T., Lindenbaum, C.,
 490 Porter, J.S., Seed, R., Skates, L.R., Stringell, T.B., Sanderson, W.G., 2013. The
 491 Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A
 492 Dilemma for Evidence-Based Conservation. PLoS One 8, e69904.
 493 doi:10.1371/journal.pone.0069904
 494
 495 Cote, I.M., Jelnikar, E., 1999. Predator-induced clumping behaviour in mussels (
 496 *Mytilus edulis* Linnaeus). J. Exp. Mar. Bio. Ecol. 235, 201–211.
 497
 498 Cranfield, H., Manighetti, B., Michael, K., Hill, a, 2003. Effects of oyster dredging
 499 on the distribution of bryozoan biogenic reefs and associated sediments in Foveaux
 500 Strait, southern New Zealand. Cont. Shelf Res. 23, 1337–1357. doi:10.1016/S0278-
 501 4343(03)00122-5
 502
 503 de Jager, M., Weissing, F.J., Herman, P.M.J., Nolet, B.A., van de Koppel, J., 2011.
 504 Lévy walks evolve through interaction between movement and environmental
 505 complexity. Science 332, 1551–1553. doi:10.1126/science.1215903
 506
 507 De Smet, B., D'Hondt, A.-S., Verhelst, P., Fournier, J., Godet, L., Desroy, N., Rabaut,
 508 M., Vincx, M., Vanaverbeke, J., 2015. Biogenic reefs affect multiple components of
 509 intertidal soft-bottom benthic assemblages: the *Lanice conchilega* case study. Estuar.
 510 Coast. Shelf Sci. 152, 44–55. doi:10.1016/j.ecss.2014.11.002

511 Dinesen, G.E., Morton, B., 2014. Review of the functional morphology, biology and
 512 perturbation impacts on the boreal, habitat-forming horse mussel *Modiolus modiolus*
 513 (Bivalvia: Mytilidae: Modiolinae). Mar. Biol. Res. 10, 845–870.
 514 doi:10.1080/17451000.2013.866250
 515
 516 Dolmer, P., 1998. The interactions between bed structure of *Mytilus edulis* L. and the
 517 predator *Asterias rubens* L. J. Exp. Mar. Bio. Ecol. 228, 137–150.
 518 doi:10.1016/S0022-0981(98)00024-0
 519
 520 Fariñas-Franco, J.M., Allcock, L., Smyth, D., Roberts, D., 2013. Community
 521 convergence and recruitment of keystone species as performance indicators of
 522 artificial reefs. J. Sea Res. 78, 59–74. doi:10.1016/j.seares.2012.10.008
 523
 524 Fariñas-Franco, J.M., Sanderson, W.G., Roberts, D., 2014. Phenotypic differences
 525 may limit the potential for habitat restoration involving species translocation: a case
 526 study of shape ecophenotypes in different populations of *Modiolus modiolus*
 527 (Mollusca: Bivalvia). Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 76–94.
 528 doi:10.1002/aqc.2496
 529
 530 Firth, L.B., Mieszkowska, N., Grant, L.M., Bush, L.E., Davies, A.J., Frost, M.T.,
 531 Moschella, P.S., Burrows, M.T., Cunningham, P.N., Dye, S.R., Hawkins, S.J., 2015.
 532 Historical comparisons reveal multiple drivers of decadal change of an ecosystem
 533 engineer at the range edge. Ecol. Evol. doi:10.1002/ece3.1556
 534
 535 Frandsen, R., Dolmer, P., 2002. Effects of substrate type on growth and mortality of

536 blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas*. Mar. Biol.
 537 141, 253–262. doi:10.1007/s00227-002-0831-8
 538
 539 Gascoigne, J.C., Beadman, H. a., Saurel, C., Kaiser, M.J., 2005. Density dependence,
 540 spatial scale and patterning in sessile biota. Oecologia 145, 371–381.
 541 doi:10.1007/s00442-005-0137-x
 542
 543 Geraldi, N.R, Bertolini, C., Emmerson, M. C. , Roberts, D., Sigwart, J.D., O’Connor,
 544 N.E., in press, Aggregation of brittle stars can provide similar ecological roles as
 545 mussel reefs, Mar. Ecol. Prog. Ser., doi: 10.3354/meps11993
 546
 547 Gormley, K.S.G., Porter, J.S., Bell, M.C., Hull, A.D., Sanderson, W.G., 2013.
 548 Predictive habitat modelling as a tool to assess the change in distribution and extent of
 549 an OSPAR priority habitat under an increased ocean temperature scenario:
 550 consequences for marine protected area networks and management. PLoS One 8,
 551 e68263. doi:10.1371/journal.pone.0068263
 552
 553 Green, D., Boots, B., O’Connor, N. E. & Thompson, R., 2016 Microplastics affect the
 554 ecological functioning of an important biogenic habitat. Envir. Sci. and Tech.
 555 10.1021/acs.est.6b04496.
 556
 557
 558 Gutierrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as
 559 ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–
 560 90.

561

562 Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and Negative Effects of
 563 Organisms as Physical Ecosystem Engineers. *Ecology* 78, 1946–1957.

564

565 Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as Ecosystem Engineers.
 566 *Oikos* 69, 373–386. doi:10.2307/3545850

567

568 Kobak, J., 2001. Light, Gravity and Conspecifics As Cues To Site Selection and
 569 Attachment Behaviour of Juvenile and Adult *Dreissena polymorpha* Pallas, 1771. *J.*
 570 *Molluscan Stud.* 67, 183–189. doi:10.1093/mollus/67.2.183

571

572 Koppel, J. Van De, Rietkerk, M., Dankers, N., Herman, P.M.J., 2005. Scale-
 573 Dependent Feedback and Regular Spatial Patterns in Young Mussel Beds. *Am. Nat.*
 574 165, E66–E77.

575

576 Kostylev, V.E., Erlandsson, J., Ming, M.Y., Williams, G. a., 2005. The relative
 577 importance of habitat complexity and surface area in assessing biodiversity: Fractal
 578 application on rocky shores. *Ecol. Complex.* 2, 272–286.
 579 doi:10.1016/j.ecocom.2005.04.002

580

581 Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: approaches
 582 and future directions. *Hydrobiologia* 685, 1–17. doi:10.1007/s10750-011-0974-z

583

584 Lenth, R. V, 2016. Least-Squares Means: The R Package lsmeans. *J. Stat. Softw.* 69,
 585 1–33. doi:10.18637/jss.v069.i01

586

587 Lindenbaum, C., Bennell, J.D., Rees, E.I.S., McClean, D., Cook, W., Wheeler, A.J.,
 588 Sanderson, W.G., 2008. Small-scale variation within a *Modiolus modiolus* (Mollusca:
 589 Bivalvia) reef in the Irish Sea: I. Seabed mapping and reef morphology. J. Mar. Biol.
 590 Assoc. UK 88, 133–141. doi:10.1017/S0025315408000374

591

592 Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C.,
 593 Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., Bay, M., 2006.
 594 Depletion, Degradation and Recovery Potential of Estuaries and Coastal Seas. Science
 595 (80-.). 312, 1806–1809.

596

597 Maas Geesteranus, R.A., 1942. On the formation of banks by *Mytilus edulis* L. Arch.
 598 Néerlandaises Zool. 6, 283–325.

599

600 Magorrian, B.H., Service, M., 1998. Analysis of underwater visual data to identify the
 601 impact of physical disturbance on horse mussel (*Modiolus modiolus*) beds. Mar.
 602 Pollut. Bull. 36, 354–359.

603

604 Mauck, R. a., Harkless, K.C., 2001. The effect of group membership on hiding
 605 behaviour in the northern rock barnacle, *Semibalanus balanoides*. Anim. Behav. 62,
 606 743–748. doi:10.1006/anbe.2001.1798

607

608 Meadows, P.S., Shand, P.S., 1989. Experimental analysis of byssus thread production
 609 by *Mytilus edulis* and *Modiolus modiolus* in sediments. Mar. Biol. 101, 219–226.

610

611 Mrowicki, R.J., O'Connor, N.E., 2015. Wave action modifies the effects of consumer
612 diversity and warming on algal assemblages. *Ecology* 96, 1020–1029.
613 doi:10.1890/14-0577.1
614

615 Navarro, J.M., Thompson, R.J., 1997. Biodeposition by the horse mussel *Modiolus*
616 *modiolus* (Dillwyn) during the spring diatom bloom. *J. Exp. Mar. Bio. Ecol.* 209, 1–
617 13.
618

619 Nicastro, K.R., Zardi, G.I., McQuaid, C.D., Pearson, G. a, Serrão, E. a, 2012. Love
620 thy neighbour: group properties of gaping behaviour in mussel aggregations. *PLoS*
621 *One* 7, e47382. doi:10.1371/journal.pone.0047382
622

623 O'Connor, N.E., 2010. Shore exposure affects mussel population structure and
624 mediates the effect of epibiotic algae on mussel survival in SW Ireland. *Estuar. Coast.*
625 *Shelf Sci.* 87, 83–91. doi:10.1016/j.ecss.2009.12.011
626

627 Okamura, B., 1986. Group living and the effects of spatial position in aggregations of
628 *Mytilus edulis*. *Oecologia* 69, 341–347. doi:10.1007/BF00377054
629

630 Pearce, T., Labarbera, M., 2009. A comparative study of the mechanical properties of
631 Mytilid byssal threads. *J. Exp. Biol.* 212, 1442–1448. doi:10.1242/jeb.025544
632

633 Pérez, I., Anadón, J.D., Díaz, M., Nicola, G.G., Tella, J.L., Giménez, A., 2012. What
634 is wrong with current translocations? A review and a decision-making proposal.
635 *Front. Ecol. Environ.* 10, 494–501. doi:10.1890/110175

636

637 Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for
638 Biologists, Experimental design and data analysis for biologists. doi:10.1016/S0022-
639 0981(02)00278-2

640

641 R Development Core Team, R., 2015. R: A Language and Environment for Statistical
642 Computing. R Found. Stat. Comput. doi:10.1007/978-3-540-74686-7

643

644 Ragnarsson, S. a., Burgos, J.M., 2012. Separating the effects of a habitat modifier,
645 *Modiolus modiolus* and substrate properties on the associated megafauna. J. Sea Res.
646 72, 55–63. doi:10.1016/j.seares.2012.05.011

647

648 Rees, E.I.S., Sanderson, W.G., Mackie, a. S.Y., Holt, R.H.F., 2008. Small-scale
649 variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. III.
650 Crevice, sediment infauna and epifauna from targeted cores. J. Mar. Biol. Assoc. UK
651 88, 151–156. doi:10.1017/S0025315408000052

652

653 Rees, I., 2009. Assessment of *Modiolus modiolus* in the OSPAR area.

654 Reimer, O., Tedengren, M., 1997. Predator-induced changes in byssal attachment,
655 aggregation and migration in the blue mussel, *Mytilus edulis*. Mar. Freshw. Behav.
656 Physiol. 30, 251–266. doi:10.1080/10236249709379029

657

658 Roberts, C., 1975. Investigations into a *Modiolus modiolus* (L.) (Mollusca: Bivalvia)
659 community in Strangford Lough,. North. Ireland. Rep. Underw. Assoc. 1.

660

661 Roberts, D., Allcock, L., Fariñas-Franco, J.M., Gorman, E., Maggs, C.A., Mahon,
 662 A.M., Smyth, D., Strain, E.M. a, Wilson, C.D., 2011. *Modiolus* Restoration Research
 663 Project : Final Report and Recommendations.
 664
 665 Roberts, D., Davies, C., Mitchell, A., Moore, H., Picton, B., Portig, A., Preston, J.,
 666 Service, M., Smyth, D., Strong, D., Vize, S., 2004. Strangford Lough Ecological
 667 Change Investigation (SLECI) (2).
 668
 669 Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years
 670 of image analysis. Nat. Methods 9, 671–675. doi:10.1038/nmeth.2089
 671
 672 Seed, R., Brown, R. a, 1978. Growth as a strategy for survival in two marine bivalves,
 673 *Cerastodroma edule* and *Modiolus modiolus*. J. Anim. Ecol. 47, 283–292.
 674
 675 Seed, R., Brown, R. a, 1977. A comparison of the reproductive cycles of *Modiolus*
 676 *modiolus* (L.), *Cerastoderma* (= *Cardium*) *edule* (L.), and *Mytilus edulis* L. in
 677 Strangford Lough, Northern Ireland. Oecologia 30, 173–188.
 678 doi:10.1007/BF00345419
 679
 680 Seed, R., Suchanek, T.H., 1992. Population and community ecology of *Mytilus*, in:
 681 Gosling, E.M. (Ed.), The Mussel *Mytilus*: Ecp;pgy, Physiology, Genetics and Culture.
 682 Elsevier, London, pp. 87–169.
 683
 684 Service, M., 1998. Recovery of benthic communities in Strangford Lough following
 685 changes in fishing practice. ICES Counc. Meet. Pap.

686

687 Service, M., Magorrian, B.H., 1997. The Extent and Temporal Variation of
688 Disturbance to Epibenthic Communities in Strangford Lough, Northern Ireland. J.
689 Mar. Biol. Assoc. United Kingdom 77, 1151–1164.

690

691 Snover, M.L., Commito, J.A., 1998. The fractal geometry of *Mytilus edulis* L. spatial
692 distribution in a soft-bottom system 223, 53–64.

693

694 Strong, J.A., Service, M., Moore, H., 2016. Estimating the historical distribution,
695 abundance and ecological contribution of *Modiolus modiolus* in Strangford Lough,
696 Northern Ireland. Biol. Environ. 116B, 1–16. doi:10.3318/BIOE.2016.1

697

698 Sugihara, G., M May, R., 1990. Applications of fractals in ecology. Trends Ecol.
699 Evol. Personal Ed. 5, 79–86.

700

701 Thrush, S.F., Hewitt, J.E., Funnell, G.A., Cummings, V.J., Ellis, J., Schultz, D.,
702 Talley, D., Norkko, A., 2001. Fishing disturbance and marine biodiversity: The role
703 of habitat structure in simple soft-sediment systems. Mar. Ecol. Prog. Ser. 223, 277–
704 286. doi:10.3354/meps223277

705

706 Tokeshi, M., Arakaki, S., 2012. Habitat complexity in aquatic systems: Fractals and
707 beyond. Hydrobiologia 685, 27–47. doi:10.1007/s10750-011-0832-z

708

709 Uryu, Y., Iwasaki, K., b, Hinoue, M., 1996. Laboratory experiments on behaviour
710 and movement of a freshwater mussel, *Limnoperna fortunei* (Dunker). J. Molluscan

711 Stud. 62, 327–341. doi:10.1093/mollus/62.3.327
 712
 713 van de Koppel, J., Gascoigne, J.C., Theraulaz, G., Rietkerk, M., Mooij, W.M.,
 714 Herman, P.M.J., 2008. Experimental evidence for spatial self-organization and its
 715 emergent effects in mussel bed ecosystems. *Science* 322, 739–742.
 716
 717 van der Zee, E.M., Tielens, E., Holthuijsen, S., Donadi, S., Eriksson, B.K., van der
 718 Veer, H.W., Piersma, T., Olff, H., van der Heide, T., 2015. Habitat modification
 719 drives benthic trophic diversity in an intertidal soft-bottom ecosystem. *J. Exp. Mar.*
 720 *Bio. Ecol.* 465, 41–48. doi:10.1016/j.jembe.2015.01.001
 721
 722 wa Kangeri, A.K., Jansen, J.M., Barkman, B.R., Donker, J.J.A., Joppe, D.J., Dankers,
 723 N.M.J.A., 2014. Perturbation induced changes in substrate use by the blue mussel,
 724 *Mytilus edulis*, in sedimentary systems. *J. Sea Res.* 85, 233–240.
 725 doi:10.1016/j.seares.2013.06.001
 726
 727
 728
 729

FIGURES

Figure 1. Representation of clumping behaviour of *M. modiolus* at: (A) low, (B) medium and (C) high, density. Left column represent *M. modiolus* outline as laid at the start of the experiment in one replicate of each treatment, right column represent outline at the end of two weeks in the same replicates.

Figure 2. Means ($\pm$ SE) of (a) cumulative distance of mussels' movement in each mesocosm and (b) percent of mussels aggregated, in three experimental treatments with insert showing responses of *M. modiolus* and *M. edulis* separately for clarity, (c) percent of mussels of both species attached to shells, and (d) the fractal dimension (D) of aggregations formed by *M. modiolus* and *M. edulis* in all three experimental treatments. White bars represent the no sediment added treatment, grey bars represent sediment added treatment and black bars represent the sediment with shells added treatment. Lower case letters denote groups of means that are significantly different from each other based on post hoc tests ($p < 0.05$).

Figure 3. Means ($\pm$ SE) of (a) cumulative distance (cm) of *M. modiolus* movement in each mesocosm after one and (b) after two weeks, (c) percent of aggregated *M. modiolus*, and (d) fractal dimension (D) of *M. modiolus* aggregations. White bars represent the low density, grey bars represent medium density, and dark black bars represent high density. Lower case letters denote groups of means that are significantly different from each other based on post hoc tests ($p < 0.05$).

755 Figure 1

756
757
758

Figure 2