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Substratum type and conspecific density as drivers of mussel patch formation

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ABSTRACT

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

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 carbon storage in the form of shell deposits (Brown and Seed,

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1976; Burrows et al., 2014; Cook et al., 2013; Fariñas-Franco et al., 2013; Geraldi et al., in press; Navarro and Thompson, 1997; Ragnarsson and Burgos, 2012; Rees et al., 2008).

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

A better understanding of how reef-forming species aggregate to form these complex reefs is essential to design more effective restoration practices, such as species translocation, aimed at reintroducing eradicated populations to establish functioning and stable reefs. Fast aggregation should result in a reef containing many small interstitial spaces, which promotes further successful settlement (Comely, 1978; Roberts, 1975) by providing refuge from predators (Dolmer, 1998; Okamura, 1986). Few studies to our knowledge, however, have tested whether substratum type or initial mussel density affects mussel aggregation behaviour (e.g. wa Kangeri et al., 2014 for substratum type), and the complexity of their formations (aggregations). If substratum type and density alter mussel aggregation behaviour, it is likely that their fractal organisation will be affected. Understanding these mechanisms, therefore, is an important prerequisite to improve restoration success (Beck et al., 2009).

While the relationships between bivalve aggregation density and survival, growth, reproduction and predation rates have been studied widely (e.g. Okamura, 1986, Dolmer, 1998, Nicastro et al., 2012), the environmental factors and conditions driving aggregation of these reef-forming bivalves are not yet understood. Differences in substratum type can affect mussel aggregation patterns, thus, affecting attachment strength (Babarro and Comeau, 2014; Christensen et al., 2015; wa Kangeri et al., 2014). Density is another important factor that alters how individuals aggregate (Gascoigne et al., 2005). In general, a greater density of adult mussels stimulates attachment of mussels to the substratum (Kobak, 2001), which can be an important predictor for spatial self-organisation (van de Koppel et al., 2005; van de Koppel et al., 2008) and size of aggregations (Capelle et al., 2014), ultimately having the potential to affect the stability of the whole reef (Bertness & Grosholz, 1985, Capelle et al., 2014). To date comparatively more research has been done on more common mussel species (e.g. *M. edulis*) than less abundant species (e.g. *M. modiolus*; Dinesen and Morton, 2014; Ragnarsson and Burgos, 2012). Although mytilid mussels may be functionally similar in many ways, it is also possible that their unique natural histories may underpin different behavioural and physiological responses to environmental conditions. While many studies have examined the aggregation behaviour of *M. edulis* (e.g. Maas Geesteranus, 1942), only one study, to our knowledge, has assessed the aggregation of *M. modiolus,* however this did not manipulate substrata or include soft-sediment representative of local field conditions (Roberts et al., 2004), thus knowledge regarding initial patch and reef formation for this species is still lacking.

In response to the need to develop optimal restoration methods (Pérez et al., 2012), the primary aim of this study was to test whether differences in substratum type and mussel density affected the aggregation behaviour of *M. modiolus* and to identify the mechanisms driving patch and subsequently reef formation in this species. We also tested whether the behaviour of *M. modiolus* differed from that of the well-studied mussel, *M. edulis*, which is taxonomically distinct but often considered functionally similar. The comparison between species will allow us to determine whether it would be prudent to include available data describing *M. edulis* movement to develop restoration methods for *M. modiolus*. Further, we assessed how substratum type and density can affect patch complexity of resulting aggregation to gain insights on the availability and size range of interstitial spaces within the mussel habitat and can be used as a proxy for refuge availability (Kostylev et al., 2005; Tokeshi and Arakaki, 2012), at the initial stages of patch formation before three dimensional reef accretion 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