In situ biodeposition measurements on a *Modiolus modiolus* (horse mussel) reef provide insights into ecosystem services

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**Abstract**

Horse mussel (*Modiolus modiolus*) shellfish reefs are a threatened and declining habitat in the North East Atlantic and support high levels of biodiversity. Shellfish can influence the surrounding water column and modify the quality of material that reaches the seabed by filtering water, actively depositing particles and changing the benthic boundary layer due to surface roughness. In the present study *M. modiolus* biodeposition was measured in a field location for the first time. The results show that *M. modiolus* enhance sedimentation and contribute to the downward flux of material to the seabed. Approximately 30% of the total sediment deposition was attributed to active filter feeding and overall, the presence of horse mussels enhanced deposition two fold. The results are discussed in terms of the potential for horse mussel reefs to provide ecosystem services to society, through functions such as benthopelagic coupling and sediment stabilisation. Highlighting the societal benefits supplied by marine habitats can help prioritise conservation efforts and feed into the sustainable management of coastal water bodies.

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**1. Introduction**

Horse mussels (*Modiolus modiolus*) can occur in dense aggregations forming ‘biogenic reefs’ or ‘beds’, which support a diverse range of associated species (Fariñas-Franco et al., 2014; Rees et al., 2008). *M. modiolus* are known to filter large volumes of water (Navarro and Thompson, 1996) and reefs provide a spatial refuge for many other invertebrates (Wilman, 1985; Kent et al., 2016), making them ecologically important. Filter feeders act as a natural top-down control on phytoplankton concentrations (Newell, 2007), indeed, oyster reef restoration has been used as an attempt to improve water quality and reduce eutrophication (Coen et al., 2007). Grabowski and Peterson (2007) highlight the ecosystem services provided by oyster reefs, including provisioning services (e.g. oyster production) and regulating services (e.g. water filtration and carbon sequestration), although there are very few measurements of long-term burial and sequestration of carbon for shellfish reefs (Kellogg et al., 2014). Walles et al. (2015b) estimate oyster reef accretion rates, demonstrating the importance of shellfish reefs for shoreline protection through sediment stabilisation. Navarro and Thompson (1997) illustrate the potential for *M. modiolus* to modify benthopelagic processes through aquarium-based measurements of biodeposition, however, no in situ measurements of *M. modiolus* deposition exist to our knowledge.

Benthic filter feeders are exposed to a range of suspended particles including plankton, detritus and mineral grains of various sizes (Ward and Shumway, 2004). Deposition by shellfish can vary seasonally (Haven and Morales-Alamo, 1966) and feeding rate is influenced by abiotic factors including flow rate (Walne, 1972) and temperature (Kittner and Riisgård, 2005). Filtration by mussels can have a significant effect on hydrodynamic processes occurring at the seabed-water column interface, for example, by increasing the velocity gradient in near-bed layers (van Duren et al., 2006).

Sediment deposition in marine systems is primarily controlled by physical processes (e.g. currents and waves) and chemical processes, such as the cohesive forces acting between fine clay particles (Montserrat et al., 2009). Shellfish beds alter seabed surface roughness, increasing drag and modifying flow (as shown for *Atrina zelandica* beds (Green et al., 1998) and oyster reefs (Styles, 2015)). van Leeuwen et al. (2010) suggest that active deposition (by filtration) in combination with the increased drag coefficient (due to seabed roughness) causes high deposition on a *Mytilus edulis* reef (Fig. 1, processes 2 and 3). As well as fine sediment becoming
Fig. 1. Five sediment processes occurring on a hypothetical biogenic shellfish habitat based on 1, Lampitt (1985); 2, van Duren et al. (2006); 3, van Leeuwen et al. (2010); 4, Doering (1989); 5, van Duren et al. (2006).

trapped within the biogenic structure, enhanced deposition can occur in the wake of a mussel bed due to reduced flow; as demonstrated for mussel beds (Donadi et al., 2013) and oyster beds (Walles et al., 2015a). Mussel beds effect benthic sediment characteristics (e.g. grain size (Mayer et al., 1985) and organic matter (van der Zee et al., 2012), and the presence of bivalves can also influence sediment resuspension, possibly due to burrowing or the production of pseudofaeces (Willows et al., 1998).

The processes illustrated in Fig. 1 can vary hourly, daily and seasonally (e.g. due to the response of phytoplankton to seasonal changes in nutrient and light availability: Lampitt, 1985) and are modulated by mixing, e.g. storms (Baileywatts, 1978). Resuspension is an important process in tidal areas such as sea lochs (Overnell and Young, 1995), as it can resuspend nutrients, enhancing primary productivity in the water column (Doering, 1989). Tides influence mixing and sedimentation, exemplified in estuaries where currents and waves during the spring-neap cycle are steering factors for erosion, resuspension and deposition (Allen et al., 1980).

Much research has been carried out into feeding and biodeposition of commercially important bivalves, specifically the blue mussel, M. edulis (e.g. Bayne et al., 1993; Hatcher et al., 1995; Tsuchiya, 1980) and the oyster, Crassostrea gigas (e.g. Deslous-Paoli et al., 1992; Dupuy et al., 2000), however, information on non-commercial shellfish species such as M. modiolus is lacking. Biogenic reef forming filter feeders are able to mediate the quality of the material that reaches the seabed (Navarro and Thompson, 1996) and reef fauna assimilate the energy into their tissues, making it available for higher trophic levels (Yeager and Layman, 2011). In bivalves, particles filtered from the water column are partly used for metabolism and growth, while the end product is excreted as faeces and pseudofaeces (Deslous-Paoli et al., 1992). On a M. modiolus reef, the accumulation of dead shell, biodeposits and animal remains can be observed as a raised structure on the seabed and such structures can form an undulating wave formation on the seabed that can persist for centuries (Lindenbaum et al., 2008).

When mussels occur in high densities to form beds or biogenic reefs, the mussel assemblage will influence the surrounding water column. Widdows et al. (2009) found that mussel assemblages induce resuspension of sediment, which enhances feeding activity and causes large scale clearance of particles from the water column. Prins et al. (1996) measured clearance rates of up to 7.1 m² m⁻² h⁻¹ for example, using a flow through tunnel on an intertidal M. edulis bed. In addition to the active and passive processes occurring as a result of the individual M. modiolus, it might be expected that there would be an influence of the mussel assemblage itself (Schwindt et al., 2004), which may further enhance deposition. Collectively, these processes will be referred to as the ‘reef effect’ for the purposes of this study.

Direct measurements of biodeposition rates occurring in situ have the benefit of being exposed to natural conditions yet have rarely been attempted due to the difficulty of undertaking subtidal studies. Zhou et al. (2006) measured scallop biodeposition rates in situ using PVC cylindrical traps suspended underneath longlines in order to recreate the conditions the animals would be exposed to when cultured. However, Storlazzi et al. (2011) warned against the use of cylindrical sediment traps to achieve absolute measures of deposition due to the modification of hydrodynamics around the trap, which can influence the total amount of sediment obtained.

The aim of the present study was to measure sedimentation in situ on a M. modiolus reef. M. modiolus habitats are on the OSPAR Threatened and Declining list, with declines recorded in Northern Ireland (Strain et al., 2012) and Scotland (Thurstan et al., 2013). Gaining an understanding of the scale of functional processes occurring on M. modiolus reefs will help show the value of such habitats through the ecosystem services that they provide. The experiment was designed to test the hypotheses that: 1) live M. modiolus enhance sedimentation by active biodeposition; 2) the physical structure created by M. modiolus reef increases sediment deposition by passive processes; and 3) M. modiolus reefs increase sedimentation through the reef effect described above.
2. Materials and methods

2.1. Study site

Experiments took place at two sites off Port Appin, in Loch Linnhe, Scotland (Fig. 2). One site was on a M. modiolus reef (56° 33′ 1.8″ N, 005° 25′ 26.4″ W) and the second ‘off-reef’ control site with no M. modiolus was located to the north-east of the reef (56° 33′ 56.59″ N, 5° 24′ 29.95″ W). Both sites were at 22 m below chart datum, on a gently sloping seabed. Flow rate at the M. modiolus reef can reach 0.18 m s⁻¹ on a flood tide (R. Cook, unpub. data).

2.2. Experimental design

Twenty-two experimental treatments were deployed using SCUBA divers at each site (12 boxes and 10 tiles). The boxes were constructed using a 6 L container (20 cm × 25.8 cm surface area) with a 4 cm thick layer of concrete inserted into the bottom to weigh the box down, and this was covered in a layer of scouring pad (Fig. 3C). The scouring pad material was used to restrict resuspension, following Babcock and Smith (2000), to ensure that the sediment and biodeposits remained in the box. An O-ring on the lid created a seal so that no sediment would be lost during diver retrieval. Each box was held in place using 1.25 m steel rods hammered into the seabed.

Twelve boxes were deployed at each site representing four replicates of three different experimental treatments. Four of the boxes contained three live adult M. modiolus (10.5–12.5 cm in length), four contained three ‘dead’ M. modiolus of the same length (shells held together with concrete, see Fig. 3A), and four contained no M. modiolus (‘box only’ treatment, Fig. 3C). Mussel density at the reef site had been recorded the year before (Moore et al., 2012), and therefore, the number of animals in the live and dead treatments were chosen to represent this natural density (approximately 40 mussels m⁻²). Live M. modiolus were collected on the 19th June 2012 and kept in a mesh bag attached to a nearby pontoon to reduce disturbance to the mussels during transportation (See Supplementary Fig. 1 for M. modiolus size distribution at Port Appin). To control for the ‘box effect’, four scouring pads were deployed at each site on plastic tiles (14 cm × 14 cm) but not in boxes.

The treatments were distributed at random around a central marker on the seabed in two concentric rings to ensure even exposure from currents at all tidal states. A predetermined random order was used to pack the boxes into deployment sacks. Each treatment was placed on the seabed a minimum of 2.5 m from the next in the circle. The treatments were distributed in the same way at the reef and off-reef site to compare sites. The boxes were

![Fig. 2. Site location with UK map insert, showing the location of Loch Linnhe. Experimental sites are represented by red circles. M. modiolus reef is located to the south-west and the 'off-reef' control site to the north-east. Brown polygon shows the estimated M. modiolus reef outline (from Moore et al., 2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)](image-url)
deployed with lids on and the scouring pads on tiles were transported to the seabed in plastic zip-lock bags. Once the divers had distributed the boxes and scouring pads, lids and bags were removed starting with those upstream to prevent disturbed sediment entering the boxes and scouring pads. The boxes were left on the seabed on the 10th July 2012 for seven days spanning a spring/neap tidal cycle.

During recovery, lids were placed on all boxes (Fig. 3D) and scouring pads on tiles were placed in bags. To avoid any resuspended sediment created by the divers entering and contaminating the boxes, recovery was made starting downstream and working upstream. All boxes were lifted to the surface and the scouring pads on tiles were carefully placed into zip-lock bags and carried to the surface by the divers. One scouring pad treatment and one box only treatment leaked during transportation and were therefore not analysed. Six scouring pads on tiles were left at each site so that three could be retrieved after 21 days and the final three retrieved 51 days after deployment to measure the saturation point of the scouring pads. This was to ensure that the scouring pads in the boxes were not becoming saturated during the seven day experiment.

The horse mussels and scouring pads in the boxes were rinsed off, and the water was filtered on pre-ashed Whatman GF/C filters (1.2 μm pore size) following Navarro and Thompson (1997), then rinsed through with distilled water to remove salt. Water from the zip-lock bags was stored in sample buckets and the scouring pads rinsed until the water ran clean. The water from the scouring pad samples was also filtered. The filters were dried at 100 °C until they reached a constant weight to measure total particulate matter (TPM). The dried filters were then ashed at 450 °C for two hours following Bayne et al. (1993). From this it was possible to calculate particulate organic matter (POM) as the difference between TPM and the ashed weight. TPM of the surface water was taken in July 2014 and analysed in the same way as for the boxes and scouring pads (Supplementary Table 1).

2.3. Data analysis

TPM was converted to g m⁻² for each treatment (i.e. one scouring pad or box) by dividing the weight of the sediment by the area over which it was collected. The TPM data were square root transformed and tested for normality (Anderson Darling test) and equal variances (Bartlett test). TPM collected from the treatments was compared using a two-way ANOVA with ‘site’ and ‘treatment’ as fixed factors. Site had two levels: reef and off-reef, while treatment had four levels: live, dead, box only and scouring pad. Non-significant terms (<0.05) were subsequently removed. A Tukey post-hoc multiple comparison test was used to investigate differences between treatments. All univariate analyses were carried out in R version 2.9.1 (R Core Development Team, 2011).

To compare the results to Navarro and Thompson (1997), data were treated differently; the weight of sediment deposited was converted to mg day⁻¹ mussel⁻¹. Then the average sediment deposited by control (dead) mussels was subtracted from that deposited by live mussels to account for any background deposition and therefore estimate the active biodeposition rate.

The POM data were assessed for overall distribution and log transformed. Following this, the data were analysed in the same way as TPM. POM was then calculated as a proportion of TPM to give the fraction of organic content of the seston (f). This converted data (f) did not meet the criteria for a parametric test and were therefore compared using a Kruskal-Wallis test. Median sediment deposition figures are reported for all analyses.

3. Results

The scouring pads continued taking on sediment throughout the 57 day saturation experiment with the variability increasing ten fold between 21 and 57 days (see Supplementary Table 2).

Comparison of TPM showed significant differences between treatments (ANOVA, F = 12.31, p < 0.001). TPM in the live treatment (60.01 g m⁻²) was significantly greater than in the dead treatment.
(p = 0.04) and the box only treatment (p < 0.001), as shown by Tukey post hoc pairwise comparisons. The dead mussel treatment was significantly different to the box only (p = 0.04), with an extra 16.15 g m\(^{-2}\) in the dead treatment (Fig. 4). The difference between the deposition in the live and dead boxes was 19.28 g m\(^{-2}\) (approximately 30% of the total sediment deposited). When calculated as biodeposition rate (faeces and pseudofaeces) for an individual M. modiolus, values range from 0.90 mg mussel\(^{-1}\) day\(^{-1}\) to 14.33 mg mussel\(^{-1}\) day\(^{-1}\) with an average (±1SE) of 5.20 mg mussel\(^{-1}\) day\(^{-1}\) ± 1.74.

There was no significant difference between the scouring pads recovered on day 7 and the box only treatment (p = 0.86), suggesting no influence of the box. There was also no significant difference in TPM between the two sites (reef and off-reef) (ANOVA, F = 0.17, p = 0.68).

POM was found to differ significantly between treatments (ANOVA, F = 25.13, p < 0.001). Sediment from the live treatment had two times more organic material than the box only treatment and 42% more organic material than the dead treatment (9.70 g m\(^{-2}\) in the live treatment compared to 6.85 g m\(^{-2}\) in the dead, p = 0.02). POM in the live M. modiolus treatment was significantly greater than the box only (p < 0.001) and scouring pad treatments (p < 0.001), as shown in Fig. 5. However, when expressed as a proportion of the TPM, there was no significant difference in organic content between treatments (X\(^2\) = 2.48, p = 0.48), although the proportion of organic material was slightly higher in the live mussel treatment compared to the box only (19% and 16% respectively).

4. Discussion

In the present study, the presence of live M. modiolus doubled deposition from a background measure of 30 g m\(^{-2}\) to 60 g m\(^{-2}\), and of this, 41% of the enhanced deposition was due to the passive, structural effect of the M. modiolus (represented by dead mussel shells). Although M. modiolus biodeposition rates have been measured before in an aquarium setting (Navarro and Thompson, 1997), this is the first time that M. modiolus deposition has been quantified in situ on a natural biogenic reef. The development of this method is an important step towards furthering our understanding of sediment accumulation and sequestration by benthic habitats in general.

Unlike conventional cylindrical sediment traps, low profile sediment traps made from artificial turf and scouring pads have been used effectively in flood plain management and coral reef experiments (Babcock and Smith, 2000; Steiger et al., 2003). In the present study, scouring pads were left for up to 57 days and these continued to accumulate sediment throughout this period. This indicates that the boxes did not become saturated during the seven day experiment in this environment. Furthermore, there was no significant difference between the sediment collected in the box only treatment and the scouring pads, indicating that there was no overall ‘box effect’. The boxes were therefore suitable for determining relative deposition rates for the purposes of this experiment. The scouring pad material within the boxes successfully retained M. modiolus biodeposits in an area of moderate tidal flow (up to 0.18 m s\(^{-1}\)) and the boxes were small and compact for ease of deployment in the field. The high variability in deposition after 21 days deployment suggests that the scouring pads would not be effective if used for prolonged periods of time, but were nevertheless effective in the present context.

The average biodeposition rate of 4.92 mg mussel\(^{-1}\) day\(^{-1}\) was slightly lower than measurements made by Navarro and Thompson (1997) using flow-through chambers during the phytoplankton bloom (April–May 1988). At the peak of the bloom, their maximum deposition rate was 40.9 mg mussel\(^{-1}\) day\(^{-1}\) dropping to 4–8 mg mussel\(^{-1}\) day\(^{-1}\) at the end of the bloom. The present measurements were made after the bloom in July (normally in May

Fig. 4. Total particulate matter (g m\(^{-2}\)) collected in experimental treatments. Combined data from Port Appin Control site and M. modiolus site over 7 days. Treatments: scouring pads (n = 7), box only (n = 7), dead M. modiolus boxes (n = 8) and live M. modiolus boxes (n = 8). Treatments that share a capital letter are not significantly different (p > 0.05).

Fig. 5. Particulate organic matter (POM) of sediment (g m\(^{-2}\)) collected in situ over 7 days. Treatments include scouring pads (n = 7), box only (n = 7), dead M. modiolus boxes (n = 8) and live M. modiolus boxes (n = 8). Treatments that share a capital letter are not significantly different (p > 0.05).
in Loch Linnhe: Overnell et al., 1995), and therefore correspond well with the lower values measured by Navarro and Thompson (1997), hence representative of the biodeposition rate for the majority of the year.

*M. modiolus* are large bivalves, able to filter seawater at a rate of 1–4 l h⁻¹ (Navarro and Thompson, 1996), making them very effective water pumps. The data presented here show that *M. modiolus* are capable of significantly enhancing the flow of suspended particulate matter from the water column to the benthos. This process acts to control coastal turbidity levels (Zhou et al., 2006) and is an important supporting ecosystem service as it regulates nutrient cycling (Strong et al., 2016; Townsend et al., 2011). Furthermore, enhanced deposition of organic material by *M. modiolus* may provide food for associated infauna and more widely enhance fish and bird populations, as has been shown for oyster reefs (van der Zee et al., 2012; Yeager and Layman, 2011). Evidence shows that *M. modiolus* reefs enhance the abundance of commercially important shellfish (Kent et al., 2016); however the influence of *M. modiolus* reefs on the wider foodweb has not yet been demonstrated.

Horse mussel reefs promote the abundance of associated epifauna including filter feeders, such as bryozoans (Farinas-Franco et al., 2014). The additional deposition by associated filter feeders is likely to be substantial for large reefs but was not considered in the present study. Likewise, *M. modiolus* shell production and accumulation was not considered in the present study, yet vertical reef accretion by unexploited oyster reefs (*Crassostrea gigas*) has been described by Walles et al. (2015b). Using estimates of reef accretion and carbonate production based on field observations, Walles et al. (2015b) demonstrate the benefits of sediment stabilisation and coastal protection provided by such habitats if left undisturbed. Reef extent and height data for a dense and biodiverse *M. modiolus* reef are available from Lindenbaum et al. (2008), which indicates that a possible 1.87 million m³ of sediment has built-up (373 ha × 0.5 m average reef height); testament to the scale of what might be bound-up in these habitat types.

In the present study, there was no difference in sedimentation between the reef samples and the off-reef control site samples. The increase in sedimentation caused by live *M. modiolus* was a relatively small proportion of the total amount of sediment deposited into the boxes (approximately 30%) suggesting that there is a large amount of background deposition. This is a similar proportion to that measured *in situ* by Ten brink et al. (1995), using sediment cores that were microscopically analysed and found to contain 20% mussel pellets by volume in the top 4 cm of a *Mytilus edulis* bed. However, the relatively small contribution of sediment caused by biodeposition relative to background deposition makes it difficult to detect a ‘reef effect’ as described by Jones et al. (2011). This maybe because the reef used in this study is only 2 ha (Fig. 2) and does not show the same undulating reef formation as the larger (up to 385 ha), more dense reefs recorded by Hirst et al. (2012), for example. Future experiments that incorporate factors such as suspended sediment concentration would be useful and experiments on different reef formations may yet elucidate a ‘reef effect’ as hypothesised in this study.

With wide scale loss of shellfish reefs, including oyster reefs (Beck et al., 2011) and *M. modiolus* reefs (e.g. Rees, 2009; Strain et al., 2012; Thurstan et al., 2013), it is very likely that we have also experienced a decline in the associated ecosystem services provided by such habitats (Strong et al., 2016). *M. modiolus* reefs are highly sensitive to physical impacts, such as mobile fishing gear (Cook et al., 2013), and are therefore protected in Marine Protected Areas (MPAs) in Scotland as well as Special Areas of Conservation (SACs) throughout the NE Atlantic. Policy makers and managers are starting to consider the ecosystem services and societal benefits of spatial protection for productive marine habitats (e.g. in Scotland’s National Marine Plan; Marine Scotland, 2015). Marine management measures should not only take into account the fisheries benefits of shellfish reef habitats (e.g. the nursery function), but also wider benefits such as coastal protection, water quality improvement and benthopelagic coupling.

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**Appendix A. Supplementary data**

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2016.11.014.

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