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Are biodiversity offsetting targets of ecological equivalence feasible for biogenic reef habitats?

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Abstract

Structurally complex habitat is declining across temperate marine environments. This trend has been attributed to changes in land use and increasing coastal development, which are activities likely to continue with governments supporting ongoing economic growth within the marine realm. This can compromise biodiversity, and biodiversity offsetting is increasingly being heralded as a means to reduce the conflict between development and conservation. Offset schemes are often evaluated against targets of 'ecological equivalence' or 'like-for-like' but these terms can be difficult to define and quantify. Although targets of equivalence have been generally shown to be feasible in terrestrial environments, the complex and dynamic nature of the marine and coastal realms present difficulties when aiming for strict equivalence targets as measures of success. Here, we investigated four intertidal biogenic reef habitats formed by the tube worm *Sabellaria alveolata* within, and in proximity to, Swansea Bay (Wales, UK). The aim was to identify measurable biodiversity components for *S. alveolata* reef habitat, and to investigate the natural spatio-temporal variation in these components, to determine whether a target of equivalence was feasible. We also looked to identify the most important drivers of species assemblages within the reefs. Results showed that biodiversity both *S. alveolata* formation and tube aperture condition showed a significant interaction between site and season with community composition varying significantly by site only. Site was found to explain the highest variation in community composition, followed by substrate type, and geographical position. These results highlight how widely coastal habitats can vary, in both space and time, and therefore calls into question a strict target of ecological equivalence when planning biodiversity offsets in coastal environments.

Keywords

Biodiversity offsetting, no net loss, *Sabellaria alveolata*, equivalence, compensation, mitigation hierarchy, coastal offsets, environmental impact assessment

1. Introduction

Loss of structurally complex habitat has been identified as one of the primary causes of biodiversity loss in coastal environments over the past century, a trend largely attributed to anthropogenic activities such as pollution, coastal development, climate change and land based human activities (Millennium Ecosystem Assessment, 2005a; Slingenberg et al., 2009). Coastal zones are some of the most biologically diverse and productive marine ecosystems, however they occupy less than 5% of the Earth's land area (Millennium Ecosystem Assessment, 2005; Sukhdev, 2008). Yet, they host more than 45% of the global population, and 75% of the world's largest urban aggregations (Balk et al., 2009; CIESIN, 2005; Neumann et al., 2015; Slingenberg et al., 2009; Small and Nicholls, 2003). Projections foretell a more than twofold increase in 'ocean economy' between 2010 and 2030 (European Commission and Directorate-General for Maritime Affairs and Fisheries, 2012; Halpern et al., 2015; Organisation for Economic Development, 2016), which indicates an increasing friction between economic development and biodiversity conservation efforts in coastal areas worldwide (Allsopp et al., 2009; Broderick, 2015).

In an attempt to minimise the implications of such impacts on biodiversity, developments are subject to regulatory frameworks based on the concept of a 'mitigation hierarchy'. This requires demonstration, firstly, that attempts have been made to ensure that negative biodiversity impacts are avoided, minimised and restored, with the last resort for any residual impacts to be addressed via biodiversity offsetting measures (BBOP, 2009; Gardner et al., 2013). Biodiversity offsetting can be defined as 'measurable conservation outcomes resulting from actions designed to compensate for significant residual adverse biodiversity impacts arising from project development after appropriate mitigation measures have been taken' (BBOP, 2013). They are increasingly heralded as a means to facilitate economic development whilst maintaining conservation objectives (Madsen et al., 2010). However, the science of ecological restoration, rehabilitation and creation that underpins offsetting efforts is still considered to be in its infancy (Quétier et al., 2014; Suding, 2011), with an increasing number of studies concluding that offsetting efforts are often ineffective (Moreno-Mateos et al., 2012, 2015).

In the terrestrial environment, biodiversity offsetting has been subject to a certain level of academic scrutiny, however, less attention has been devoted to the extension of the practice in marine environments (Bas et al., 2016; Gonçalves et al., 2015; Niner et al., 2017). This is also reflected in the lack of specific coastal and marine offsetting policy, with only six countries (US, Canada, Australia, France, Germany, Columbia) having national offsetting policies that are directly applicable to the marine environment (Niner et al., 2017).

Biodiversity offsetting differs from other types of compensatory action in that it requires 'measureable' outcomes (BBOP, 2009; Bull et al., 2013; Maron et al., 2012). This requires a demonstration of equivalence between biodiversity losses and gains (Bull et al., 2013), however how to measure ecological equivalence is one of the most debated of all technical offset issues (Gardner et al., 2013; ICMM and IUCN, 2012; Quétier and Lavorel, 2011). Current best practice recommendations for implementing offsetting suggest that they should be 'in-kind' or 'like-for-like' offsets (BBOP, 2012), meaning that gains from the biodiversity offset must comprise of the same biodiversity components as those impacted (Maron et al., 2012; Bull et al., 2015).

In terrestrial environments, a target of 'in kind equivalence' or 'like for like' has been shown to often be feasible (Defra, 2012). In contrast, the more complex and dynamic nature of coastal and marine environments means that it may be less feasible to recreate the physical factors that govern the distribution and success of certain biotopes (Cook and Clay, 2013). Connectivity between ecosystems operates in three dimensions, and the high biological and physical heterogeneity of habitats and species on a range of spatial and temporal scales presents difficulties when planning offsets in the marine environment (Crowder and Norse, 2008; Niner et al., 2018). The question remains, whether setting a target of 'like-for-like' is realistic to determine the success of offsetting projects in coastal and marine environments. If not, how much variation may be acceptable given natural variation in space and time?

Demonstrating equivalence between impacts and offsets requires the identification of a suite of metrics that accurately describe all biodiversity elements of interest. Adequately defining the elements of biodiversity that are most important is a crucial element of offset design, but is often challenging (Bull et al., 2016; Maron et al., 2016). Biodiversity elements can be broadly categorised into type, component and attribute (New Zealand Department of Conservation, 2014). While other categorisations could be used, this provides an intuitive, tractable and published framework in which to develop our study. The type of biodiversity to be offset is the key biodiversity feature of concern, and can be an ecosystem, a habitat or species. Biodiversity components are characteristics used to describe the biodiversity type and they represent the elements of biodiversity that are of primary interest for which no net loss is to be achieved.

Biodiversity attributes are the measurable elements which comprise the biodiversity components. The three levels, biodiversity type, components and attributes, can be used to collectively describe the biodiversity at both impact and offset sites (Figure 1a).

In this study, we decided to investigate the feasibility of reaching a target of ecological equivalence for the reef building tube worm *Sabellaria alveolata*. The habitat was identified as being subject to significant residual impact within the Environmental Impact Assessment of a proposed tidal lagoon in Swansea Bay, Wales (UK). *S. alveolata* is classified under 'reefs' as an Annex I habitat in the EU Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Habitats Directive), and is listed as a 'marine habitat to be protected by the designation of Special Areas of Conservation (SAC's)' (European Commission and Office for Official Publications of the European Communities, 2000). It is generally considered that any biodiversity offset should be carried out on a like-for-like basis, i.e. non-flexible in that the same type of habitat and measured biodiversity components must be recreated or restored as the one impacted, in particular if that habitat is designated (Defra, 2012).

In order to investigate the feasibility of a target of 'like-for-like' equivalence for *S. alveolata* habitat, the study had the following objectives:

i) Identify biodiversity components and measurable attributes which could be used to determine ecological equivalence in *S. alveolata* reefs;
ii) Investigate the natural spatio-temporal variation of measured biodiversity components;
iii) Investigate which factors influence species assemblages associated with *S. alveolata* reefs;
iv) Explore how factors modified by *S. alveolata* as an ecosystem engineer, as well as factors external to the influence of *S. alveolata* (spatio-temporal effects), influence associated community composition.

2. Materials and Methods

2.1 Study sites

Four *S. alveolata* reefs were chosen to be sampled, all of which were located along the northern coastline of the Bristol Channel (Wales, UK) (Figure 2): two sites within Swansea Bay ((A)

Tawe, (B) Port), and two sites along the wider Glamorgan coastline at (C) Porthcawl and (D) Dunraven. This coastline is often exposed to severe hydrodynamic forces due to strong winds and tides generated in the Bristol Channel, as well as North Atlantic Swells. Swansea Bay receives some protection from Mumbles Head, an area of headland which can provide shelter from prevailing south-westerly wave conditions. *S. alveolata* within Swansea Bay colonises glacial till as well as pebble and small stone, while at Porthcawl and Dunraven reefs are cemented to Blue Lias limestone platforms as well as some mixed cobble substrate.

2.2 Identifying suitable biodiversity components for *S. alveolata* reefs.

Best practice guidance on biodiversity offsetting suggests that any Equivalence Assessment Method (EAM), used to measure biodiversity losses and gains (Bezombes et al., 2017) should describe all biodiversity components of interest, which should align with clearly stated policy or conservation objectives (Maseyk et al., 2016). With that logic, we identified biodiversity components outlined in Severn Estuary SAC conservation objectives for biogenic reef habitats (Natural England and Countyside Council for Wales, 2009), as they were considered to be applicable across EU member states and were also in line with the high levels of protection given to Annex I habitats within the Habitats Directive. The conservation objectives for *S. alveolata* are as follows, 'That the feature will be considered to be in favourable condition when, subject to natural processes, each of the following conditions are met':

i) The total extent and distribution of *S. alveolata* reef is maintained;
ii) The community composition of *S. alveolata* reef is maintained;
iii) The full range of different age structures of *S. alveolata* reef are present;
iv) The physical and ecological processes necessary to support *S. alveolata* reef are maintained.

It was decided that the study would focus on three measurable biodiversity components from the above criteria: a) a measure of extent and distribution; b) a measure of community composition and c) a measure of the range of age structures. Having identified suitable biodiversity components, we then looked to identify measurable attributes to describe these components (Figure 1b).

2.3 Identifying measurable attributes to describe biodiversity components for *S. alveolata* reefs

a) Measurement of total extent and distribution

The distribution of *S. alveolata* appears to be geographically limited to between Morocco and the southwest of Scotland (Crisp, 1964). In Great Britain, the vast extent of *S. alveolata* has been recorded on the west coast, with isolated records also seen in the south and north of eastern England (Gubbay, 1998). The distribution of *S. alveolata* relates to the specific environmental conditions it requires to colonise an area successfully. *S. alveolata* exhibits natural temporal and spatial variability, and can be affected by a number of factors such as extreme cold and frost events (Firth et al., 2015), burial by sand (Allen et al., 1999), damage through trampling (Plicanti et al., 2016), competition for space with species such as *Mytilus edulis* (Cunningham, 1984; Holt et al., 1998) and naturally variable recruitment (Holt et al., 1998). This study looked to explore spatio-temporal changes in *S. alveolata* by using percentage cover as a measure of distribution.

b) Measurement of community composition

S. alveolata is an ecosystem engineer that builds three-dimensional structures which can qualify as 'reefs' (Holt et al., 1998). Ecosystem engineers modify, create or destroy habitats that "directly or indirectly modulate the availability of resources to other species" (Jones et al., 1994). For this reason, ecosystem engineers are often reported to host a more diverse range of species than adjacent non-engineered habitats (Ataide et al., 2014, De Smet et al., 2015). Physical ecosystem engineering appears to be of particular importance in extreme environments (e.g., thermic, hydrodynamic stress) such as temperate intertidal areas (Bouma et al., 2009; Jones et al., 1997). The biogenic reefs created by *S. alveolata* are recognised as potential community enhancers and can be seen as biodiversity 'hotspots', where species diversity deeply contrasts with that of surrounding sediments (Jones et al., 2018; Porras et al., 1996; Dubois et al., 2002; Schlund et al., 2016). By creating variation in an otherwise homogenous environment, and by stabilising loose substrate and restricting water flow to form pools, they can provide niches for a large array of species (Egerton, 2014).

This study explored spatio-temporal changes in the composition of communities associated with *S. alveolata*. In addition, in order to investigate the influence of *S. alveolata* as an ecosystem engineer in temperate intertidal environments, we also explored how much of the variation in community composition was as a result of the biodiversity components associated with the tube worm reefs (extent, formation, condition), as well as additional factors that may be modulated by *S. alveolata* as ecosystem engineers. A number of studies have discussed the effect that engineer species can have on community composition (Ataide et al., 2014; De Smet et al., 2015, Jones et al., 1997, Stachowicz, 2001) and following a detailed literature search, we selected 7 variables that could be modified directly by *S. alveolata* (Table 1).

In order to control for spatio-temporal effects external to the influence of *S. alveolata*, we also investigated how much variation could be explained by an additional four factors; site, season, position on the shore and distance to Mean Low Water (MLW) (Table 1).

c) Measurement of age structures

As the conservation objective refers to the age structure of *S. alveolata* 'reef', this is taken as a reference to morphological developmental phases of tube aggregations, as opposed to that of the individual worms. Because *S. alveolata* larvae prefer to settle on active colonies or the remains of old colonies, morphology of reefs cannot be directly related to the age of individual polychaetes (Gruet, 1986). However, *S. alveolata* colonies follow a well-documented cycle of growth and decay (Gruet, 1982; 1986; Wilson, 1971; 1974; 1976), of which one or all phases may be observed at any one time. The cycle is linked in part to larval settlement and recruitment, but is also influenced by physical factors associated with hydrodynamics (Gruet, 1986). Gruet (1982) divided these growth phases into three types of reef formation: sheet, hummock and reef. Further work building on this classification by Egerton (2014) added an additional categorisation of patchy formation. Following initial site visits, we also chose to include the category of 'encrusting' formation, as we felt that based on *S. alveolata* communities in our study area that this was missing from the classification. These classifications of reef formation were used as a proxy for a measure of reef 'age structure'.

d) Measurement of condition of age structures

To supplement the measurement of reef age structure, a measure of reef health was also recorded. Reefs are formed from a coalescence of sand tubes built by individual worms (Le Cam et al., 2011). Whilst submerged, their head and tentacles protrude from the tube in order to gather particles for the maintenance of tube structures as well as gathering food (Dubois et al., 2009). For this reason, it is assumed that individuals in healthy condition will create un-smothered and intact tubes, whereas unhealthy individuals are likely to display worn tube apertures, or even tubes completely smothered by sediment (Dubois et al., 2003). Tube aperture condition was used in this study as a proxy for the health of the colony.

2.3 Sampling Design

All four sites were surveyed between June and September 2016 (Summer) and between February and April 2017 (Winter). Survey sites were selected from Phase 1 Habitat maps created by the Countryside Council for Wales (CCW) showing presences of *S. alveolata* biotopes around the Swansea and Glamorgan coastlines. Once selected, *S. alveolata* reefs at each survey site were divided into a 50 x 50m grid using QGIS. Due to the differences in area of each of the four sites, a random sample of 30 grid intersections were selected. Each grid intersect was marked and the coordinates transferred to GPS (Garmin eTrex Legend HCx). The GPS was used to locate the selected grid intersects at each site and once located a 1m^2 quadrat was placed at random in the area surrounding the point. Within each quadrat, percent cover of *S. alveolata* was quantified as a proxy for distribution, and percent formation type and percent tube aperture condition were recorded as proxies for age structure and health. A photographic guide to the classification of *S .alveolata* formation, type and status (Figure 3) was used to increase accuracy of estimation and standardise recordings. Substrate type associated with *S. alveolata* reef was also recorded. Benthic species visible within the quadrats were enumerated and recorded to the lowest taxonomic level possible, with the same amount of time spent on each quadrat (approx. 5 minutes).

Other *S. alveolata* reef variables were also recorded within each quadrat, including percentage cover of macroalgae, standing water and barnacle cover.

2.4 Statistical Analysis

Data were analysed using univariate and multivariate methods using the PRIMER v7 software package with PERMANOVA add on (Anderson et al., 2008; Clarke and Gorley, 2015).

Square-root transformed data was used to create a Bray-Curtis dissimilarity matrices for each of the biodiversity components, a) percentage *S. alveolata* cover, b) community composition, c) percentage *S.alveolata* formation, d) percentage tube aperture condition.

Spatial and temporal differences in habitat structure and community composition variables were tested using a permutation analysis of variance fixed model (PERMANOVA) (Anderson et al., 2008) (PRIMER v7, Primer-E Ltd, 239 Plymouth, UK). Two-way crossed PERMANOVA for factors SEASON (Two levels; fixed) and SITE (Four levels; fixed) was used to examine patterns of variation in habitat structure and associated community composition, using 9999 permutations. Where significant differences were found, PERMANOVA pairwise comparisons were used to identify the origin of the differences.

Similarity percentages analysis SIMPER was performed to identify species contributing to differences between sites and seasons, based on Bray-Curtis similarities of square root transformed abundance data (Clarke and Warwick, 2001).

Macrofaunal species diversity was estimated using species richness and Hill's (1973) heterogeneity of diversity indices: N_1 = exp(H') and N_2 = 1/SI, as recommended by Gray (2000). N_1 is sensitive to the number of medium-density species, whereas N_2 is sensitive to the number of very abundant species (Whittaker, 1972). To investigate differences in diversity measures between both sites and seasons, two way Analysis of Variance (ANOVA) was used. Where significant differences were obtained, Tukey's honestly significant difference (HSD) *post-hoc* tests were carried out. All univariate analysis was carried out using R statistical software (R Core Team, 2013).

A distance based linear model (DistLM) was built to identify which factors were significant predictors for the biodiversity component of community composition. DistLM is a multivariate multiple regression routine, in which a resemblance matrix of species abundance data is regressed against a set of explanatory (environmental) variables (Anderson et al., 2008). Environmental variables were normalised and evaluated using an Euclidean distance matrix. Permutation methods were used to assess statistical significance of each predictor variable. DistLM selection was based on the BEST selection procedure with 9999 permutations based on adjusted R^2 selection criteria (Sokalr and Rohlf, 1981). A Draftsman plot was carried out prior to DistLM regression to avoid multicollinearity among predictor variables that could bias results (McArdle & Anderson, 2001). If two variables were found to be strongly correlated (R^2 > 0.80), one was removed from the analysis (Dormann et al., 2013). To assess the amount of variation in community composition explained by each set of predictors (reef variables or spatio-temporal), overall variation was partitioned using a DistLM model that included only the significant predictors identified in both sets of predictors. Fitted DistLM models were visualised using the distance-based redundancy analysis (dbRDA) routine (PRIMER v7).

3. Results

3.1 Spatio-temporal variation in biodiversity components

a) Total extent and distribution of *S. alveolata* (percentage cover)

During the summer sample season, average percent cover of *S. alveolata* ranged from 33.40 ± 2.14% at the Port site to 42.77 ± 3.31% at the Dunraven site. Percent cover increased marginally at each site during the Winter sample season, with the highest increase recorded at the Porthcawl site from 35.53 ± 1.32% in summer to 45.37 ± 4.31% in the winter (Appendix 1). Permutational analysis of variance (PERMANOVA) found no significant difference in percent cover *S. alveolata* between sites or between seasons (Table 2).

b) Community composition of *S. alveolata*

PERMANOVA identified a significant difference in community composition between sites, but not between seasons (Table 3). *Post-hoc* pairwise PERMANOVA tests indicated significantly different community composition among all sites (Table 4). SIMPER analysis showed that species assemblages at Tawe and Porthcawl sites were most dissimilar at 89.59% (Table 5). The gastropods *Littorina littorea* and *Steromphala umbilicalis* accounted for 46.7% of the dissimilarity, although dissimilarity/SD of below 1 indicates that *L. littorina* would have been distributed unevenly within sites; e.g. they were abundant in some quadrats but absent from others. *S. umbilicalis* and *L. littorea* were also the highest contributing species to dissimilarity between Tawe and Dunraven as well as Porthcawl and Dunraven sites. High abundance of the invasive gastropod *Crepidula fornicata* at the Port site caused dissimilarity when compared with the other three sites, although the species also had a dissimilarity/SD value below 1, indicating it was patchy in its distribution.

Two way Analysis of Variance (ANOVA) found a significant difference in species richness and both Hill's indices (N1 and N2) between sites ($P < 0.001$), but not between seasons (Figure 4; Table 6). Post-hoc comparisons using Tukey HSD test indicated that species richness was significantly different between all sites ($P < 0.001$), except between Tawe and Dunraven sites ($P = 0.438$). Kruskall Wallis *pos- hoc* analysis found that this was also true of Hill's N1 between sites (all sites, $P < 0.05$, apart from Tawe and Dunraven, $P = 0.138$), but not of Hill's N2, where non-significance was reported between Tawe and both Port ($P = 0.057$) and Dunraven (P =

0.425) sites. However, Hill's N2 was found to be significantly different between all other sites ($P < 0.001$) (Table 7).

c) Range of age structures

Formation assemblages showed location specific trends, with sites grouped in closest proximity (Port and Tawe; Porthcawl and Dunraven) to each other displaying similar changes over sampling seasons (Figure 5). Port and Tawe sites both saw decreasing percentage cover of encrusting and reef formations between summer and winter sample seasons, as well as increases in percentage cover of patchy, hummock and sheet formation types. In contrast, between summer and winter sample seasons, Porthcawl and Dunraven saw increasing percentage cover of encrusting formation as well as decreases in patchy formation. Dunraven was the only site to show an overall increase in percentage reef cover, and a decrease in sheet formation in the winter. No hummock formation was recorded at Porthcawl in either sample season.

Two factor PERMANOVA analysis showed a significant interaction between site and season (Table 8) indicating that all variables analysed showed a temporal pattern depending on site. The presence of a significant interaction generally indicates that the tests of the main effects may not be meaningful (Underwood, 1997). As suggested by Anderson (2001) we then performed *Post hoc* pairwise PERMANOVA which found that only Port and Tawe and Tawe and Dunraven had significantly different formation assemblages during the Summer sample season, however, during the Winter sample season, these were the only site pairings to not show significant differences (Table 9).

d) Tube aperture condition

Tube aperture condition showed overall seasonal trends, with each site showing decreases in the percentage cover of both crisp and worn tube apertures from summer to winter sample seasons. This was matched with increases in the average percent cover of both dead and newly settled tubes apertures from summer to winter seasons (Figure 6).

PERMANOVA analysis found a significant interaction between site and season with regards to tube aperture condition (Table 10). *Post hoc* PERMANOVA analysis found that all sites were significantly different during the winter sample season, however tube aperture condition at Port and Tawe and Tawe and Porthcawl were not significantly different during the summer sample season (Table 11).

3.2 Variation in community assemblages in relation to environmental factors.

Distance-based linear models (DistLM) were constructed to quantify the degree to which one or more of the environmental variables, including biodiversity components a, c and d, explained the associated species community structure. The overall best model explained 32.4% of the variation and contained all of the included variables (% *S. alveolata* cover, % formation, % condition, % macroalgal cover, % standing water cover, % barnacle cover, geographic position, distance to mean low water, site, season and substrate). Of all variables retained in the BEST model, site explained the most variation (19.7%, $P = 0.001$), followed by substrate (10.0%, $P = 0.001$) and geographical position (9.3%, $P = 0.001$). Of the *S. alveolata* biodiversity components, % *S. alveolata* cover explained 0.9% of the variation and was not found to be significant ($P = 0.06$). Both % formation and % condition were found to be significant predictors ($P < 0.05$), explaining 3.2% and 7.6% of the variation respectively. The full model was visualised via dbRDA ordination (Figure 7) and broadly groups the samples by site. The first two axis explained 79.2% of the fitted variation and 31.1% of the total variation. Species assemblages tended to be structured according to site, which aligns with the results of the DistLM.

The partitioning of variance showed that factors modified by *S. alveolata* explained 27.3% of variation, whereas factors external to the influence of *S. alveolata* explained 26.5% of the total variation in the biological community composition. Both were found to be significant ($P = 0.001$). The shared effects of the two groups accounted for 26.6% of the variation (Figure 8).

4. Discussion

A key element of Biodiversity Offsetting is the concept of 'ecological equivalence'. The term has no universally agreed definition (Rayment et al., 2014), however it is generally accepted that an offset is considered 'equivalent' when it is 'in-kind' (EC, 2000; Defra, 2012), and provides habitat, functions or other attributes similar to those impacted (BBOP, 2009; Bennett and Gallant, 2017). Accurate assessment of equivalence requires a suite of measurable biodiversity components to account for losses and gains in biodiversity (Maseyk et al., 2016). In this study, we identified two measureable biodiversity components suitable to assess equivalence for the Annex I reef habitat, *S. alveolata*, and investigated how they varied naturally in space and time. *S. alveolata* extent was not found to differ between site or season. However, significant interactions between site and season were found for both formation and tube aperture condition. Species composition was found to vary significantly between sites only. The findings of this study suggest high natural variability in the structure and condition of the *S. alveolata* habitat, as well as associated species assemblages. This calls into question the feasibility of a strict like-for-like target of ecological equivalence as a measure of success, for coastal offset projects carried out in highly dynamic coastal environments. It suggests that it would be unlikely that recreated or relocated habitat would reach a strict target of equivalence naturally, and could be deemed as having failed, although they may support a unique and persistent ecosystem that may be equally as 'valuable' in its biodiversity outside of the constraints of a strict 'like-for-like' framework of evaluation.

Determining which elements of biodiversity to offset is key to project design, but is often challenging to clearly define (Bull et al., 2016; Maron et al., 2016). Measures tend to be conceived at local or regional levels, on a case-by-case basis, making it difficult to compare the performance of offsetting projects in relation to one another (Gonçalves et al., 2015). In the absence of an agreed suite of components for *S. alveolata* reefs, we based our selection on the conservation objectives stated in SAC guidelines for *S. alveolata*, to ensure they aligned with the broader conservation objectives of the EU Habitats Directive, as has been recommended in guidance literature (BBOP, 2009; Slingenberg et al., 2009). This method can then facilitate a certain level of standardisation between projects, as they are evaluated against a common goal of maintaining the 'favourable conservation status' of the habitat as outlined in the Habitats Directive.

A measure of habitat structure is included as a biodiversity component in many EAM's due to its influence on associated community compositions (Gonçalves et al., 2015). This relationship is supported by our results, which showed *S. alveolata* formation and condition had a significant influence on community composition. It is well documented that *S. alveolata* reefs in degraded condition are often found to have higher diversity and species richness than actively growing reef structures (Porras et al., 1996; Dubois et al., 2002; Desroy et al., 2011), although these studies differ from this study as they refer primarily to infaunal assemblages. This relationship was true of the Swansea Port reef, which had the highest diversity and species richness across all sites and was characterised by high percentage cover of patchy and encrusting formations in worn and dead condition. However, this was in contrast to Porthcawl reef, which was also characterised by degraded reef features but was found to have the lowest diversity and abundance of species across sites. This could be explained by the difference in exposure between the two sites, as Swansea Port is largely sheltered from prevailing winds and wave action by a large breakwater, as opposed to Porthcawl which is the most exposed of all four sites. Exposure has been observed as influencing community structure within *S. alveolata* in a number of studies (Gruet, 1971, 1982; Schlund et al., 2016), which report higher species and taxonomic richness of species in more sheltered areas compared to those subject to higher energy hydrodynamic conditions. Our results suggest that the influence of *S. alveolata* habitat structure on associated community composition seems to vary across a gradient of exposure, where a lack of more robust reef formation to provide protection at sites of high wave exposure can lead to lower species richness and diversity. Whereas, at medium to low exposure sites, large reef structures can dominate and outcompete other species for space, resulting in reduced species richness and diversity.

This highlights some of the difficulty involved in recreating habitats in such a dynamic environment as the coastal zone. Even if an exact copy of what was lost in terms of habitat structure were to be recreated elsewhere, the influence of external factors may prevent an exact replication of species composition unless adequately addressed (Hannan and Freeman, 1977). This is in contrast to a common assumption in some habitat creation and restoration projects that high similarity in the physical template of a particular ecosystem, would naturally lead to a higher similarity in associated species assemblages (Rosgen, 1994, 1998) . The concept of self-design or 'build it and they will come' is an appealing approach to practitioners looking to implement biodiversity offsets within limited time and budgets. However, it must be considered that intertidal communities will be subject to strong abiotic gradients such as those of vertical, wave, sediment and salinity, all of which are abiotic filters that drive species assemblages at each site (Lhotsky et al., 2016; Török and Helm, 2017) and which will vary between impact and offset sites.

This also challenges another assumption often made when planning biodiversity offsets, that increasing proximity to the impact site increases the likelihood of ecological equivalence being reached (BBOP, 2009; Brownlie and Botha, 2009; Kiesecker et al., 2009; McKenney and Kiesecker, 2010; Salzman and Ruhl, 2000). The present study did find that sites in closest proximity (Port and Tawe) were found to be most similar, in terms of their associated community composition, but were not most similar in terms of their habitat structure. Furthermore, the similarity in species composition with proximity did not hold true as the distances increased between sites, which may suggest a non-linear relationship. Sites in close proximity may be subject to similar environmental conditions and have access to the same species pool on a regional scale, yet at a local scale, potential recolonising species are further subject to both abiotic and biotic filtering, and so it would be unwise to assume that a similar assemblages will always be established (Hobbs and Norton, 2004). This is likely the reason that our results showed 'site' to have the largest influence on community composition, emphasising the importance of suitable site selection to reaching equivalence in species composition.

Conversely to species composition, our observations show that both formation and tube aperture condition differed more as a result of seasonal effects (Figure 3). The structural development of reefs has been shown to be dependent on a precarious balance between biological and physical forces, the main of which is that of hydrodynamics, which can have both positive and negative effects on reef growth and condition (Gruet, 1986). In the current study, the primary differences in habitat structure between seasons were two fold. Firstly, Port, Tawe and Porthcawl sites all showed decreasing percentage cover of reef formation in winter surveys, although the opposite occurred at Dunraven where reef formation was shown to almost double (Table 3). Low temperatures (Pawlik, 1988; Wilson, 1971) coupled with increasing frequency of storm events during winter months have been shown to contribute to degradation and fragmentation of reef structures (Gruet, 1986). This hypothesis is further supported by the increase of dead tube apertures across all sites between summer and winter seasons, indicating that mortality rates of *S. alveolata* increase winter months, which could lead to a weakening of the reef structure. Secondly, all sites showed an increase in newly settled tube apertures from summer to winter surveys. Enhanced metamorphosis of *S. alveolata* larvae has been shown to occur with increasing agitation (Wilson, 1968), which may have been facilitated by the increased wave action in winter months. The shown increase in mortality of adult worms during the winter season may have also led to increased settlement, as the gregarious nature of *S. alveolata* larvae means that conspecific tube sand is the preferred substrate, with dead reef lacking the competition for space with adult worms being the optimum (Wilson, 1968).

Temporal variation in habitat structure is an important aspect to consider when planning a monitoring and evaluation period for any coastal or marine offset site, with temporal changes in structure evident across a number of habitats (Koch et al., 2009). Basing equivalence calculations on, for example, winter survey results could result in non-equivalence being concluded, whereas, as in this case, survey results from a summer sample season could indicate much higher similarity. This suggests that sampling timings should be as consistent as possible, and that both summer and winter sampling may need to be carried out to gain an accurate assessment of habitat dynamics. Another solution may be the use of multivariate statistical frameworks such as in this study, which have been proven as a robust strategy for assessing losses and gains against baseline conditions (as in multivariate before and after/control impact (M-BACI) methodologies (Downes et al., 2002; Underwood, 2000), whilst allowing for the control of natural variation. Such methods can also allow for detailed comparisons to be made through time and the use of ordination means that samples can be visualised through time by charting their changing positions in 'ordination space' summarised as a 'change vector' (Halpern, 1988; McCune et al., 2002; Smith and Urban, 1988). This allows for both a visual and quantitative assessment to be made of direction (towards or away from) and magnitude (length of vector) of any progress made by offset against baseline conditions (for further discussion see McCune et al., 2002; Urban, 2006) which can aid in the interpretation of results, and to the understanding of results to a variety of different stakeholders, with varying technical knowledge.

The use of 'species composition' as a biodiversity component is apparent in many EAMs (BBOP, 2013; ICMM, 2012). However, our results highlight how its inclusion must be carefully considered. Factors such as the presence of invasive species in the species pool of the impact site, as was the case for the Swansea Port site, raise the question of whether a strict like-for-like restoration of the impacted species composition is a sensible direction to pursue. An offset could be deemed to be unsuccessful if a similar community composition to that impacted is not recreated. However, in this case, the offset could have a more natural composition than that of the impact site. This is also true of the use of diversity indices as measures of success, as high abundances of invasive species can be masked by high levels of diversity and species richness at a site. The identification of a set of 'key reference species' native to the impacted habitat may be a better way of evaluating success in the recreation of equivalent community composition in offset sites.

In practice, no two components of biodiversity will ever be precisely equivalent (Salzman and Ruhl, 2000) and so all offsets are 'out of kind' to some degree (Moreno-Mateos et al., 2015).

This logic has led to some academics to call for further investigation into the effect of incorporating more flexibility into offset design (Bull et al., 2015; Habib et al., 2013). The difficulties in achieving ecological equivalence, as well as the uncertainty of being able to re-establish some habitats elsewhere, raises the question of whether 'trading up' could be an option to pursue. In the case of protected features of Special Areas of Conservation (SAC's), biodiversity offsets must legally be 'like-for-like' as outlined in the Habitats Directive. However, outside of these protective provisions, the option of creating or enhancing a habitat that has equivocal or higher 'value' could be considered as an 'out of kind' offset and has been suggested as an option in some pilot biodiversity offset schemes (Defra, 2012). Habitats such as seagrass beds or bivalve reefs, which may support similar or more diverse species assemblages than those recorded within *S. alveolata* reefs, may provide functions and services in addition to biodiversity, such as carbon sequestration and water filtration (Barbier et al., 2011; Filguera et al., 2015; Vaughn, 2017). Restoration of bivalve reefs habitats has been explored by a number of studies in the UK and overseas (McLeod et al., 2012; Peterson et al., 2003; Roberts et al., 2011) and so could be considered less uncertain and of higher value in terms of services it provides. However, regional ecological priorities should be considered before 'trading up' is agreed, as it could lead to habitats that are easier to recreate being chosen over more difficult habitats, which could endanger those habitats in the longer term (Bull et al., 2015). A more relaxed, out-of-kind type of biodiversity offsetting raises questions about how habitats are assigned biological 'value' and how that value is likely to be different depending on the stakeholder.

5. Conclusion

This paper outlines the complex nature of biodiversity offsetting, and the difficulty in attaining a target of ecological equivalence in *S. alveolata* habitat, due to its naturally high spatial and temporal variation. It brings forward the question of what is it we are offsetting? Is it the loss of the specific impacted habitats themselves or their associated species? If it is the habitats specifically then offsets must focus on like for like equivalence in type and area. However, if the aim is to provide equivalent habitat for other species, then an 'out of kind' offset may be more feasible. Our results have shown that achieving equivalence in both factors will be difficult and a target set within the constraints of strict like-for-like carries considerable uncertainty and is likely to fail. In particular, this study enforces the on-going need for solid guidance and policy frameworks to be developed around biodiversity offsetting. When determining a methodology for biodiversity offsetting in highly dynamic coastal environments, our findings point to the strong influence of location and timing on targets of ecological equivalence.

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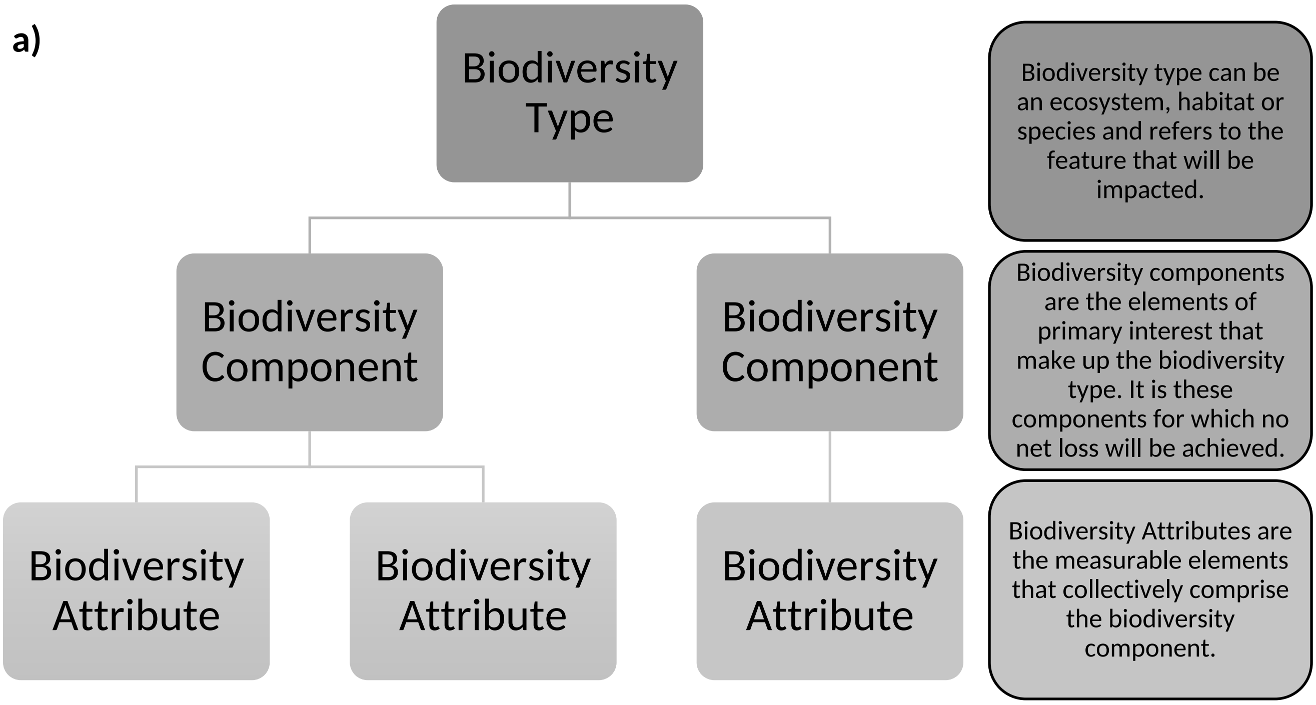
Figures

a)



b)

Biodiversity Type	**Biodiversity Component**	**Biodiversity Attribute**
Sabellaria alveolata habitat	a) Extent and Distribution	% cover *S. alveolata*
	b) Species Composition	Abundance of associated species
	c) Range of age structures	% Hummock formation
		% Sheet formation
		% Reef formation
		% Patchy formation
		% Encrusting formation
	d) Tube aperture condition	% Newly Settled tube apertures
		% Crispy tube apertures
		% Worn tube apertures
		% Dead tube apertures

Figure 1 (a) Conceptual diagram of the hierarchy levels used to categorise biodiversity in the design of offsets based on the Guidance of Good Practice Biodiversity Offsetting in New Zealand (Department of Conservation, 2014), with hypothetical example (b). Modified from Maysek et al. (2016). Collectively, this hierarchy describes ‘biodiversity’ in the context of the offset. In this example, the proposed tidal lagoon development in Swansea Bay will impact on *S. alveolata* habitat ‘type’ of biodiversity.

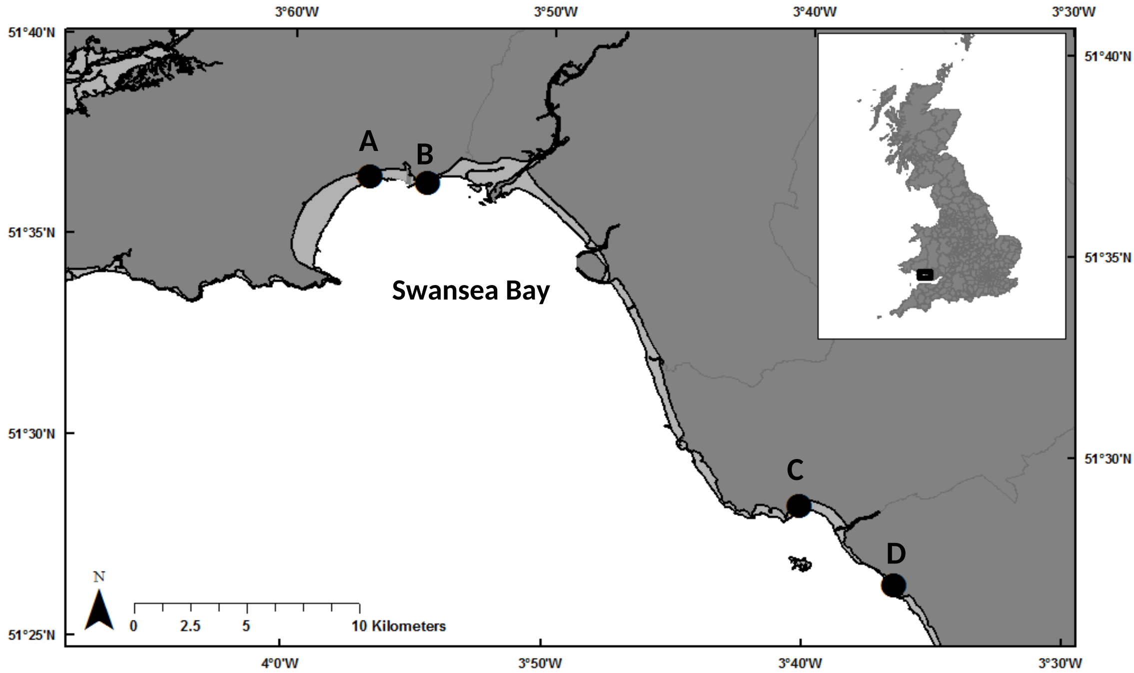
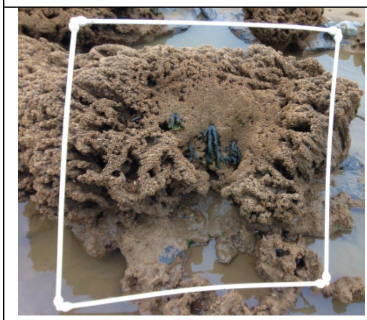
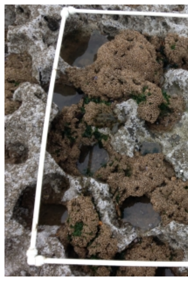


Figure 2 Study site Swansea Bay, South Wales, UK. Black dots indicate the location of the four *S. alveolata* reefs surveyed (A. Tawe (potential impact site), B. Port, C. Porthcawl, D. Dunranven).

a) Formation categories			
Reef	Hummock	Sheet	Pat
			
Large mounds which are greater than $1m^2$	Raised mounds which are greater than $30cm^2$	Flat crusts which are greater than $30cm^2$	Small crusts which are les

b) Tube aperture health categories		
Crisp Apertures	Worn Apertures	Dead Apertures
		
New growth of tubes can be seen, the apertures are crisp with a ‘porch’ over the tube opening.	There is no clear porch over the tube opening, however apertures can still be seen. Lacking the light,	Tubes have merged into a blo sediment. Can often be detach the substratum.

Tend to be a light, sandy colour when compared with worn tubes.	sandy colouring. Often covered in silt or fine sediment.	

Figure 3. Classification of the a) *S. alveolata* formation categories and b) *S. alveolata* tube aperture health ca
(2014) and Gruet (1982).

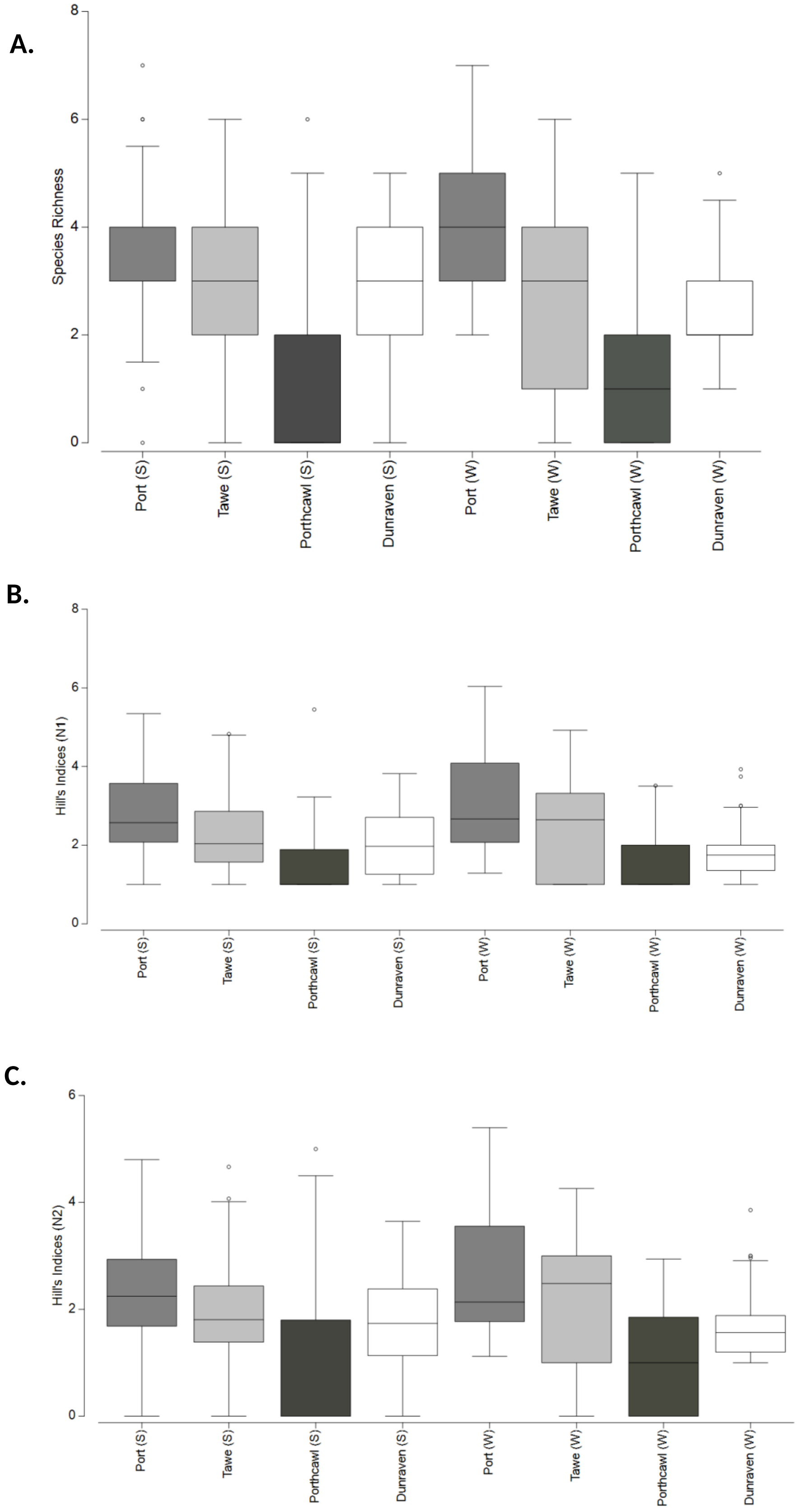


Figure 4 (A) Variations of species richness and Hill's indices (N1, N2) according to site sampled (Port, Tawe, Porthcawl and Dunraven) and sample season, summer (S), winter (W).

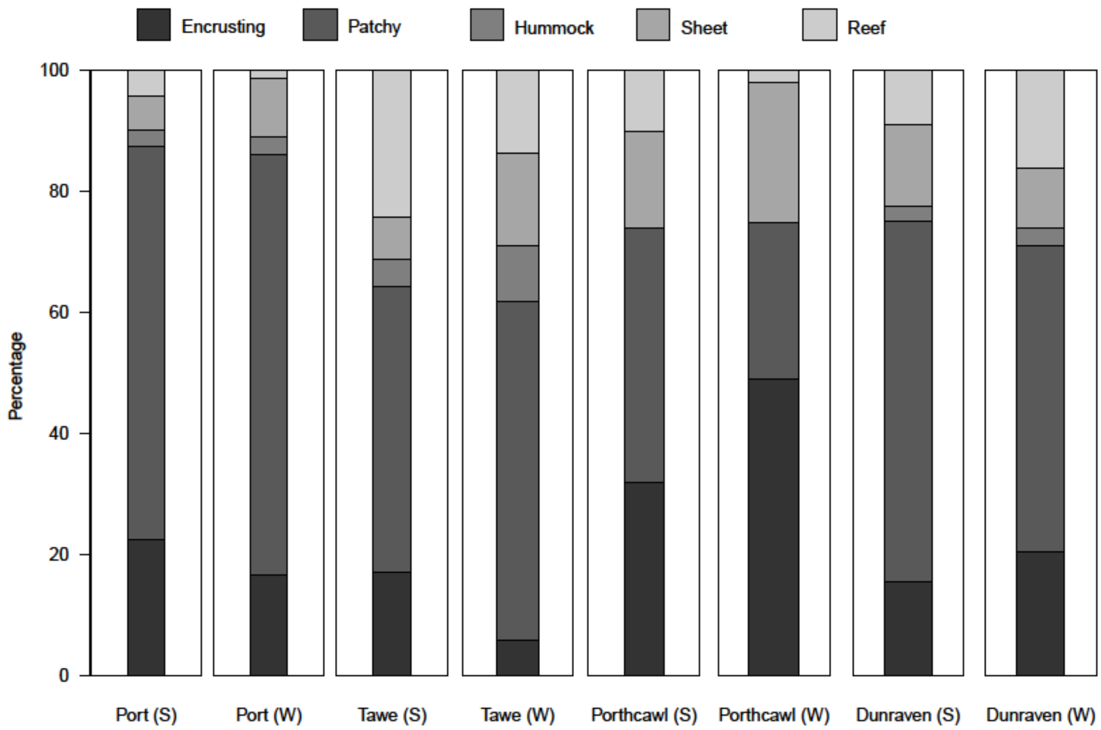


Figure 5 Mean proportion of *S. alveolata* formation, for each site in both summer (S) and Winter (W) sample seasons. Width of each bar indicates the overall mean percentage cover of *S. alveolata*, scaled within standard width boxes.

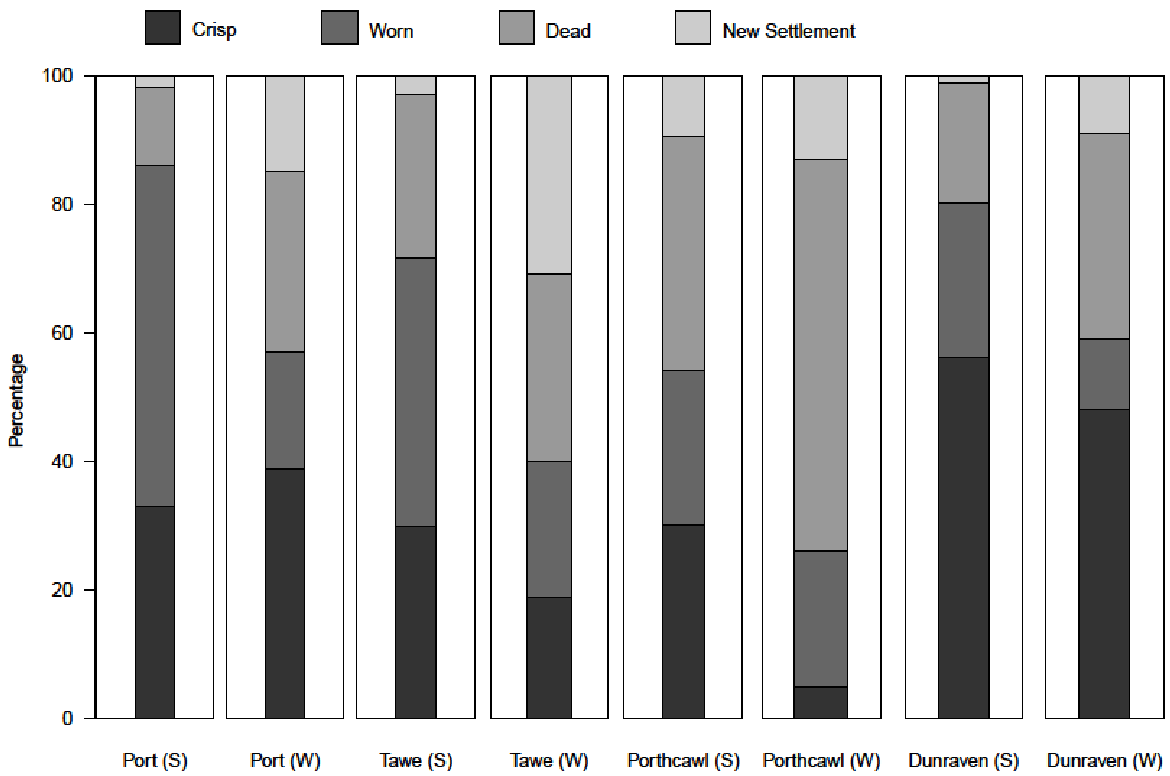


Figure 6 Mean proportion of *S. alveolata* tube aperture condition for each site in both summer (S) and Winter (W) sample seasons. Width of each bar indicates the overall mean percentage cover of *S. alveolata,* scaled within standard width boxes.

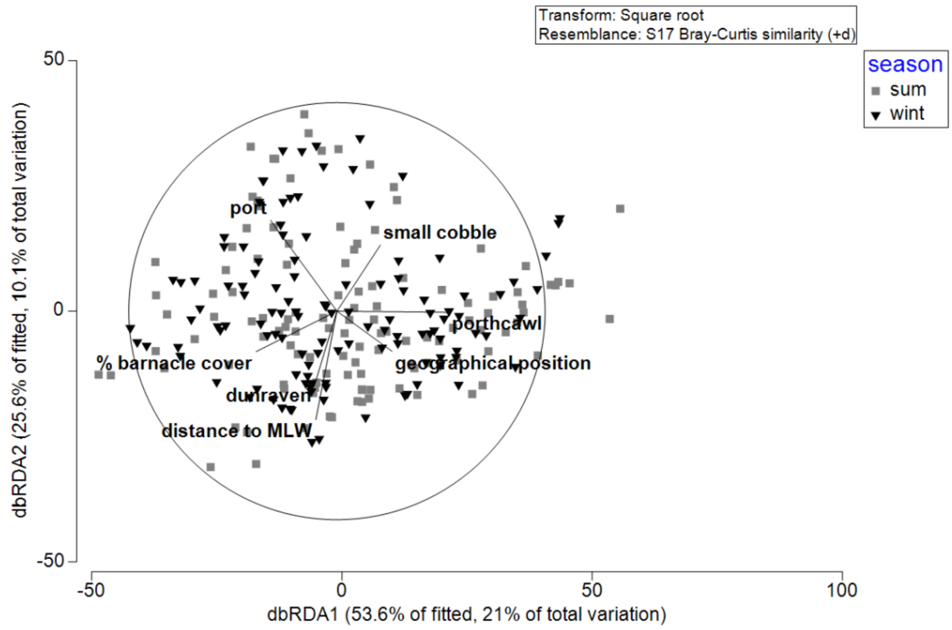


Figure 7 Distance based redundancy analysis (dbRDA) ordination of BEST fitted model for the community composition associated with *S. alveolata* reef habitat, based on Bray-Curtis similarities after square root transformation of abundances. Visualised according to sample season: sum – summer, wint – winter. Habitat characteristics significantly linked and showing correlation > 0.3 to the variation in the data are superimposed.

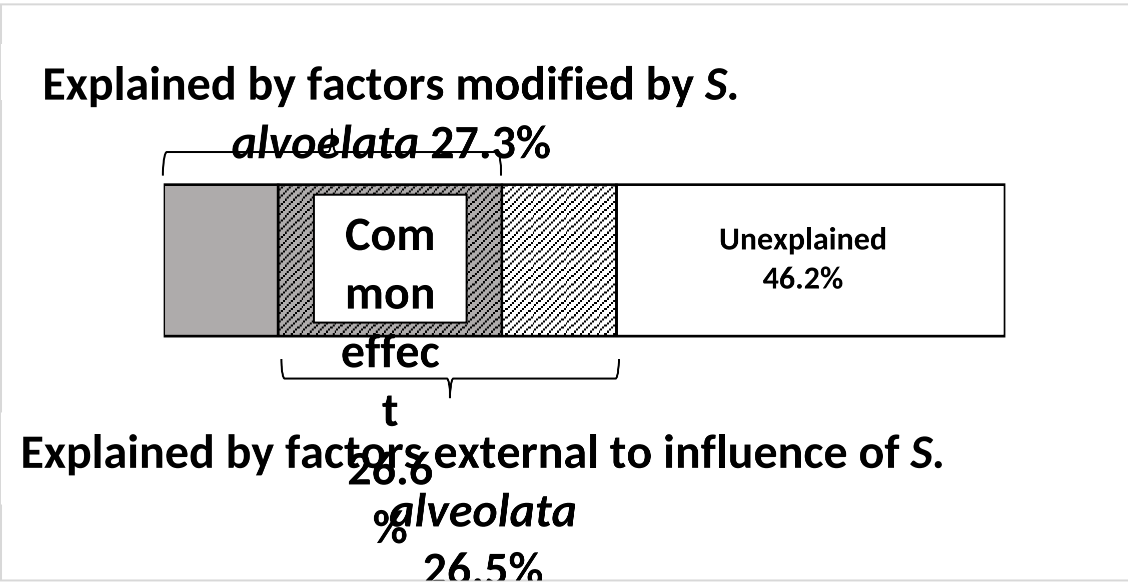


Figure 8 Schematic of variance partitioning distance-based linear model (DISTLM) showing the relative effects of reef variables and spatio-temporal variables on the composition of associated reef species.

Tables

Table 1. Factors that influence community composition in temperate, intertidal communities including a) those that can be modified by the ecosystem engineer *S. alveolata* and b) those factors which are external to the influence of *S. alveolata*

	Effects on associated community composition
a) Factors modified by *S. alveolata*	
% cover *S. alveolata*	Species richness is often found to be higher within S. alveolata aggregations than that of surrounding sediments (Jones et al., 2018; Mettham et al., 1989). However, can dominate and outcompete species for space (Cunningham et al., 1984).
% *S. alveolata* formation	Species assemblages has been shown to vary according to S. alveolata formation, due to differences in surface topography and spatial heterogeneity (Dubois et al., 2002; La Porta and Nicoletti, 2009; Porras et al., 1996)
% *S. alveolata* tube aperture condition	Tube aperture condition is indicative of the health of S. alveolata and clearing/fliter feeding (La Porta and Nicoletti, 2009; Dubois et al., 2003) Healthy *S. alveolata* have high filtration rates and are consumers of newly settling larvae (Andre et al., 1993), which can influence the ability of other species to colonise certain areas.
% associated macroalgal cover	S. alveolata provide a hard substrate on which macroalgae can attach. Macroalage can influence species assemblages, in particular grazing species (Wells et al., 2007)
% associated barnacle cover	Barnacle species have been shown to competition with *S. alveolata* for space (Fodrie et al., 2014) and food (Dubois and Colombo, 2014) and therefore *S. alveolata* will have an influence on their distribution. Barnacles are a key food source for a number of intertidal species (Paine, 1966) and are also ecosystem engineers (Mendez et al., 2015) and so any modification of their distribution is likely to influence species assemblages.
% standing water	Ecosystem engineers can modify hydrological regimes and act as barriers and breakwaters (Borsje et al., 2011; Bouma et al., 2014), restricting drainage of the lower shore, creating rock pools and therefore increasing associated species diversity (Holt et al., 1998)
Substrate type	As Ecosystem engineers, S. alveolata stabilise loose sediment and substrate, which in turn can increase heterogeneity in the surrounding benthos, which has been shown to influence structure of species assemblages (Ambrose and Anderson, 1990; Barros et al., 2001; Cusson and Bourget, 1997)

b) Factors external to influence of *S. alveolata*	
Site	Spatial differences in intertidal species compositions are well documented, as a result of factors such as abiotic and biotic filtering (Hobbs and Norton, 2004)
Geographical position (lat/long)	It is well documented that a number of gradients influence the composition of organisms on temperate, rocky shores (Menge, 2000)
Season	Temporal differences in intertidal species compositions have been found in a number of studies (Menconi et al., 1999)
Distance to MLW	This is taken as a proxy for time spent exposed to air This is known to result in vertical zonation of species, depending on their tolerance to exposure (Dayton et al., 1971; Menge, 1976)

Table 2 Results of multivariate permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities (square root transformed) of percent cover of *S. alveolata* reefs between sites and seasons in Swansea Bay, UK.

Source	DF	MS	Psuedo-F	Unique Perms	p (perm)
Season	1	555.7	1.2943	9940	0.2577
Site	3	954.1	2.2221	9945	0.072
Season x Site	3	155.2	0.36154	9954	0.8396
Residual	232				
Total	239				

Table 3 Results of multivariate permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities (square root transformed) of community composition of *S. alveolata* reefs between sites and seasons in Swansea Bay, UK.

Source	DF	MS	Psuedo-F	Unique Perms	p (perm)
Season	1	3069.2	1.9049	9940	0.0885
Site	3	31305	19.429	9934	0.0001
Season x Site	3	2010.5	1.2479	9918	0.2299
Residual	232				
Total	239				

Table 4 Results of *post hoc* pairwise PERMANOVA analysis of the differences in community composition of *S. alveolata* reef habitat between sites (Port, Tawe, Porthcawl and Dunraven).

Group	T	Unique perms	P(perm)	Average % similarity
Port, Tawe	2.671	9945	0.0001	40.26
Port, Porthcawl	6.8979	9942	0.0001	30.73
Port, Dunraven	4.463	9950	0.0001	36.84
Tawe, Porthcawl	4.4197	9940	0.0001	38.95
Tawe, Dunraven	2.5478	9958	0.0001	39.81
Porthcawl, Dunraven	4.7372	9950	0.0001	39.76

Table 5 Percentage contribution of species to pairwise dissimilarities between each of the sample sites, based on Bray-Curtis similarity indices (SIMPER).

	Mean±SE		Dissimilarity/SD	Contribution to dissimilarity %	Total dissimilarity between sites %
	Port	**Tawe**			71.69
Crepidula fornicata	5.0 ± 1.0	2.0 ± 0.6	0.92	19.67	
Littorina littorea	4.0 ± 1.1	6.8 ± 2.3	1.03	19.16	
Steromphala umbilicalis	2.5 ± 0.4	3.5 ± 0.6	1.18	15.76	
Nucella lapulis	3.6 ± 0.7	1.9 ± 0.3	1.04	15.71	
	Port	**Porthcawl**			88.57
Crepidula fornicata	5.0 ± 1.0	0.1 ± 0.1	0.92	21.45	
Nucella lapulis	3.6 ± 0.7	1.1 ± 0.6	1.11	18.33	
Littorina littorea	4.0 ± 1.1	0.1 ± 0.0	0.89	15.95	
Steromphala umbilicalis	2.5 ± 0.4	1.4 ± 0.4	1.11	15.27	
	Port	**Dunraven**			75.45
Steromphala umbilicalis	2.5 ± 0.4	6.1 ± 0.9	1.15	18.63	
Crepidula fornicata	5.0 ± 1.0	0.1 ± 0.0	0.90	18.07	
Littorina littorea	4.0 ± 1.1	3.3 ± 1.2	1.03	16.21	
Nucella lapulis	3.6 ± 0.7	1.2 ± 0.3	1.08	15.38	
Spirobranchus triqueter	1.7 ± 0.3	0.2 ± 0.1	0.91	10.88	
	Tawe	**Porthcawl**			89.59
Littorina littorea	6.8 ± 2.3	0.1 ± 0.0	0.90	25.34	
Steromphala umbilicalis	3.5 ± 0.6	1.4 ± 0.4	1.01	21.36	
Nucella lapulis	1.9 ± 0.3	1.1 ± 0.6	0.97	14.87	
Crepidula fornicata	2.0 ± 0.6	0.1 ± 0.1	0.57	11.25	
	Tawe	**Dunraven**			76.59
Steromphala umbilicalis	3.5 ± 0.6	6.1 ± 0.9	1.05	26.55	
Littorina littorea	6.8 ± 2.3	3.3 ± 1.2	1.01	21.63	
Nucella lapulis	1.9 ± 0.3	1.2 ± 0.3	0.86	13.47	
Crepidula fornicata	2.0 ± 0.6	0.1 ± 0.0	0.56	9.06	
	Porthcawl	**Dunraven**			86.88
Steromphala umbilicalis	1.4 ± 0.4	6.1 ± 0.9	1.22	37.12	
Littorina littorea	0.1 ± 0.0	3.3 ± 1.2	0.82	16.82	
Nucella lapulis	1.1 ± 0.6	1.2 ± 0.3	0.65	12.56	
Actinia equina	0.1 ± 0.1	0.6 ± 0.2	0.57	7.67	

Table 6 Results of two way Analysis of Variance (ANOVA) for measures of a) species richness, b) Hill's Indices (N1) and c) Hills Indices (N2)

a) Species richness

Source	DF	SS	MS	F	P
Season	1	2.80	2.82	1.32	0.251
Site	3	235.50	78.50	36.86	< 0.001
Season x Site	3	5.50	36.86	0.86	0.464
Residual	232	494.10	0.86		

b) Hill's Indices (N1)

Source	DF	SS	MS	F	P
Season	1	0.32	0.32	0.31	0.581
Site	3	71.32	23.77	22.77	< 0.001
Season x Site	3	2.30	0.77	0.767	0.533
Residual	232	242.23	1.04		

c) Hill's Indices (N2)

Source	DF	SS	MS	F	P
Season	1	1.45	1.45	1.27	0.262
Site	3	81.57	27.19	23.69	< 0.001
Season x Site	3	0.98	0.33	0.28	0.837
Residual	232	266.31	1.15		

Table 7. Results of Tukey's RSD p*ost hoc* test of the differences in a) species richness, b) Hill's indices (N1) and c) Hill's diversity indices (N2) between study sites.

a) Species richness

Group	diff	P (adj)
Port, Tawe	-1.050	< 0.001
Port, Porthcawl	-2.767	< 0.001
Port, Dunraven	1.450	0.438
Tawe, Porthcawl	1.717	<0.001
Tawe, Dunraven	0.400	<0.001
Porthcawl, Dunraven	-1.317	< 0.001

b) Hill's Indices (N1)

Group	diff	P (adj)
Port, Tawe	- 0.548	0.020
Port, Porthcawl	-1.49	< 0.001
Port, Dunraven	0.950	< 0.001
Tawe, Porthcawl	0.941	< 0.001
Tawe, Dunraven	0.403	0.138
Porthcawl, Dunraven	-0.538	0.020

c) Hill's Indices (N2)

Group	diff	P (adj)
Port, Tawe	-0.500	0.057
Port, Porthcawl	-1.606	< 0.001
Port, Dunraven	0.794	< 0.001
Tawe, Porthcawl	1.11	< 0.001
Tawe, Dunraven	0.298	0.425
Porthcawl, Dunraven	-0.813	< 0.001

Table 8 Results of multivariate permutational analysis of varience (PERMANOVA) based on Bray-Curtis dissimilarities (square root transformed) of the formation of *S. alveolata* reefs between sites and season in Swansea Bay, UK.

Source	DF	MS	Psuedo-F	Unique Perms	p (perm)
Season	1	3202.2	1.0445	9969	0.3707
Site	3	17459.0	5.6945	9931	0.0001
Season x Site	3	7289.6	2.3777	9927	0.0142
Residual	232				
Total	239				

Table 9 Results of *post hoc* pairwise PERMANOVA analysis of *S. alveolata* formation of *S. alveolata* reef habitat between sites (Port, Tawe, Porthcawl and Dunraven), across each sample season (summer, winter).

Group	Summer			Winter		
	t	Unique perms	P(perms)	t	Unique perms	p (perm)
Port, Tawe	2.0134	6171	0.0093	1.2994	493	0.1568
Port, Porthcawl	1.3618	1483	0.1424	3.3377	72	0.0004
Port, Dunraven	0.88712	1997	0.5012	1.7991	226	0.0265
Tawe, Porthcawl	1.4592	2382	0.0943	3.3072	962	0.0001
Tawe, Dunraven	1.834	2778	0.0218	1.4237	1279	0.0987
Porthcawl, Dunraven	1.4973	269	0.0921	2.227	290	0.0044

Table 10 Results of multivariate permutational analysis of varience (PERMANOVA) based on Bray-Curtis dissimilarities (square root transformed) of the % tube aperture condition of *S. alveolata* reefs between sites and season in Swansea Bay, UK.

Source	DF	MS	Psuedo-F	Unique Perms	p (perm)
Season	1	41843	39.323	9960	0.0001
Site	3	15883	14.927	9947	0.0001
Season x Site	3	6582.2	6.1858	9945	0.0002
Residual	232				
Total	239				

Table 11 Results of post hoc pairwise PERMANOVA analysis of *S. alveolata* tube aperture condition of *S. alveolata* reef habitat between sites (Port, Tawe, Porthcawl and Dunraven), across each sample season (summer, winter).

Group	Summer				Winter			
	t	Unique perms	P(perms)	Average % similarity	t	Unique perms	p (perm)	Average % similarity
Port, Tawe	1.6581	9967	0.0785	54.16	2.6697	9972	0.0036	58.48
Port, Porthcawl	2.4336	9961	0.0013	45.40	4.4008	9961	0.0001	47.95
Port, Dunraven	2.884	9967	0.0006	53.77	1.8492	9970	0.0464	63.03
Tawe, Porthcawl	1.5602	9948	0.0835	51.82	3.2434	9971	0.0001	56.82
Tawe, Dunraven	2.7872	9974	0.0032	56.62	5.6128	9961	0.0001	52.92
Porthcawl, Dunraven	2.8085	9964	0.0002	50.13	6.392	9958	0.0001	43.01

Appendices

Appendix 1. Mean percentage cover calculated for each of the surveyed condition status metrics. Results are shown for each site, for both summer and winter surveys with standard error (SE).

Reef Condition Status metrics	Port		Tawe		Porthcawl		Dunraven	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Overall % Cover	33.40 ± 2.14	33.86 ± 2.04	34.47 ± 3.56	38.46 ± 2.80	35.53 ± 1.32	45.37 ± 4.31	42.77 ± 3.31	42.93 ± 2.83
Formation								
Encrusting	22.22 ± 4.02	16.67 ± 3.60	16.91 ± 4.40	5.88 ± 2.87	31.37 ± 6.56	49.02 ± 7.07	15.49 ± 5.64	20.42 ± 4.77

Patchy	**64.44 ± 4.52**	**69.35 ± 4.36**	**46.47 ± 5.83**	**55.94 ± 5.94**	**41.18 ± 6.96**	**25.88 ± 6.14**	**59.58 ± 5.72**	**50.70 ± 5.89**
Hummock	**2.73 ± 1.48**	**2.87 ± 1.49**	**4.41 ± 2.51**	**9.31 ± 3.48**	**0 ± 0**	**0 ± 0**	**2.39 ± 1.51**	**2.82 ± 1.98**
Sheet	**5.56 ± 2.11**	**9.72 ± 2.83**	**6.91 ± 3.02**	**15.15 ± 4.27**	**15.69 ± 5.14**	**23.14 ± 5.91**	**13.52 ± 3.93**	**9.86 ± 3.56**
Reef	**4.12 ± 1.77**	**1.39 ± 1.03**	**23.82 ± 5.11**	**13.72 ± 4.15**	**9.80 ± 4.21**	**1.96 ± 1.96**	**9.01 ± 3.32**	**16.20 ± 4.35**
Condition								
Crisp	**33.06 ± 3.29**	**38.91 ± 2.59**	**30.07 ± 3.94**	**18.63 ± 2.76**	**30.14 ± 4.65**	**5.06 ± 1.61**	**56.06 ± 4.03**	**47.61 ± 3.26**
Worn	**53.10 ± 3.20**	**18.24 ± 2.22**	**41.84 ± 4.18**	**20.91 ± 2.36**	**23.96 ± 3.87**	**20.78 ± 2.55**	**24.04 ± 2.93**	**10.94 ± 2.03**
Dead	**12.00 ± 2.11**	**28.01 ± 2.06**	**25.29 ± 3.05**	**28.88 ± 2.31**	**36.39 ± 4.68**	**60.47 ± 4.02**	**18.49 ± 3.22**	**31.59 ± 2.86**
New Settlement	**1.85 ± 1.30**	**14.94 ± 1.73**	**2.94 ± 2.06**	**30.35 ± 2.25**	**9.41 ± 3.39**	**13.00 ± 3.02**	**1.14 ± 1.41**	**8.94 ± 2.22**

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