Are we there yet? Management baselines and biodiversity indicators for the protection and restoration of subtidal bivalve shellfish habitats

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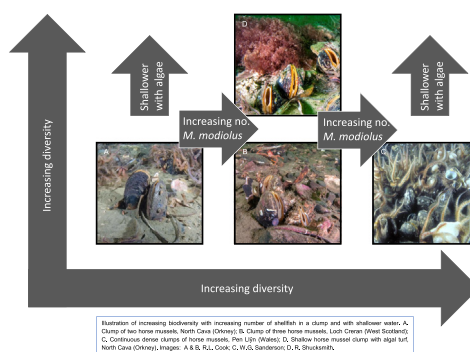[d] Scottish Natural Heritage, Silvan House, 231 Corstorphine Rd, Edinburgh EH12 7AT, UK
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HIGHLIGHTS

- *Modiolus modiolus* reefs are hotspots of biodiversity across their biogeographical range.
- Large biodiversity dataset were collected at 16 reefs in the Eastern Atlantic.
- Very high biodiversity was recorded at low numbers of *M. modiolus* as the keystone species.
- Latitudinal and environmental biodiversity gradients were observed.
- Shellfish reef conservation baselines of biodiversity need to be site-specific.

GRAPHICAL ABSTRACT

Illustration of increasing biodiversity with increasing number of shellfish in a clump and with shallower water. A, Clump of two horse mussels, North Cava (Orkney); B, Clump of three horse mussels, Loch Creran (West Scotland); C, Continuous dense clumps of horse mussels, Pen Llŷn (Wales); D, Shallow horse mussel clump with algal turf, North Cava (Orkney). Images: A & B, R.L. Cook, C, W.G. Sanderson; D, R. Shucksmith.

ARTICLE INFO

ABSTRACT

Biodiversity loss and degradation of natural habitats is increasing at an unprecedented rate. Of all marine habitats, biogenic reefs created by once-widespread shellfish, are now one of the most imperilled, and globally scarce. Conservation managers seek to protect and restore these habitats, but suitable baselines and indicators are required, and detailed scientific accounts are rare and inconsistent.

In the present study the biodiversity of a model subtidal habitat, formed by the keystone horse mussel *Modiolus modiolus* (L.), was analysed across its Northeast Atlantic biogeographical range. Consistent samples of 'clumped' mussels were collected at 16 locations, covering a wide range of environmental conditions. Analysis of the associated macroscopic biota showed high biodiversity across all sites, cumulatively hosting 924 marine macroinvertebrate and algal taxa.

There was a rapid increase in macroinvertebrate biodiversity (H′) and community evenness (J) between 2 and 10 mussels per clump, reaching an asymptote at mussel densities of 10 per clump. Diversity declined at more northern latitudes, with depth and in coarser substrata with the fastest tidal flows. Diversity metrics corrected for species abundance were generally high across the habitats sampled, with significant latitudinal variability caused by current, depth and substrate type. Faunal community composition varied significantly between most sites and was difficult to assign to a 'typical' *M. modiolus* assemblage, being significantly influenced by regional environmental conditions, including the presence of algal turfs.

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Within the context of the rapid global increase in protection and restoration of bivalve shellfish habitats, site and density-specific values of diversity are probably the best targets for conservation management and upon which to base monitoring programmes.

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1. Introduction

Biodiversity loss and the degradation of natural habitats are being caused by direct human impacts throughout the world's oceans (Cardinale et al., 2012; Ceballos et al., 2015; Dirzo et al., 2014; McCauley et al., 2015; Schratzberger and Somerfield, 2020). Correspondingly, there has been a rapid increase in conservation management initiatives such as the designation of Marine Protected Areas (MPAs) and marine habitat restoration programmes (Handley et al., 2020; UNEP-WCMC and IUCN, 2019; Barbosa et al., 2019; Gordon et al., 2020; Nilsson et al., 2016).

Structurally complex marine habitats such as coral and shellfish reefs are often described as biodiversity hot-spots and are especially sensitive to anthropogenic impact from bottom-contacting fishing gear (Hawkins, 2012; Roberts, 2007; Turner et al., 1999) as well as climate change related impacts (Bruno et al., 2018; Halpern et al., 2008). Amongst these biogenic reefs are the once widespread shellfish reefs, now globally scarce or "imperilled" (Beck et al., 2011). Oyster and mussel habitats have become the focus of protective or restorative initiatives in the European Northeast Atlantic where they are "priority habitats" (e.g. Fariñas-Franco et al., 2018b; OSPAR Commission, 2009a; Pogoda et al., 2020, 2019). Similar initiatives have been advancing rapidly in other regions such as the USA and Australia with other oyster and mussel species (Baggett et al., 2015; Birch et al., 2013; Damiano and Wilberg, 2019; Gillies et al., 2017; Mcleod et al., 2019; Sea et al., 2022; Wilberg et al., 2013).

MPA designation and protection coupled with ecological restoration of degraded or lost habitats can lead to substantial recovery of habitat structure and ecological function (Duarte et al., 2020; Roberts et al., 2017; zu Ermgassen et al., 2020). However, restoration and protection require a clear understanding of what constitutes an un-impacted state in order to inform conservation goals and establish indicators and target for success (Crouzeilles et al., 2017; Plumeridge and Roberts, 2017; Roberts et al., 2017). Modern-day habitat and data scarcity as well as inter-generational 'sliding baselines' (c.f. Pauly, 1995) hamper the clarification of these conservation management goals and the opportunity to develop indicators.

To be useful in conservation, biodiversity indicators need to be able to inform assessments of the state of the environment (e.g. "Good Environmental Status" under the European Marine Strategy Framework Directive 2008/56/EC; Borja et al., 2013; Van Hoey et al., 2010), inform assessments of the management effectiveness of MPAs, and/or the achievement of habitat restoration goals (Jones et al., 2016; Watson et al., 2014; Baine, 2001; Diefenderfer et al., 2003). Furthermore, biodiversity conservation objectives and indicators also need to accommodate climate change scenarios (Frost et al., 2016; Graham et al., 2020; Rilov et al., 2020). Biodiversity indicators therefore need to be responsive to spatial and temporal change and able to differentiate between natural and anthropogenic drivers (Boldt et al., 2014; Pearson and Rosenberg, 1978; Woods and Verones, 2019), and, as appropriate, determine restoration success (Matthews et al., 2009). Indicators also need to be reliable, easy to use by practitioners, and the methods to measure them replicable and cost-effective (Borja et al., 2009; Borja and Dauer, 2008). To avoid excess cost and effort, emphasis should also be placed on determining if existing indices are sufficiently effective before developing new ones (Borja and Dauer, 2008). Existing, 'classic' univariate biodiversity indices, for example, are easy to calculate and often responsive to anthropogenic impacts (Johnson et al., 2008; van Loon et al., 2018).

Biogenic reefs are often the most species rich types of benthic habitat (De Smet et al., 2015; Trigg et al., 2011) and, of these, subtidal shellfish habitats such as those formed by horse mussels (*Modiolus modiolus*

Linnaeus, 1758) and European oysters (*Ostrea edulis*, Linnaeus, 1758) are usually described as one of the richest and most diverse in the North Atlantic (Hagmeier and Kändler, 1927; Kenchington et al., 2007; Korringa, 1946; Möbius, 1877; Roberts, 1975; Robinson et al., 2012; Thorson, 1957).

M. modiolus is a large mussel species of slow growth and longevity (Fariñas-Franco and Roberts, 2018; Brash et al., 2018) which forms biogenic habitats distributed across the temperate regions in the northern Atlantic and Pacific Oceans (Gormley et al., 2015; Halanych et al., 2013). The associated community of these habitats has a multi-layered structure (Magorrian et al., 1995) of rich epifauna attached to the mussels, and mobile scavengers and predators attracted by the feeding opportunities enhanced by the complexity of the habitat (Bertolini et al., 2018; Fariñas-Franco et al., 2013; Navarro and Thompson, 1997; Ragnarsson and Burgos, 2012; Sanderson et al., 2008). A diverse, small invertebrate fauna inhabit the microhabitats and benefit from enhanced sedimentation and faecal material resulting from the filter feeding of the bivalves (Kent et al., 2016; Lee et al., 2020; Lindenbaum et al., 2008; Wildish et al., 1998). Several *M. modiolus* habitat types have been described, ranging from individual to clumped mussels, to bioherms and even with algal turfs (e.g., Lindenbaum et al., 2008; Mair et al., 2000; Ojeda and Dearborn, 1989). This variability has created uncertainty about what conservation management should achieve and if, as biogenic concretions, they fit definition of 'reef' that could grant them protection under conservation legislation in Europe, e.g., Council Directive 92/43/EEC (the EU Habitats Directive; see Morris, 2015).

Horse mussel habitats have suffered marked declines from dredge and trawl fisheries targeting associated commercial species such as scallops (Cook et al., 2013; Kenchington et al., 2007; Strain et al., 2012; Strong et al., 2016). In contrast, the European native oyster (*O. edulis*) was directly targeted and is therefore known to have been formerly widespread in European shelf seas (see e.g., Fariñas-Franco et al., 2018b; Pogoda, 2019 and references therein), and suffered massive losses in the late 1800s and early 1900s (Beck et al., 2011; Korringa, 1957; Thurstan et al., 2013). Records of the oyster habitat and its rich associated biota are exceedingly rare (Hagmeier and Kändler, 1927; Mistakidis, 1951; Möbius, 1877; Smyth and Roberts, 2010). Horse mussel habitats, however, were never targeted in the same way as oyster habitats and, although now rare and declining, probably represent an extant model subtidal shellfish habitat for the NE Atlantic, and therefore present an opportunity to study the biodiversity of subtidal biogenic shellfish habitats. Furthermore, there is growing evidence that oyster habitats and horse mussel habitats shared closely overlapping subtidal niches (e.g. Thurstan et al., 2013). By studying the biodiversity associated with subtidal biogenic horse mussel habitats, there is therefore potential to inform the management of subtidal shellfish habitats as a whole in the Northeast Atlantic (see Bromley et al., 2016; Fariñas-Franco and Roberts, 2018; Helmer et al., 2019; Pogoda, 2019; Pogoda et al., 2019; Smaal et al., 2015) and other biogenic reef types.

1.1. Aims and objectives

The present study set out to investigate horse mussel habitats from across the distributional range in Europe. The aim was to establish if biodiversity indices could be explained by environmental factors, and biotic factors such as the density of horse mussels. The present work also sought to establish whether horse mussel community assemblages or 'biotopes' could be repeatably described. The results were considered within the context of protective and restorative conservation management goals and potential biodiversity monitoring indicators for them.

2. Methods

Sixteen horse mussel (*Modiolus modiolus*) habitats were sampled between 1999 and 2014, largely during routine monitoring surveys conducted by the authors and commissioned by National Conservation Bodies (NCBs) in the United Kingdom. All sites were in scientific scuba diving depths (<30 m), had a near or fully marine salinity regime and were found in Boreal and Temperate waters where seasonal temperatures varied to differing degrees (depending on the latitude) between 5 and 16 °C (Sanderson et al., 2008; Tyberghein et al., 2012). Some sites were in tidal narrows, whilst others were off open coasts or semi-enclosed fjordic systems such as sea lochs. Tidal currents at sites varied from negligible to ~2kn (100 cm s^{-1}) and benthic sediments also varied from variously muddy, shelly substrates to gravels (see Appendix B).

2.1. Study areas

The sites were located within seven broad geographical areas: Norway, Shetland, Orkney, Northwest Scotland, West Scotland and the Irish Sea (Fig. 1; Appendix A). These locations were discovered during localised, targeted habitat survey and mapping exercises and span the latitudinal range of the habitat in the Northeast Atlantic, from the Norwegian fjords in the north, to the southern distributional limit in the Irish Sea off Wales (UK) and the Isle of Man (Halanych et al., 2013; OSPAR Commission, 2009b). Repeat surveys were conducted at some of these sites, e.g., Loch Creran (1999, 2005) and String Rock, Loch Alsh (1999, 2004, and 2011). Off Pen Llŷn (Wales); the ridge and trough sub habitats formed by the horse mussel bioherms were targeted separately (see also Sanderson et al., 2008).

2.2. Survey and sampling design

The full extent of the horse mussel habitat was not known at all sites but had been estimated for many; varying widely between 0.01 km^2 to 3.75 km^2 (see Table 10 in Hirst et al., 2012). At each sampling location, scientific divers collected four replicate clumps of horse mussels with associated biota and sediments, each clump from within a 25 × 25 cm quadrat. Samples were randomly selected over a 100 m distance but stratified to areas where *M. modiolus* was present. Clumps of *M. modiolus* and sediments were scoped carefully into a 5 L plastic bucket with a trowel, ensuring a 10 cm penetration into the benthos. The bucket was sealed with a lid, placed inside a bag, and recovered to the surface. On return to the laboratory the samples were sieved through a 0.5 mm mesh and all biota retained. Samples from Pen Llŷn (Wales; Fig. 1; Appendix A) were collected using a suction sampler within a similar 25 × 25 cm quadrat (see Rees et al., 2008). However, greater benthic penetration meant that a minor volumetric standardisation was applied to data prior to analyses. The retained biota were identified to as high a taxonomic resolution as possible (lowest possible taxonomic level, usually to species level) and enumerated. The World Register of Marine Species (WoRMS; http://www.marinespecies.org/) was used for taxonomic standardisation. More details of survey design and site selection are given in technical reports elsewhere (e.g., Hirst et al., 2013; Mair et al., 2000, 2009, 2010; Moore et al., 2006, 2012, 2013; Rees et al., 2008; Sanderson et al., 2014, all listed in Appendix A).

2.3. Statistical analyses

For consistency, larval stages of macrofauna, pelagic species or meiofauna such as cumaceans, copepods, ostracods, nematodes and tubificid oligochaetes, were removed from the dataset, which was also truncated
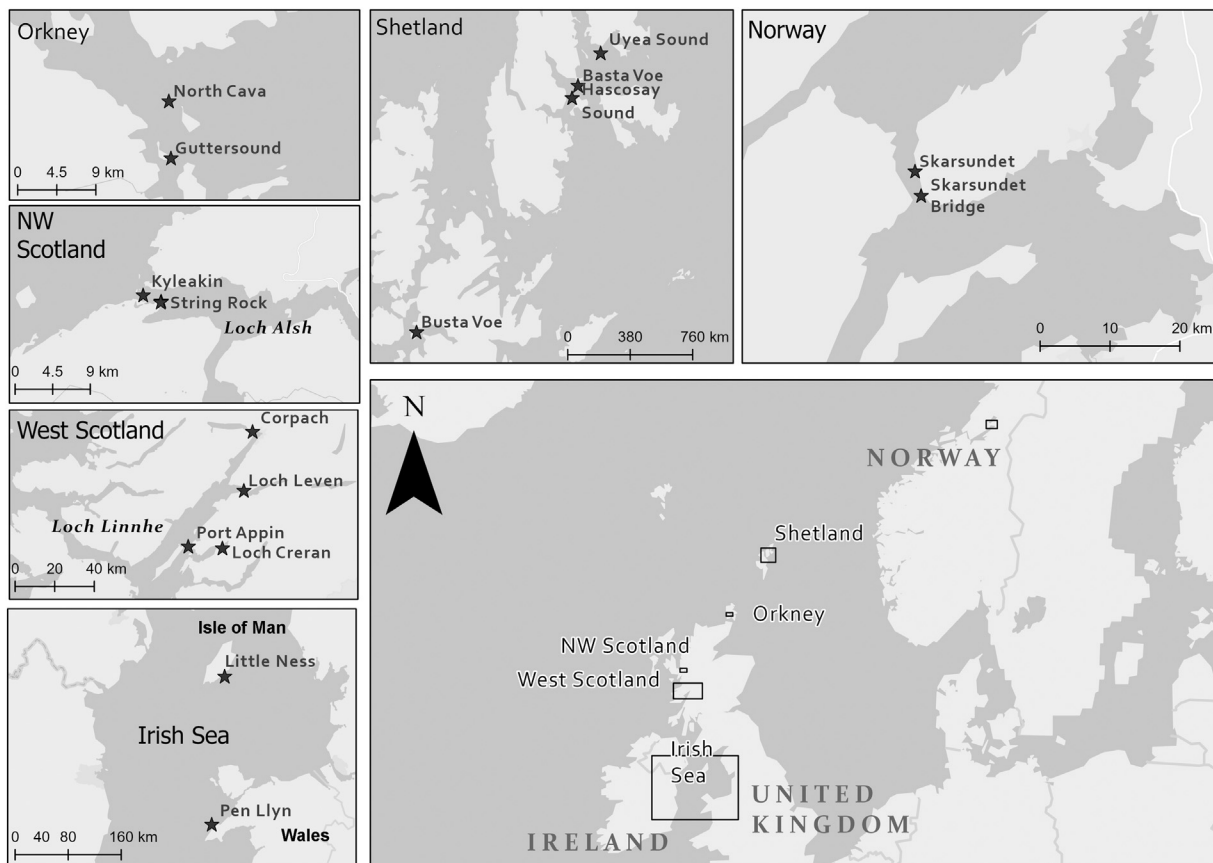

Fig. 1. Sampling locations in the present study. Map created using ArcGIS® Desktop: Release 10. ArcGIS® is the intellectual property of Esri and was used under license. Copyright © Esri. www.esri.com. Light gray canvas map © Esri.

to remove taxa not identified to at least genus level, and algae and colonial taxa recorded only as 'present' or inconsistently enumerated across the samples. The biodiversity of samples was characterised using the *vegan* package in R (Oksanen et al., 2013; R Development Core Team, 2022) to calculate: total number of taxa (S); abundance of macroinvertebrate fauna (N); two metrics of diversity adjusted for N, Margalef's species richness (d), Shannon diversity (H'); and a Pielou's measure of evenness (J) (see Magurran, 2004). These metrics were chosen because they are most reported in the literature (see Magurran, 2004) and therefore most widely applicable in management.

PERMANOVA models, also included in the vegan package (*adonis* function), were used to investigate the effects of environmental parameters (i.e., tidal current and depth), *M. modiolus* numbers and macroalgae abundance on the variability of macroinvertebrate biodiversity. Tidal current and depth data were obtained from Bio-Oracle (Tyberghein et al., 2012) and GEBCO (www.gebco.net) and extracted using ARCGIS Pro v2.7.1 (Esri Inc.). Potential latitudinal gradients in biodiversity and community composition were also investigated. Non-independence of errors was accounted for by including sample site (nested within each of the 16 *M. modiolus* habitats) as a random factor in the models. For those locations that were revisited, i.e., Loch Creran (1999, 2005) and Loch Alsh (1999, 2004, and 2011), interannual effects (if any) were investigated by running separate GLMMs using site as a random factor.

Correlation between biodiversity indices and continuous variables (depth, latitude, *M. modiolus* density, number of algae species recorded and tidal current) was investigated using Spearman's coefficient and correlogram charts plotted in R. The 'keystone' role of *M. modiolus* (c.f. Ragnarsson and Burgos, 2012; Fariñas-Franco et al., 2018a) was further investigated by examining the relationship between horse mussel numbers and diversity indices using curve model fitting in R (Wickham, 2009; R Development Core Team, 2017). A full list of all sites sampled, and the environmental variables recorded is available in the appendices (Appendix B).

Multivariate community data examined in R (R Development Core Team, 2022) and PRIMER 6 (Clarke and Gorley, 2006) were standardised to account for volumetric differences between samples and fourth root transformed to compensate for highly abundant species such as the calcareous tube-building *Spirobranchus* spp. polychaetes. A Bray-Curtis similarity matrix was ordinated using non-metric multidimensional scaling and tested with CLUSTER and SIMPROF analyses to investigate groups of similar sample stations across all sampling locations. Environmental factors explaining variability in community composition were investigated using PERMANOVA mixed models (Anderson, 2005) and fitted as vectors in the multidimensional scaling (MDS) ordination plots using the *envfit* function in the 'Vegan' R package (Oksanen et al., 2013). Broad sampling location and prevalent tidal current were used as the fixed categorical factors while *M. modiolus* abundance per clump, latitude and depth were covariates in the model. Sampling site nested within location was included in the model as a random factor to further explain the residual model variance and account for potential spatial autocorrelation. SIMPER analysis was conducted in Primer 6 (Clarke and Gorley, 2006) to determine the taxa responsible for within and between group community similarities and differences.

3. Results

A total of 924 fauna and flora taxa were recorded across all horse mussel habitats studied, including 1 Bacteria, 7 Chromista, 43 algae, and 863 macroinvertebrates. Algae were recorded in Loch Creran (3), Little Ness (8), Loch Linnhe (12), Busta Voe in Shetland (13) and Loch Alsh (35). Coraline algae (e.g., *Pseudolithoderma extensum*), *Peyssonnelia dubyi, Phycodris rubens, Delesseria sanguinea, Pterothamnion plumula, Heterosiphonia japonica* and *Polysiphonia* spp., were amongst the typical species whilst Corallinacea (encrusting red algae) were often recorded on horse mussel shells. Algae were dominated by red foliose and filamentous turf species numbering a total of 40 taxa. Five species of Chlorophyta (green algae) were also commonly associated with *M. modiolus* clumps. Fauna belonged to most major

macroinvertebrate phyla, including the colonial Porifera, Tunicata and Bryozoa (see Fig. 2 and Appendix C for full list). Total taxa per clump ranged from 29 (Shetland-Uyea Sound) to 155 (Little Ness, SW Isle of Man) (Table 1 and Appendix C; Fig. 1). The highest number of taxa per site was recorded at Little Ness (296) followed by Loch Alsh (252), and Loch Leven (251). The lowest number of taxa was recorded in Norway (80) and Shetland-Uyea Sound (88). The full list of sites surveyed and taxa recorded in each is available in Appendices A and C.

Species rich communities were recorded in a range of horse mussel habitat types from circalittoral (>30 m deep), open coast bioherm structures in tidal flows in the Irish Sea, off Pen Llŷn (Fig. 1), with an average of 100 taxa per sample, to enclosed sea loch habitats off the west coast of Scotland, where 160 taxa were recorded in one clump from Loch Alsh (see Figs. 1 & 3). In Shetland and Orkney (Fig. 1), sites ranged from sheltered sea loch (or 'voe') habitats with low flow to tidal sounds with an average species richness that varied between 65 (Uyea Sound, Shetland, ~16 m depth) and 102 taxa (Basta Voe, Shetland, ~20 m depth). Norwegian horse mussel habitat was recorded on gravel substrate overlying bedrock in the strongest tidal currents and with the second lowest number of taxa in a clump (35) in Skarsundet (~20 m depth; Figs. 1 & 2).

Macroinvertebrate abundance (N) was highest in the samples from Pen Llŷn where over 1500 individual specimens were recorded from the bioherm ridges (see Lindenbaum et al., 2008; Rees et al., 2008). Crevice fauna and infauna were conspicuously abundant, including the bivalves *Hiatella arctica, Kurtiella bidentata* and *Nucula* spp., and the porcelain crab *Pisidia longicornis*. Other sites, such as Loch Alsh (West Scotland), had similarly abundant macroinvertebrate fauna but polychaetes such as *Pholoe inornata* and *Sphaerosyllis hystrix* dominated. In addition to Pen Llŷn, some communities also had well developed barnacles and other encrusting taxa (e.g., Loch Linnhe and Loch Creran) or, where horse mussels occurred semi-infaunally (e.g. Uyea and Hascosay Sound, Shetland), a higher proportion of abundant sediment-dwelling taxa were found in the mud and byssal-matrix (e.g. capitellids and tubificid oligochaetes).

Overall, biodiversity indices such as Margalef's richness (d) and Shannon (H') were very high across all sites (Tables 1 & 2; Fig. 2). Average H' values were above 3 in most habitats in Scotland and the Irish Sea (Little Ness, Pen Llŷn) (Table 1). The exceptions were mixed substrate sites with more gravel, e.g., in Shetland (especially Uyea Sound), and cobble and gravel, e.g. Skarsundet. Under those conditions, biodiversity was low, largely because infauna and crevice fauna were less dominant.

PERMANOVA showed horse mussel abundance was a significant factor in explaining the total number of species and Margalef's richness but not Shannon diversity (H') and evenness (J) Table 2), which was overall high regardless of *M. modiolus* numbers, and did not vary significantly across the surveyed areas. Tidal current was a significant factor explaining variance in some biodiversity metrics: the number of species and richness being lower at high current speeds. Substrate type significantly predicted biodiversity, especially dominance-type indices (H' and J). Habitats with abundant *M. modiolus* shell and mixed shell gravel were the most biodiverse while those horse mussel communities on bedrock and coarse sand and gravel had significantly lower biodiversity, dominated by a few taxa, compared with all other seabed types. Although horse mussel habitats in more exposed coastlines (e.g., Pen Llŷn, Little Ness, and North Cava, in Orkney) had significantly more associated taxa, all other biodiversity indices did not show significant variation in faunal diversity regardless of exposure. There was a significant effect of latitude and longitude on all biodiversity metrics considered, explaining most of the of total variance and decrease in biodiversity in more northerly horse mussel habitats (Table 2).

Biodiversity indices were positively correlated with the number of horse mussels per clump, depth, current, exposure and presence of macroalgae, but negatively correlated with latitude and longitude (Fig. 4).

The relationship between *M. modiolus*, as the keystone, habitat-forming species, and the biodiversity metrics (richness S and Shannon biodiversity H') was best explained by an exponential curve reaching an asymptote at ca. 70 taxa and H' = 4 at approximately 10 mussels per clump (Fig. 5).

Fig. 2. A. Collecting 'clump' samples, North Cava; B. Horse mussel community with red algal turf, North Cava; C. Ophiuroids and octopus (*Eledone cirrhosa*, L.) on dense horse mussel bed, Hascosay Sound; D. Epifaunal bryozoans *Reteporella grimaldii* (Jullien) and *Plagiooecia patina* (L.), Skarsundet; E. Cryptic, crevice-dwelling *Galathea intermedia* (Lilljeborg) amongst horse mussels, Haskosay Sound. F. Star fish (*Asterias rubens*, L.) on dense horse mussels, Pen Llŷn. G. Edible crab (*Cancer pagurus*, L.) and hermit crab (*Pagurus bernhardus*, L.) on shallow horse mussel bed, Hascosay Sound. A,C,E,G Richard Shucksmith, B Robert Cook, D Joanne Porter, F William Sanderson.

Interannual differences in biodiversity indices for those sites that were revisited, i.e., Loch Creran in 1999 and 2005 and Loch Alsh in 1999, 2004 and 2012, were not significant (Appendix 2).

In total, 732 species were included in the multivariate analyses after data were further truncated to remove colonial and encrusting species; for which abundance values could not be consistently assigned. Multidimensional scaling was a useful representation of the data (Fig. 6: stress level 0.21), showing distinct infaunal community groupings loosely based on broad geographical location (e.g., 'Orkney'; Fig. 1) and/or sampling site within location (e.g., North Cava, Fig. 1). Irish Sea (Pen Llŷn and Isle of Man) and Norwegian assemblages were the most distinct groupings (25 % CLUSTER Bray-Curtis similarity) while the Scottish sites clustered into three main groups: Loch Linnhe and Orkney; Loch Creran and the Busta

Voe site (in Shetland); Loch Alsh and Shetland (Fig. 6). SIMPROF clustering identified a total of 16 significant (at $\alpha = 0.05$) community groups which, with few exceptions, corresponded with distinct sampling sites. According to the *envfit* analysis, latitude, *M. modiolus* density, depth and exposure significantly explained the ordination ($p < 0.001$) while current ($p = 0.378$) and algal richness ($p = 0.501$) did not. The goodness of fit expressed by the correlation coefficient between significant environmental factors and ordination scores (r^2) were 0.45 (exposure), 0.33 (latitude), 0.24 (depth) and 0.18 (*M. modiolus*).

PERMANOVA models (Table 3) indicated that the composition of infaunal communities associated with horse mussels was significantly influenced by all environmental factors, including the abundance of *M. modiolus* (p < 0.001; Table 3). Most of the variation in macroinvertebrate community

Table 1

Biodiversity indices recorded from *Modiolus modiolus* beds (N = 74) in Northern Europe (see Fig. 1 for locations). S_total = Total number of taxa (infaunal and epifaunal); S = Total number of taxa (infaunal); d = Margalef's richness; N = Total abundance of individuals; H′ = Shannon-Wiener's diversity; J = Pielou's evenness.

|		Norway	Shetland	Orkney	Loch Alsh	Loch Creran	Loch Linnhe	Little Ness	Pen Llyn
S (total)	Mean	40.75	56.08	89.13	100.19	85.63	90.67	147.00	94.57
	SE	2.17	4.57	5.74	3.95	1.69	3.93	3.98	7.16
	Max	45	82	107	123	91	105	155	132
	Min	35	29	70	73	79	71	136	77
S	Mean	37.75	49.08	85.5	90.5	76.13	82.58	125.75	88
	SE	1.49	3.13	5.48	4.03	2.17	3.87	4.96	5.82
	Max	41	64	103	116	86	98	137	120
	Min	34	28	67	67	68	62	113	74
N	Mean	152.5	468	524.63	833.5	423.63	341	907.5	831.71
	SE	14.13	52.3	106.08	92.69	40.06	17.41	96.83	178.65
	Max	192	805	994	1505	636	446	1152	1599
	Min	126	170	209	398	275	252	711	461
d	Mean	7.32	7.94	13.73	13.42	12.51	13.98	18.35	13.12
	SE	0.18	0.51	0.47	0.44	0.45	0.57	0.57	0.53
	Max	7.61	10.49	15.03	15.8	14.35	16.57	19.79	16.13
	Min	6.82	4.36	11.7	10.34	10.92	11.02	17.06	11.87
H	Mean	2.98	2.71	3.57	3.45	3.65	3.79	3.96	3.41
	SE	0.07	0.11	0.09	0.08	0.05	0.05	0.05	0.07
	Max	3.17	3.43	3.88	3.83	3.8	4.09	4.09	3.58
	Min	2.86	2.02	3.23	2.46	3.43	3.42	3.86	3.17
J	Mean	0.82	0.7	0.81	0.77	0.84	0.86	0.82	0.76
	SE	0.01	0.02	0.03	0.02	0.01	0.01	0.01	0.02
	Max	0.87	0.85	0.92	0.85	0.87	0.92	0.83	0.82
	Min	0.8	0.55	0.7	0.58	0.81	0.8	0.81	0.7
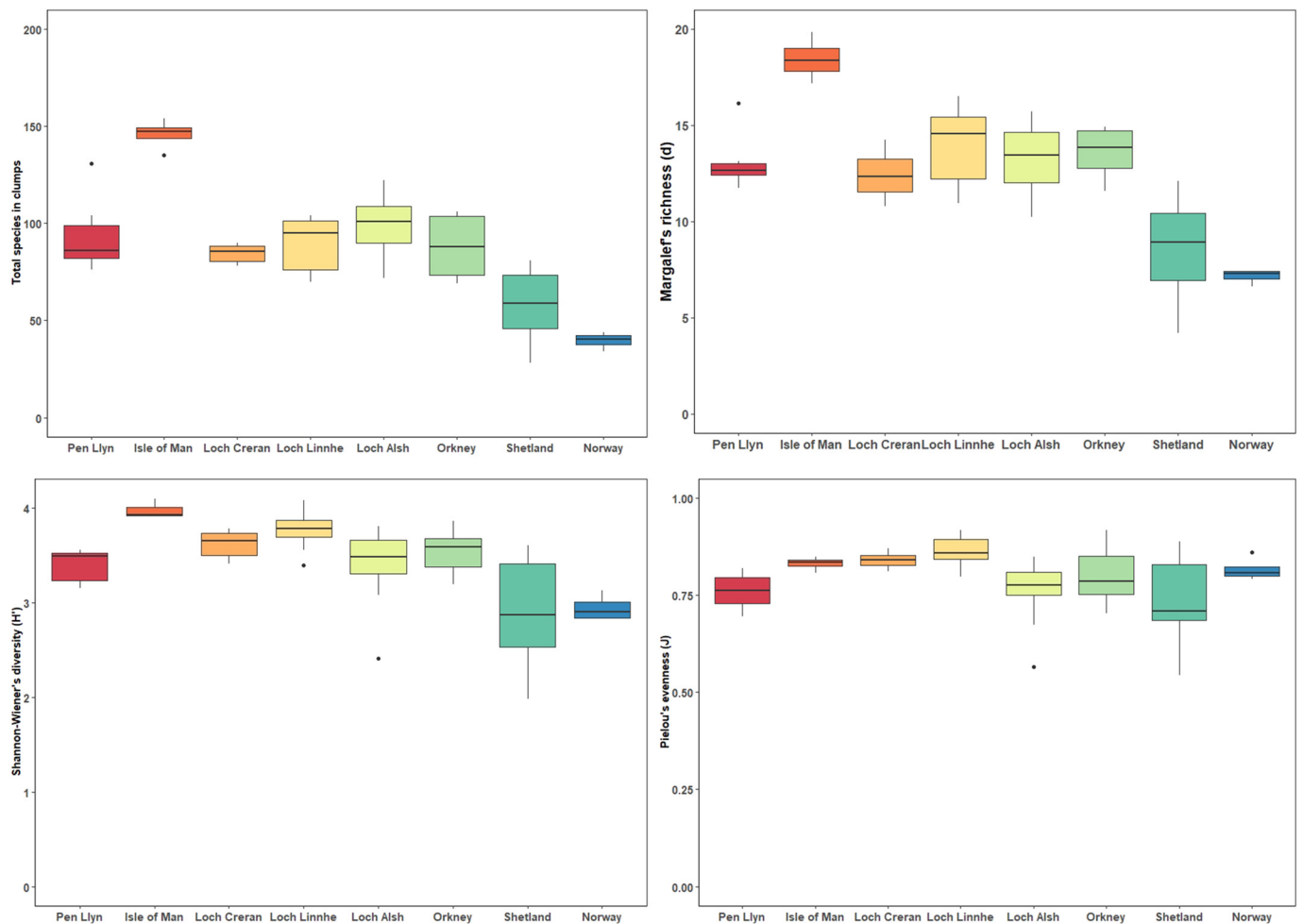
Fig. 3. Biodiversity characteristics of horse mussel (*M. modiolus*) habitats surveyed in the present study. Box represents the interquartile range; line indicates median and whiskers are maximum and minimum observed values (*n* = 71).

Table 2

Results of permutational multivariate anova (PERMANOVA) models for biodiversity indices in *M. modiolus* beds across the species' Northern European range. R^2 indicates contribution of each factor to the total observed variance. *P* values in bold denote statistical significance at α = 5 % (0.05). Location is included as a random factor in the models to control for location specific effects.

Source	Total species (St)			Richness (d)			Shannon (H)			Evenness (J)		
	F-value	R^2	P	F-value	R^2	P	F-value	R^2	P	F	R^2	P
Current	31.06	0.10	**0.01**	12.09	0.05	0.07	1.14	0.01	0.59	14.69	0.11	**0.001**
Depth	12.89	0.04	**0.01**	15.10	0.06	**0.004**	9.47	0.05	**0.001**	4.05	0.03	**0.01**
Latitude	107.36	0.35	**0.01**	93.77	0.35	0.11	54.95	0.29	**0.04**	7.68	0.06	0.16
Macroalgae	9.42	0.14	0.15	4.66	0.02	0.18	0.86	0.05	0.28	0.01	0.00	0.96
M. modiolus	44.52	0.12	**0.01**	18.84	0.07	**0.02**	2.94	0.02	0.45	0.02	0.31	0.97
Substrate	7.16	0.02	**0.03**	10.76	0.20	**0.02**	10.79	0.27	**0.01**	8.36	0.03	**0.01**
Exposure	415.2	0.02	**0.07**	2.07	0.02	0.59	1.53	0.02	0.22	1.80	0.46	0.16
Residuals		0.20			0.23			0.33				

composition found by the model was explained by the fixed factor substrate type (i.e., gravelly or mixed gravel and fine sediment) and Location as the random factor (29 % and 15 %, respectively). Current, wave exposure and depth explained between 8 and 9 % of the total variation, while *M. modiolus* abundance explained 3 %. Residual variation not explained by the model amounted to 23 % of the total observed variance in the multivariate species data (Table 3). Overall regional variability (latitude and longitude) drove the groupings, with a clear effect of *M. modiolus* abundance in combination with current, depth and exposure; more distinct communities were found in deeper, more exposed locations, with fastest tidal flows (Pen Llŷn and Little Ness), at higher latitudes (distinctively Norway) and those communities where macroalgae were present (Loch Alsh) (Fig. 7).

SIMPER analysis of significant groupings created by SIMPROF (see Fig. 6 and Appendix D) showed that most communities aggregated regionally (by location) with most of the between-group variability attributed to differences in the abundances of many of the same species. A notable exception were the sites at the latitudinal extremes, Pen Llŷn and Little Ness, in the southern edge, and Norway in the northern. In the Norwegian beds, characterised by gravelly substrate and bedrock, the *M. modiolus* communities were the most distinct, dominated by *Ophiura robusta*, *Astarte* spp. and

Limaria loscombi species not found in samples from Scotland and the Irish Sea. In Shetland *M. modiolus* habitats were largely dominated by ophiuroids and capitellid polychaetes.

4. Discussion

The present study is the most comprehensive, geographically wide-ranging, and consistent subtidal shellfish community study to date. Sixteen locations were described from across the biogeographic range of horse mussel (*Modiolus modiolus* L.) habitats in the Northeast Atlantic. Community composition varied between most sites, with horse mussel density, and especially with substrate type, such that a 'typical' universal community was not evident and could not be reasonably asserted. Statistically, significant relationships between diversity, horse mussel abundance, tidal current, latitude, depth and algal abundance were shown. Within the context of the conservation management for the protection or restoration of horse mussel communities, it would be unwise to seek to achieve or maintain an idealised community composition. However, protective or restoration management can aim to achieve a given level of biodiversity associated with the abundance of the habitat-forming shellfish, while accounting for site-specific differences in environmental conditions of tidal flow, wave exposure, depth, and latitude (Table 4).

Despite the lack of evidence of clearly defined biotopes in the present study, there were, nevertheless, associated species recorded at some sites that had previously been noted as characteristic, or found in former descriptions of horse mussel biotopes (see Connor et al., 2004; Cook et al., 2013; Erwin, 1990; Fariñas-Franco et al., 2018b; Fariñas-Franco and Roberts, 2018; Kent et al., 2017, 2016; Magorrian and Service, 1998; Moore et al.,
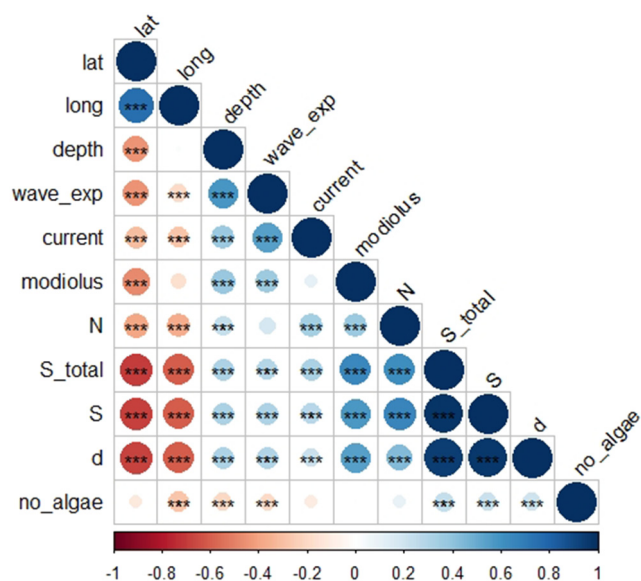
Fig. 4. Spearman's correlation matrix showing relationship between biodiversity, horse mussel (*M. modiolus*) abundance and environmental parameters. Colour of circles represents negative (red) or positive (blue) correlation between the parameters; size indicates strength of the correlation (Spearman's coefficient value) between pairwise comparisons. Asterisks indicate significance levels: below 0.05 (*), 0.01 (**), and 0.001 (***) (n = 71).
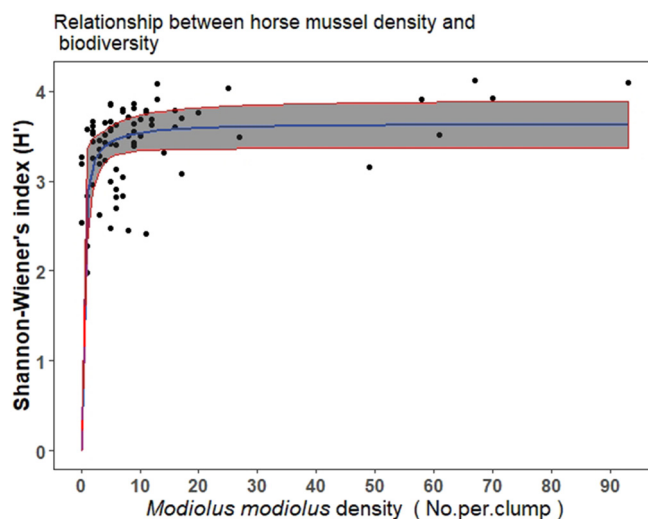
Fig. 5. Number of horse mussels (*M. modiolus*) recorded in each clump plotted against Shannon's diversity index (H′). Fitted hyperbolic curve with 95 % confidence intervals and coefficient of determination (R^2).

Fig. 6. MDS plot of squared root transformed Bray-Curtis similarity for species and abundance data collected across all horse mussel beds (*M. modiolus*; n = 74). 2D stress value (0.19) represents good representation of multivariate relationships. Symbols represent significant SIMPROF groups and circles indicate 50 % similarity. PLl = Pen Llŷn; LC = Loch Creran; BustaV = Busta Voe; BV = Basta Voe; US = Uyea Sound; HS = Hascosay Sound; LA_SR = String Rock, Loch Alsh; LA_KA = Kyle Akin, Loch Alsh; GS = Guttersound; NC = North Cava; CP = Corpach; PA = Port Appin; LL = Loch Leven; Nor = Norway.

2012; Roberts et al., 2004, 2011; Sanderson et al., 2014, 2008). Attempts to classify horse mussel biotopes (e.g., Connor et al., 2004; Magorrian and Service, 1998) have previously been based on relatively few, inconsistent records, because the habitat type is "threatened and declining" in the NE Atlantic (OSPAR Commission, 2009b) and therefore rarely sampled. With advances in the discovery and consistent sampling of the remnant habitats presented here, it is now apparent that a continuum of community types exists, reflecting increased diversity linked to increasing density of the 'keystone' horse mussels. Functionally, shellfish habitats will increase habitat provisioning in the form of hard substrate for epibiota, and crevices for cryptic species. More shellfish per unit area will also increase pelagic-benthic coupling from the increased filter-feeding biomass and produce more faecal and pseudo-faecal deposition for detritivores (zu Ermgassen et al., 2020; Kent et al., 2016; Lee et al., 2020). Those horse mussel habitats with algal turfs, and sometimes kelps in shallower water (e.g., upper sublittoral and lower infralittoral areas of Loch Linnhe and Alsh, Figs. 1, 2 & 8; see Graphical Abstract) are likely to further increase habitat complexity; adding primary production that will contribute to enhance biomass and diversity further (Smale et al., 2013; Teagle et al., 2017). When found in the strongest tidal currents, however (i.e., samples from Norway), the depositional sediments appear to not be retained in the clump and byssal matrix to the same extent, leading to a porous gravelly matrix and a reduced

infaunal community, with a higher percentage of crevice fauna that shelter between the mussels (e.g., *Astarte* spp., *H. arctica*). Intuitively, habitats found in stronger tidal currents might be expected to experience increased food supply, supporting more individuals per unit area and greater diversity (Lesser et al., 1994; Wildish and Kristmanson, 1985), however, this relationship is not shown in the present study. In the present work tidal flow rates were categorically estimated from charts and from the direct experiences of the diving scientists rather than measured accurately in situ and for this reason, any increase in biodiversity associated with moderate increases in tidal flow were probably undetected. A conceptual model based on the present findings and their interpretation is provided in Fig. 8 and the graphical abstract.

The significant latitudinal factor in the present study is entirely consistent with previous findings and aligns with the paradigm that benthic species richness decreases latitudinally from the tropics with a mid-latitude peak that is higher in the northern hemisphere where the continental shelf is greatest (Saeedi et al., 2019; Tittensor et al., 2010). The explanation of that trend is that both the evolutionary spread from the tropics and the availability of high-productivity shelf habitats have both influenced the evolution of the biogeographical pattern of biodiversity (Chaudhary et al., 2016). The data collected for the present study extended north from the mid latitudes of the Irish Sea to Norway and showed a significant latitudinal decline in horse mussel habitat biodiversity (that was also auto correlated with a longitude trend which is probably an artefact of the shape of the coastline (Fig. 1)). This finding is important to conservation managers because the diversity at any location will 'naturally' be less the further north.

Based on the present study, seabed habitats with horse mussels are consistent biodiversity hotspots (Figs. 2 & 4), so long as clumping occurs and fine sediments are retained: Diversity is similar or higher than the usual range for what is considered a diverse habitat (see Magurran, 2004) and for other diverse benthic habitats that lack the structural complexity of mussel habitats (e.g., soft sediments, Ellingsen, 2002, Snelgrove, 1999). In this regard, horse mussels are clearly an ecosystem engineer and keystone species, increasing community diversity and evenness at relatively low densities between 2 and 10 mussels per clump and reaching what can be considered a 'climax community' in terms of biodiversity at about 10 mussels per clump (Fig. 5). Even horse mussel habitats consisting of sparse, isolated and barely clumped mussels, at densities as low as 5 mussels m^{-2} do provide habitat to a relative high number of species (>200) compared to areas from which the mussels have disappeared (see Fariñas-Franco et al., 2018a).

Table 3

Results of PERMANOVA tests for differences in the biotic assemblages associated with *Modiolus modiolus* habitats sampled across Europe (N = 74). Location is included in the model as a blocking (random) factor. Significant p values (<0.05) are indicated in bold. Total unique permutations = 999.

Source	d.f.[a]	SS[b]	Pseudo-F	R^2	P
Current	1	0.952	7.458	0.04	**0.001**
Depth	1	1.439	1.0.273	0.07	**0.001**
Latitude	1	1.859	14.522	0.09	**0.001**
Macroalgae	1	1.040	8.153	0.05	**0.001**
M. modiolus	1	0.741	5.812	0.03	**0.001**
Substrate	5	6.148	9.632	0.29	**0.001**
Exposure	2	1.13	4.442	0.05	**0.001**
Location (Blocks)	5	3.109	7.37	0.15	**0.001**
Residuals	63	8.593		0.23	
Total	74				

[a] d.f. = degrees of freedom.
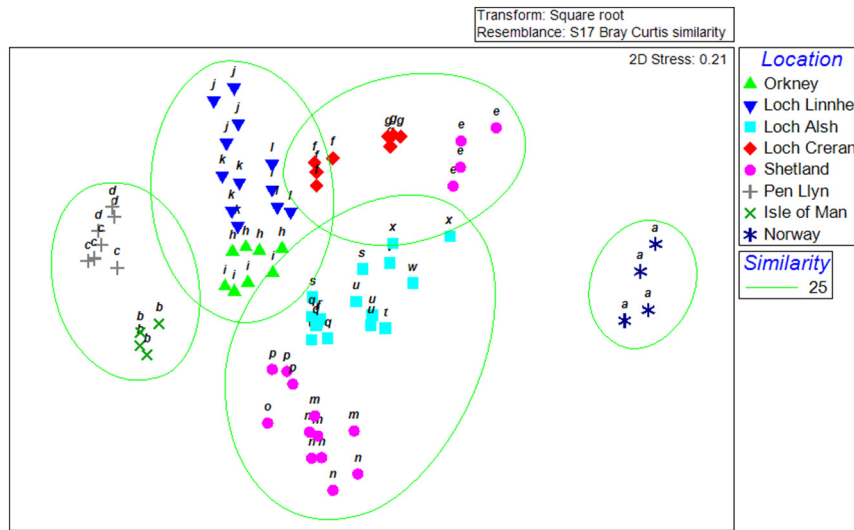[b] SS = Sums of squares.
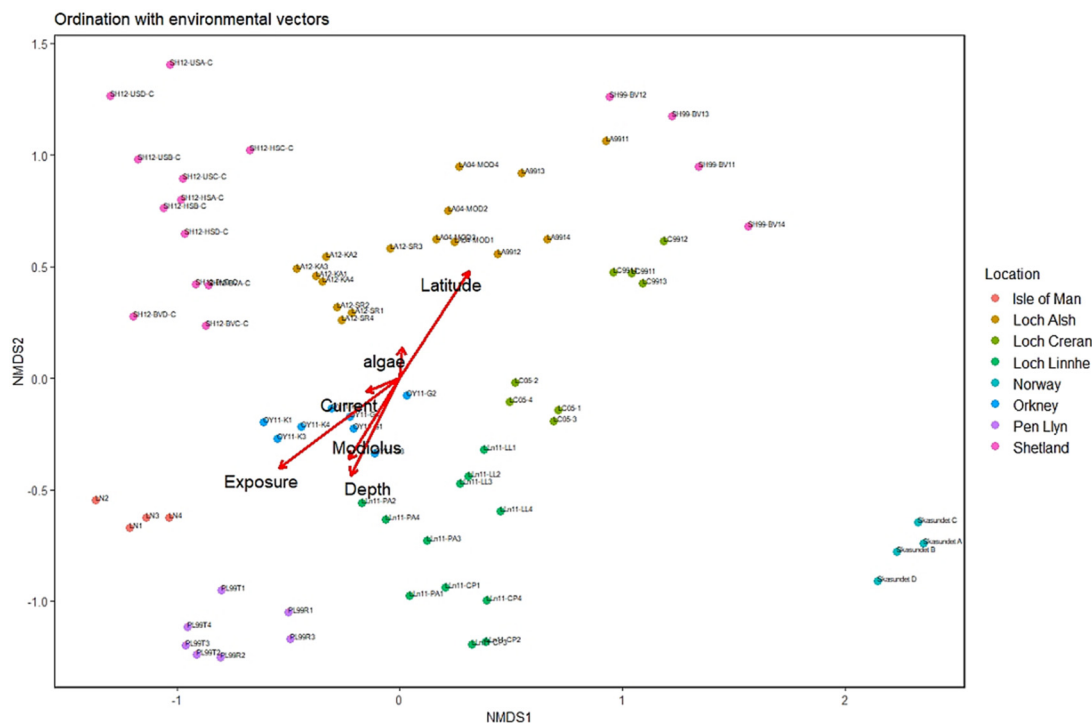
Fig. 7. MDS plot of squared root transformed Bray-Curtis similarity for species and abundance data collected across all horse mussel beds (*M. modiolus*; n = 74). 2D stress value (0.19) represents good representation of multivariate relationships. Environmental factors are plotted as vectors to explain the MDS plot ordination.

Throughout the North Sea and Northeast Atlantic, metrics for sedimentary benthic habitat condition have been based on infaunal macroinvertebrate diversity and assemblage composition (e.g., M-AMBI index: Muniz et al., 2005). These metrics have been developed as indicators in several European Directives (e.g., Borja, 2014; Borja et al., 2009; Borja and Dauer, 2008) using soft seabed benthic communities that are typically collected using van Veen or Day grab-sampling equipment. These indicators are known to respond to human impacts (Kröncke and Reiss, 2010), and rely heavily on the presence of species such as oligochaetes and detritivorous polychaetes that increase in number with pressures (cf Pearson and Rosenberg, 1978). These indicators do not have such high thresholds for biodiversity found in the present study, do not typically use the abundant epifaunal or crevice taxa reported here and would typically be obtained with grab-sampling equipment that is ineffective at sampling large shellfish habitats because they jam the grab jaws open and cause sample loss (authors pers. obs.). It is therefore highly unlikely that normal benthic reference conditions or the traditional methods of collecting samples for it can be applied to biogenic shellfish habitats.

Infaunal species diversity measured using Shannon diversity index (H′) usually ranges from 1.5 to 3.5, rarely exceeds 4, and reaches 5 in the richest benthic assemblages (Magurran, 2004). In the present, and previous studies (e.g. Moore et al., 2013), Shannon diversity reached 5 in some clump samples (Table 1). In the present study Pielou's J values were between 0.6 and 0.9, i.e., very even (Table 1). Higher Pielou's (J) evenness values, close to 1, indicate assemblages where most species are equally abundant but, although an informative index, it is probably too sensitive to variations in sampling effort, the retention of meiofauna and taxonomic zeal (e.g., identifying nematodes, cumaceans and oligochaetes) to be consistently applied and therefore, it is not recommended for monitoring time-series. The poor correlation between abundance of horse mussels and N (Fig. 4) suggests that a gross measure of macroinvertebrate abundance is also not a good indicator. When considering indicator metrics, for protection or restoration, within MPAs or over the wider predominant benthic habitats of the Northeast Atlantic, good indicators must be able to capture and discriminate the sources of natural spatial and temporal variation from anthropogenic impact (e.g. Pearson and Rosenberg, 1978). They

must also be cost effective and subject to low levels of error. Although other diversity indices exist (see Magurran, 2004 and references therein), those here are common in the literature. Overall, in most cases Shannon diversity index (H′) enables the best assessment for conservation management, whilst being stable and characteristically high.

Direct targeting by dredge fisheries is recognised as a universal source of decline for subtidal bivalve habitats such as oysters (Beck et al., 2011; Thurstan et al., 2013). Incidental impact and marked decline from abrasion caused by dredge and trawlers whilst targeting associated queen and king scallops (see Brown, 1989; Strain et al., 2012) has also been responsible for the decline in horse mussel habitats (Fariñas-Franco et al., 2018b; Kenchington et al., 2007; Strong et al., 2016). Marked reductions in diversity, and the abundances of bivalves, malacostracans, ophiuroids and polychaetes have been shown after a single pass of the fishing gear (Cook et al., 2013). Indeed, Shannon diversity has been shown to drop decisively to 1.7 in response to physical impact in Strangford Lough (Fariñas-Franco et al., 2018b). Shellfish density and corresponding diversity are therefore responsive to these prevalent pressures and, a relevant indicator that accounts for these pressures would therefore be a suitable management tool. Furthermore, since shellfish density is so closely linked to diversity, it probably offers the most cost-effective 'rapid' indicator of protective and restorative management success. An added advantage of recording an index of diversity using shellfish density is that remote camera or quadrat photography by scientific divers is unlikely to be damaging to the sensitive shellfish habitats.

Shellfish habitats are "threatened and declining" in the NE Atlantic (OSPAR Commission, 2008, 2009b) meaning that records of un-impacted habitat are relatively scarce: probably more so for species such as European flat oysters because they were a historically significant fishery-target species until their collapse in the late 1800s and early 1900s (Beck et al., 2011; Thurstan et al., 2013). Consequently, there has been much debate amongst conservation managers about what the protection or restoration of shellfish habitats should achieve, especially as these aggregations of shellfish can fit the definition of reefs as biogenic concretions that provide habitats for a large number of epibiotic species under the EU and OSPAR definitions (Halanych et al., 2013; Morris, 2015; Wildish et al., 2009).

Table 4

Results of SIMPER analysis of square root transformed data showing average similarity of faunal taxa contributing to 50 % of the total similarity in *M. modiolus* faunal assemblages within broad geographical locations in the NE Atlantic (see Fig. 1).

(a) Little Ness (Isle of Man)
Average similarity: 65.64 %

Species	Average abundance	Contribution %
Nucula nucleus	8.18	4.53
Abra alba	7.36	3.91
Psamathe fusca	5.53	2.93
Onoba semicostata	6.22	2.86
Exogone (Exogone) naidina	5.5	2.75
Anomiidae indet.	5.81	2.48
Mediomastus fragilis	5.61	2.47
Polycirrus norvegicus	4.9	2.45
Lepidonotus squamatus	4.73	2.36
Pisidia longicornis	4.73	2.33
Mytilidae indet.	3.78	1.96
Paradexiospira (Spirorbides) vitrea	3.6	1.9
Aonides oxycephala	3.63	1.89
Autolytus spp.	4.21	1.85
Harmothoe sp. A	3.66	1.79
Sphaerosyllis taylori	3.59	1.75
Spio armata	3.15	1.61
Nephtys kersivalensis	2.78	1.57
Syllis variegata	3.4	1.52
Nucula sp.	2.96	1.52
Janua pagenstecheri	3.53	1.49
Hiatella arctica	2.87	1.38
Syllis armillaris	3.2	1.37

(b) Pen Llyn (Wales)
Average similarity: 59.45 %

Species	Average abundance	Contribution %
Scalibregma inflatum	8.65	4.14
Pisidia longicornis	7.42	2.97
Abra alba	7.58	2.83
Nucula nucleus	6.45	2.66
Aphelochaeta sp.	7.5	2.64
Exogone (Exogone) naidina	4.66	2.22
Pholoe sp.	5.1	2.03
Polycirrus sp.	4	1.76
Sphaerosyllis hystrix	3.97	1.75
Mediomastus fragilis	3.9	1.66
Caulleriella alata	3.6	1.64
Amphipholis squamata	3.56	1.46
Kurtiella bidentata	5.67	1.45
Parexogone hebes	3.3	1.14

(c) Loch Alsh
Average similarity: 41.73 %

Species	Average abundance	Contribution %
Pholoe inornata	7.08	2.34
Nereimyra punctata	5.82	2
Ophiopholis aculeata	4.11	1.68
Jasmineira elegans	5.82	1.52
Anomiidae indet.	5.58	1.44
Ophiothrix fragilis	4.21	1.43
Nucula nucleus	3.32	1.38
Polynoidae indet. D	3.61	1.34
Eumida sanguinea	3.43	1.29
Ostracoda indet.	5.12	1.22
Ophiocomina nigra	3.37	1.19
Hiatella arctica	2.95	1.1
Trichobranchus glacialis	2.61	1.07
Psammechinus miliaris	3.01	1
Aonides oxycephala	3.15	0.88
Pholoe inornata	7.08	2.34
Nereimyra punctata	5.82	2

(d) Loch Creran
Average similarity: 49.58

Species	Average abundance	Contribution %
Monia patelliformis	4.91	2.85
Dendrodoa grossularia	4.45	2.78
Pisidia longicornis	4.69	2.38
Lepidonotus squamatus	3.56	2.13
Phtisica marina	4	2.04
Nereimyra punctata	3.81	2.03
Pyura microcosmus	2.97	1.81
Ophiothrix fragilis	4.03	1.8

Table 4 (*continued*)

(a) Little Ness (Isle of Man)
Average similarity: 65.64 %

Species	Average abundance	Contribution %
Pholoe inornata	3.32	1.56
Mytilus edulis	2.82	1.52
Hiatella arctica	2.73	1.52
Mytilidae indet.	3.04	1.06
Eupolymnia nebulosa	1.92	0.94
Terebellides stroemii	1.64	0.93

(e) Loch Linnhe
Average similarity: 46.23

Species	Average abundance	Contribution %
Nereimyra punctata	6.24	3.66
Myrianida sp.	4.02	2.34
Harmothoe sp. B	3.36	2.06
Leptochiton asellus	3	1.86
Hiatella arctica	2.56	1.61
Mediomastus fragilis	2.74	1.35
Paradialychone filicaudata	2.22	1.27
Glycera lapidum	2.02	1.27
Pholoe baltica	1.83	1.1
Jugaria granulata	3.42	1.09
Spirobranchus lamarcki	2.04	1.03
Dipolydora coeca	1.92	1.02
Polycirrus norvegicus	1.92	0.93
Monia patelliformis	1.8	0.92
Janira maculosa	1.6	0.89
Actinaria indet.	1.85	0.78
Janira maculosa	1.6	0.89

(f) Orkney
Average similarity: 48.47

Species	Average abundance	Contribution %
Mediomastus fragilis	4.8	2.29
Nereimyra punctata	5.75	2.16
Pisidia longicornis	4.14	1.75
Onoba semicostata	5.63	1.6
Crassicorophium bonellii	6.12	1.51
Pholoe baltica	2.88	1.48
Sphaerosyllis taylori	3.37	1.42
Kefersteinia cirrata	2.91	1.36
Harmothoe sp. A	3.22	1.36
Nucula nucleus	2.23	1.28
Polycirrus norvegicus	2.6	1.25
Hiatella arctica	2.28	1.17
Ophiothrix fragilis	3.07	1.14
Pholoe inornata	2.37	1.11
Mya truncata	2.2	1.08
Leptochiton asellus	1.91	0.95
Scalibregma inflatum	1.82	0.89
Paradoneis lyra	1.81	0.86

(g) Norway
Average similarity: 61.32

Species	Average abundance	Contribution %
Ophiura robusta	5.14	7.82
Ophiopholis aculeata	4.52	6.04
Leptochiton asellus	3.65	5.41
Hiatella arctica	3.65	5.14
Astarte elliptica	2.62	3.03
Limaria loscombi	2.4	2.84
Syllis armillaris	1.57	2.35
Sphaerodorum gracilis	1.93	2.24
Liljeborgia pallida	1.39	1.91

What is clear from the present study is that conservation managers should seek to protect or restore a density of bivalve shellfish that is appropriate to the site and a diversity commensurate with that mussel density, adjusted for the latitude, and site-specific environmental factors such as depth.

5. Conclusion

Overall, the present study shows that measures of biodiversity rather than community type are of greatest potential use as indicators for the protection or restoration of bivalve shellfish habitats. Furthermore, shellfish density is probably a cost-effective 'rapid' indicator of this. There was a significant increase in community diversity and evenness between 2 and 10
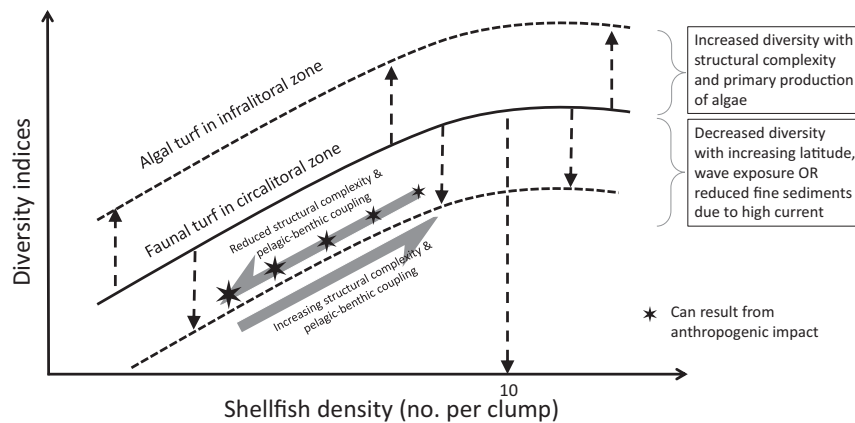
Fig. 8. Conceptual model based on the present study. Biodiversity is greater with higher numbers of horse mussels (*Modiolus modiolus*, L.) in a clump and in shallower water. Biodiversity is lower with increasing latitude and when tidal currents are sufficiently strong to prevent fine muds from being retained in the mussel clump matrix.

mussels per clump reaching a climax at low mussel densities of about 10 per clump. The crucial role horse mussels have as ecosystem engineers was therefore evident. Diversity declined at higher latitudes and with depth but was nevertheless high and stable across horse mussel habitats. Biodiversity and shellfish density are also previously known to respond to impacts from the chief anthropogenic causes of decline (dredging).

Overall, the present study is a potential model for the management of subtidal shellfish habitats. Within the context of the rapid global increase in conservation and restoration of marine biogenic habitats, and more specifically, biogenic shellfish habitats, it would seem that shellfish density indicators of biodiversity are the most appropriate, cost-effective tools for conservation management, so long as targets account for site-specific environmental characteristics.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.161001.

Data availability

All the data used in this paper is available in the supplementary materials

Declaration of competing interest

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CRediT authorship contribution statement

Fariñas-Franco: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing -Original Draft-, Writing – Review & Editing-, Visualization, Project administration. Cook: Conceptualization, Methodology, Writing -Review & Editing. Gell: Writing -Review & Editing. Harries: Investigation. Writing -Review & Editing. Hirst: Investigation. Writing -Review & Editing. Kent: Writing- Reviewing and Editing. MacPherson: Investigation. Data Curation. Moore: Investigation. Mair: Investigation. Porter: Investigation. Writing -Review & Editing. Sanderson: Conceptualization. Methodology. Validation. Investigation. Resources. Writing – Review & Editing-. Visualization. Supervision. Project administration. Funding acquisition.

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