1 Protection alone may not promote natural recovery of biogenic habitats
2 of high biodiversity damaged by mobile fishing gears
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Abstract

The horse mussel *Modiolus modiolus* (L.) is a large marine bivalve that aggregates to create complex habitats of high biodiversity. As a keystone species, *M. modiolus* is of great importance for the functioning of marine benthic ecosystems, forming biogenic habitats used to designate Marine Protected Areas (MPAs). The present study investigates the condition of *M. modiolus* beds historically subjected to intense scallop fishing using mobile fishing gears. The study, conducted seven years after the introduction of legislation banning all forms of fishing, aimed to establish whether natural habitat recovery occurs after protection measures are put in place.

Lower biodiversity and up to 80% decline in densities of *M. modiolus* were recorded across the current distributional range of the species in Strangford Lough, Northern Ireland. The decline in biodiversity in most areas surveyed was consistent with that observed in biogenic reefs impacted by mobile fishing gears elsewhere. Epifauna, including sponges, hydroids and tunicates, experienced the most substantial decline in biodiversity, with up to 64% fewer taxa recorded in 2010 compared with 2003. Higher variability in community composition and a shift towards faunal assemblages dominated by opportunistic infaunal species typical of softer substrata were also detected. Based on these observations we suggest that, for biogenic habitats, the designation of MPAs and the introduction of fishing bans alone may not be sufficient to reverse or halt the negative effects caused by past anthropogenic impacts. Direct intervention, including habitat restoration based on translocation of native keystone species, should be considered as part of management strategies for MPAs which host similar biogenic reef habitats where condition and natural recovery have been compromised.

Keywords

Benthic ecology; Biodiversity; Biogenic reefs; Ecosystem disturbance; Fishing gear; Keystone species; Marine Protected Areas; *Modiolus modiolus*
'Modiolus communities SL.kmz here'

1. Introduction

The marine environment is under intense pressure from human activities which can result in serious negative impacts on established benthic communities, e.g. by reducing their biodiversity and altering their species composition and spatial distribution (Halpern et al., 2008; Hawkins et al., 1999; Worm et al., 2006). Of those anthropogenic stressors, the use of mobile fishing gears (MFG), can have the most serious detrimental effects on the seabed,

leading to habitat fragmentation and simplification, reducing biodiversity and ultimately compromising ecosystem functioning (Cardinale et al., 2012; Watling and Norse, 1998). For example, the capture of commercially valuable species such as oysters (Cranfield et al., 1999), scallops (Bradshaw et al., 2002) and razor clams (Gaspar et al., 2011) on or in the sea bed using MFG may have major impacts on the benthos (Collie et al., 2000; Hughes et al., 2014).

The nature and extent of the impacts caused by MFG have been widely reviewed and depend on the type of gear used, the physical nature of the seabed and the composition of the benthos (Kaiser et al., 2006). Heavier gear, such as the hydraulic dredges used to collect razor clams (Gaspar et al., 2011), have greater impacts on the benthos compared with lighter gear such as trawls (Kaiser, 1998). In addition, communities on biogenic and soft, mixed substrata are regarded to be more vulnerable to impacts by MFG than those associated with other substrata (Kaiser et al., 2006). Once the negative impacts stop, slow-growing taxa with high biomass such as sponges, soft corals and some species of bivalves, are likely to take much longer to recover than communities structured by taxa with shorter life-spans (e.g. infaunal polychaetes). Periods over which MFG are used may be relatively short if the resource is depleted quickly, or long where resources are extensive. For example, landings of the European oyster *Ostrea edulis* in Strangford Lough (Northern Ireland) peaked and collapsed over a 30 year period between 1825 and 1855 (Smyth et al., 2009) whereas in the Foveaux Strait, New Zealand, oysters (*O. chilensis*) have been fished commercially for more than 100 years (Cranfield et al., 2003).

1.1. Background and aims of this study

The horse mussel *Modiolus modiolus* is a large, slow-growing bivalve that can aggregate to form structurally complex biogenic habitats of high biodiversity (Kenchington et al., 2007; Rees et al., 2008), from patchy clumps to extensive elevated beds that qualify as biogenic reefs (Fariñas-Franco et al., 2014). The high biodiversity of epifaunal and infaunal taxa associated with these *M. modiolus* aggregations is promoted by their multi-layered structure consisting of live mussels and shell fragment bound by byssal threads (Fariñas-Franco and Roberts, 2014; Sanderson et al., 2008), and large quantities of biodeposited organic material, e.g. faeces and pseudofaeces (Kent et al., 2017a; Navarro and Thompson, 1997). *Modiolus modiolus* beds also play an important role in the functioning of marine ecosystems and the provision of ecosystem services (Kent et al., 2017b, 2016) and are thus regarded as habitats of great conservation importance on a European and International level (Fariñas-Franco et al., 2014; OSPAR Commission, 2008).

In Strangford Lough, Northern Ireland (Fig. 1), *M. modiolus* was first reported in the 19th century (Dickie, 1857) and regarded as common in the 1950s (Williams, 1953). The importance of the species as a habitat-provider was first acknowledged by Roberts (1975), who identified 57 taxa from just five mussels. Considering Roberts (1975) also estimated that these particular beds occupied an area of up to 1 km², with densities of 170 horse mussels m⁻², their ecological importance as hotspots of benthic biodiversity is clear. These *M. modiolus* communities were later described as 'luxuriant' and regarded as the climax subtidal community in Strangford Lough (Erwin, 1977).

Sublittoral surveys carried out in the 1980s (Brown, 1989; Erwin, 1990) documented high *M. modiolus* densities and high biodiversity throughout the mid-section of Strangford Lough, with some of the species recorded regarded as rare or absent from *M. modiolus* beds elsewhere. To protect these and other marine and terrestrial habitats, the Lough was designated Northern Ireland's first Marine Nature Reserve (MNR), a Special Area of Conservation (SAC) and Special Protected Area (SPA), a pilot Marine Protected Area (MPA) (Cork et al., 2006) and the first Marine Conservation Zone (MCZ) in Northern Ireland (see of Yates et al., 2013 for a thorough review of conservation designations). A key feature in the designation of Strangford Lough as an SAC was the presence of biogenic reefs formed by the horse mussel *M. modiolus* (DOENI, 1994; Roberts et al., 2011).

These conservation designations were implemented after an intensive and highly destructive fishery targeting the queen scallop *Aequipecten opercularis* had developed in Strangford Lough in the early 1980s lasting approximately 10 years (Brown, 1989). The spike in landings of *A. opercularis* between 1985 and 1993 (see Fig. 2 in Strain et al., 2012) coincided with reports in the 1980s and 1990s documenting extensive damage to the *M. modiolus* reefs where *A. opercularis* were usually found, strongly suggesting MFGs (e.g. otter trawls and dredges) were the cause of the decline (Brown, 1989; Service and Magorrian, 1997). According to Strong et al. (2016) a reduction of ca. 54% of the original horse mussel beds occurred from 1986 to 2007, while *M. modiolus* densities, and typical species also declined throughout its distributional range (Roberts et al., 2004). In view of these declines and considering that none of the remaining areas occupied by horse mussels at that time could be regarded as pristine (Magorrian and Service, 1998) the conservation status of the whole Strangford Lough SAC was downgraded to 'unfavourable'.

In view of this decline, and to protect the remaining *M. modiolus* beds, the use of MFG was restricted in 1993 to a small area in the south basin of Strangford Lough (Inshore Fishing Prohibition Regulations (NI) 1993). Ten years later, in December 2003, all forms of mobile fishing were totally banned across the Lough by the Department of Agriculture and

Rural Development for Northern Ireland (DARDNI) under the Inshore Fishing (Prohibition of Fishing and Fishing Methods) (Amendment) Regulations (Northern Ireland) 2003. In order to comply with Article 2.2 of the EU Habitats Directive, the competent authorities at that time (DARDNI and the Department of the Environment - DOE) approved a restoration plan (the “*Modiolus* Restoration Plan” - MRP) that involved monitoring of the remaining *M. modiolus* beds and investigating potential restoration techniques (Anon., 2005; NIAO, 2015). Protection and policing the ban was the responsibility of DARDNI.

The present study aimed to assess natural recovery in the areas of the seabed of Strangford Lough occupied by *M. modiolus* by comparing *M. modiolus* numbers and the diversity and composition of the associated faunal assemblage at the time of the introduction of the total fishing ban (2003) and seven years later (2010). A successful experimental study of restoration that involved aquaculture and translocating *M. modiolus* on to scallop cultch and onto the seabed in Strangford Lough is described elsewhere (Elsässer et al., 2013; Fariñas-Franco et al., 2013; Fariñas-Franco and Roberts, 2014).

2. Materials and Methods

2.1. Study area

Strangford Lough is a large sea inlet 29 km long and 8 km wide at its widest point, covering an area of 150 km². It is located on the northeast of the island of Ireland (Fig. 1) lying between 54° 35' N and 54° 20' N and between 5° 41' W and 5° 34' W. The Lough is connected to the Irish Sea by a 1 km wide channel with fast tidal currents of up to 3.5 m s⁻¹ (Magorrian, 1995). Strangford Lough is divided into two distinct basins (north and south), the boundary roughly marked by an eroded glacial deposit (locally known as ‘The Long Sheelah’, see Fig. 1) located in the Lough’s mid-section. The waters in the south basin are relatively deep and mix freely with the Irish Sea whereas the northern part is characterised by shallower depths and higher water retention (Boyd, 1973; Ferreira et al., 2007; Kregting and Elsässer, 2014). The markedly different hydrographic regimes found in Strangford Lough along with its glacial origin have influenced the development of a wide range of diverse marine habitats (Brown, 1990).

2.2. Data acquisition

A random stratified survey design was used in 2010 to obtain samples representative of the spatial distribution of the *M. modiolus* habitat across the north and south basins of Strangford Lough (Fig. 1 and Appendix A; see also Elsässer et al., 2013). The sampling sites (namely Hadd Rock and Long Sheelah in the north basin, and Brown Rocks and Round Island Pinnacle in the south; Fig. 1) are fully saline, with water depths between 15 and 28 m,

and similar tidal current velocities (Kregting and Elsässer, 2014). These sites had been previously investigated in 2003 during the SLECI project (Roberts et al., 2004).

For consistency, sampling approaches used for the present case study replicated those used during SLECI, as far as it was possible. Scuba divers collected all live *M. modiolus* specimens, empty shell and underlying sediment down to ~10 cm within five random 0.5 x 0.5 m replicate quadrats placed at each of the four locations chosen (N=5x4=20 samples in total; 10 samples per basin). The samples were collected using a trowel and placed into 1 mm mesh bags. The sample bags were sent to the surface using a lift bag and transported to the laboratory in seawater where they were fixed in 4% formalin for 48 hours and washed through a 1mm mesh sieve. The live *M. modiolus* were counted and macrofauna were sorted into major phyla and preserved in 70% ethanol. All taxa were later identified to species level where possible and enumerated. In-situ notes and photographs taken by the divers were used to supplement the data. Nomenclature was checked against the World Register of Marine Species (WoRMs; <http://www.marinespecies.org/>) to ensure naming consistency.

Sample collection was conducted with the knowledge and approval of local authorities, namely DARDNI and DOE (and its Marine Division, known during the study as the Northern Ireland Environment Agency -NIEA) who also funded the studies (i.e. SLECI and the MRP). The fieldwork phase strictly followed a project specific Code of Responsible Research and Restoration Practices to minimise impact on the biogenic reef and the processes that directly or indirectly support this feature.

2.3. Data analysis

2.3.1. Univariate analyses

The biodiversity of the extant *M. modiolus* communities was characterised using a suite of representative metrics and indices, namely total abundance of macroinvertebrate fauna (N), Margalef's species richness (d), Shannon-Wiener's diversity (H') and Pielou's evenness (J). All indices were calculated using the DIVERSE function of Primer[®] 6 (Clarke and Gorley, 2006). Spatial and temporal variability in *M. modiolus* abundance and biodiversity metrics (e.g. N, d, H' and J) was investigated using generalized linear mixed models (GLMMs) with basin and sampling year as fixed factors. In addition, *M. modiolus* abundance was included as a covariate in the GLMMs investigating change in biotic indices. For all GLMMs, replicate quadrats nested within site were used as the random factor to account for potential spatial autocorrelation. Data were fitted to the models using the maximum likelihood method, Poisson (N) and Gaussian error distribution, and identity link function. Significance was

established at $\alpha = 0.05$. Exploration of the data and model residuals were undertaken to confirm assumptions of normality and sphericity and determine model goodness of fit. As a result, N was fourth root transformed to comply with the normality assumptions. It was not necessary to transform the remaining variables.

The relationship between diversity (S) and numbers of *M. modiolus* was also studied to establish its role as a foundation species. Regression analysis and curve fitting were conducted using R (R Development Core Team, 2017; Wickham, 2009), as were all other data manipulation and univariate statistical analyses.

2.3.2. Multivariate analysis

Primer® 6 with the PERMANOVA+ extension (Anderson et al., 2008) was used to investigate differences in composition of the faunal assemblages associated with *M. modiolus* beds before and after the implementation of the total fishing ban, and to identify their characterising taxa. A preliminary fourth root transformation of the raw abundance data was necessary to compensate for overabundant species (e.g. the calcareous tube-building polychaete *Spirobranchus* spp. or tubificid oligochaetes *Tubificoides* spp.). A Bray–Curtis similarity matrix was constructed to identify natural groupings among quadrat samples across the sampling period. The matrix was subjected to a non-metric multidimensional scaling (MDS) algorithm, also in Primer® 6, to represent the samples as points in a two-dimensional scale, the distances between the different points being in the same rank order as the dissimilarities calculated by the Bray–Curtis coefficient. A dummy variable was used to stabilise dispersion of sparse data (Clarke and Gorley, 2006).

Multivariate variance homogeneity was tested using PERMDISP (Anderson et al., 2008) prior to using two-way crossed permutational analyses of variance (PERMANOVA) to study differences in community composition between basins and year. PERMANOVA models were based on 999 permutations of residuals under a reduced model and Type III sums of squares (SS) to account for the asymmetry in the sampling design. Similarity percentage (SIMPER) analyses were carried out using statistically significant PERMANOVA factors as the grouping factor. The aim of the SIMPER analysis was to identify which taxa typified the faunal assemblages for each basin each sampling year, and which taxa were responsible for the differences between them.

3. Results

3.1. Changes in *Modiolus modiolus* density

The distribution (based on occurrence in 0.5 km grid squares) and the densities of *M. modiolus* in Strangford Lough have substantially declined through time (Fig. 2). A major

decline in distribution occurred in the mid-1970s followed by a further 40% decrease in extent between 1975 and 1995 and a slight decrease between 1995 and 2010 (Fig. 2A; Appendix A). Cumulative densities across the known extent of the habitat declined substantially between 1975 and 2003 and further until 2010 (Fig. 2B). Between 2003 and 2010, statistically significant decreases in *M. modiolus* density were recorded across the distributional range (Table 1; Fig. 2C). Mean densities of *M. modiolus* in the north basin showed an 83% reduction, from 80 individuals m⁻² in 2003 to 13.6 individuals m⁻² in 2010 (Fig. 2C). A similar decline (80%) was recorded in the south basin, where mean *M. modiolus* density changed from 64.6 individuals m⁻² in 2003 to 12 individuals m⁻² in 2010 (Fig. 2C).

3.2. Biodiversity and community composition

3.2.1. Univariate analyses

Total abundance of macroinvertebrates (N) was significantly higher in 2010 compared to 2003. This increase was largely limited to the north basin communities, which experienced a substantial increase in the numbers of benthic infauna compared to those in the south basin, albeit not at statistical significance (Table 1; Fig. 3A). According to the mixed model, random variation between sampling sites and between the quadrats sampled was also a key factor explaining the overall variability in N across the sites (Table 1).

In total, 282 benthic taxa were recorded across all *M. modiolus* sites surveyed in Strangford Lough, 219 taxa in 2003 and 251 in 2010 (Appendix A Table A.1). Between 2003 and 2010 total numbers of taxa decreased from 119 to 110 in the north basin whereas an increase, from 100 to 141 taxa, was recorded in the south basin over the same period. Although Margalef's richness index (d) values were not significantly different across basins or between 2003 and 2010, the interaction between year and basin was highly significant (Table 1; Fig. 3B). The boxplots and the post hoc analysis revealed that, while *M. modiolus* faunal assemblages in the north basin experienced a significant reduction in richness in 2010, those in the south basin registered an increase (Table 1 and Fig. 3B). Largely similar patterns were observed for Shannon-Wiener's diversity (H') and Pielou's evenness (J) across all sites (see model results in Table 1 and Figs. 3C, D). In the north basin, H' and J were significantly lower in 2010 than in 2003 (Table 1; Figs 3C, D). In the south basin, H' was significantly higher in 2010 compared to 2003. Similarly, J was significantly lower in the north basin in 2010, experiencing a slight increase (albeit statistically non-significant) in the south basin *M. modiolus* communities in 2010 compared to 2003 (Table 1; Figs. 3C, D).

The number of *M. modiolus* recorded across all sites was not a significant predictive factor for any of the faunal diversity metrics investigated by the mixed models ($P \geq 0.05$; Table 1). However, the relationship between the total number of taxa (S) and the abundance of *M.*

modiolus across all sites surveyed in Strangford Lough was one of exponential decay (increasing form), whereby the rapid increase in macrofaunal diversity with horse mussel numbers levels off at ca. 10 horse mussels m⁻² to an upper asymptote of 55 taxa (Fig. 4A).

To further understand the changes in total abundance of macroinvertebrates and biodiversity after the implementation of the fishing ban, all fauna recorded were grouped according to lifestyle into epifauna, crevice fauna, infauna and vagile taxa (Fig. 4B). Epifaunal taxa declined from 24 to 18 taxa in the north basin *M. modiolus* beds and from 33 to 20 taxa in the south basin ones. The decline in epifauna accounted for most of the overall decrease in biodiversity between 2003 and 2010. In 2010, 64% fewer species of sponges, cnidarians, bryozoans and tunicates were recorded in the north basin *M. modiolus* beds compared to 2003 (Figs. 4B and 5A; in the south basin *M. modiolus* beds, 29% fewer taxa of epifaunal species were recorded over the same period, Figs. 4B and 5B). In contrast, species richness of soft bottom and crevice dwelling macroinvertebrates increased regardless of location (from 35 to 42 taxa in the north basin and from 25 to 55 taxa in the south basin, Fig. 4B). Higher numbers of species of polychaetes, crustaceans (mostly amphipods) and molluscs were responsible for increases of infauna and crevice fauna diversity in the south basin communities (Fig. 5B). Although increases in infaunal polychaetes and crustaceans were also recorded in the north basin communities, mollusc numbers experienced a 40% decrease. Numbers of mobile, opportunistic species including vagile echinoderms (starfish and sea-urchins) and crustaceans (crabs and shrimp) remained relatively constant (Fig. 4B and 5A).

3.2.2. Multivariate analyses

The MDS ordination showed distinct groupings for each basin in 2003 as well as a shift in faunal community composition between 2003 and 2010, more evident in the *M. modiolus* communities sampled in the north basin of the Lough (Fig. 6). PERMDISP results showed significantly higher dispersion in communities at the same sites sampled in 2010 compared to 2003 ($F=26.13$; $P=0.01$). However, the communities were equally spread across time with no significantly different shifts in 2010 compared to 2003 ($F=0.008$; $P=0.91$). PERMANOVA analysis (Table 2) identified a strong significant change in community composition seven years after the implementation of the trawling ban (pseudo- $F_{(1,38)}=18.76$; $P<0.001$) as well as significant differences between the *M. modiolus* communities in the north and south basins (pseudo- $F_{(1,38)}=7.20$; $P<0.001$). The interaction term (basin x sampling year) was also significant (pseudo- $F_{(1,38)}=5.21$; $P<0.001$). Most of the variation in macroinvertebrate composition found by the PERMANOVA model occurred at the random quadrat level (32%)

while sampling year, basin and the interaction between the two respectively explained 29%, 18% and 20% of the variation (Table 2).

According to the SIMPER analysis, in 2003 the similarity within the samples in north basin *M. modiolus* beds was 62.84% (Appendix A; Table A.2a). Fifteen taxa contributed to 70% of the similarities within the community led by *Pisidia longicornis*, *Nucula nucleus*, *M. modiolus* and *Chlamys varia* (responsible for 34% of the cumulative similarity). In 2010 similarity decreased to 48.41%, which reflects a shift in community composition as infaunal species, particularly bivalves, dominated the assemblage (e.g. *N. nucleus*, *Abra alba* or *Thyasira flexuosa*) while *M. modiolus* and *C. varia*, two of the characterising species of the *M. modiolus* assemblages described in Strangford Lough in the past, had disappeared (Appendix A; Table A.2b). In the north basin, dissimilarities between *M. modiolus* assemblages in 2003 and 2010 were 66.1%, with 45 species contributing to 70% of the dissimilarities. The most substantial changes were decreases in abundance of habitat defining taxa, e.g. *C. varia* and *M. modiolus*, and epifauna and crevice fauna such as *Pododesmus patelliformis* (a bivalve usually attached to live *M. modiolus*) and *Pisidia longicornis*. Hermit crab *Pagurus bernhardus* and whelk *Buccinum undatum* were relatively common in 2003 but were not found in the 2010 surveys. SIMPER analysis identified increases in the relative abundance of infaunal polychaetes and amphipods as well as the tunicate *Ascidella aspersa* (Appendix A; Table A.2c).

The average pre-ban (2003) similarity within the south basin *M. modiolus* communities was 60.49% (Appendix A; Table A.2d). The community was dominated by *M. modiolus*, *P. longicornis*, *N. nucleus*, cirratulid polychaetes and brittlestar *Ophiotrix fragilis* (cumulatively responsible for ~40% of the similarities). Twelve species were responsible for 70% of such similarities (Appendix A; Table A.2d). The increase in multivariate dispersion recorded in the south basin in 2010 was matched by a decrease in the average SIMPER similarity, down to 46.5% (Appendix A; Table A.2e). In 2010, the south basin *M. modiolus* assemblage was dominated by *A. aspersa* and detritivorous and suspension feeders such as *P. longicornis*, *Melinna palmata*, *Terebellides stroemi*, *Thyasira flexuosa* and *A. alba*. *Modiolus modiolus* ranked 11th in the list.

In total, 54 species were responsible for 70% of the 66.72% average dissimilarity between the south basin assemblages (Table A.2f) recorded in 2003 and 2010. The change in community composition was largely the result of increases in the tunicate *A. aspersa* and infaunal polychaetes such as *N. latericius*, *S. inflatum* and *T. stroemi* (found in silt and biodebris) and the decline in numbers of *M. modiolus* and a number vagile taxa and epifauna associated with them, such as *O. fragilis*, *A. bifida*, and *P. patelliformis*.

4. Discussion

Ecosystem-based management of fisheries and marine protected areas relies on the identification of pressures and the measurement of impacts to develop adequate mitigation measures (Depestele et al., 2014; Reiss et al., 2014). In Europe, the increasing need to correct historical impacts and inadequate management of the marine environment is mainly driven by international conservation legislation such as the OSPAR agreement (OSPAR Commission, 2008) and European regulations (Directives), chiefly EU Directive 92/43/EEC (the Habitats Directive), and EU Directive 2008/56/EC (Marine Strategy Framework Directive or MSFD). The latter focuses on measuring ecosystem health using a functional approach (Rice et al., 2012) whereby targets and indicators are set up to identify changes in condition resulting from anthropogenic impact (Van Hoey et al., 2010). However, for habitats of high biodiversity and conservation importance it is difficult to document and assess the effects of impacts such as mobile fishing gear because experimental data are scarce and costly to obtain (Buhl-Mortensen et al., 2016). Strangford Lough SAC, where MFG were ultimately banned to protect *M. modiolus* biogenic reefs, provided an opportunity to characterise ecosystem damage by this type of fishing gear, and draw site-specific conclusions on the efficiency of fishing bans to promote natural recovery.

Although negative impacts by MFG vary in intensity and duration in different marine benthic habitats, in general, poorly sorted and hard substrates, and especially those of biogenic origin, are known to be highly sensitive (Bolam et al., 2014; Kaiser et al., 2000; Queirós et al., 2006). For bivalve biogenic reefs, one of the most imperilled marine habitats globally (Beck et al., 2009), overexploitation and habitat degradation have resulted in worldwide population declines including local extinctions. For example, the iconic flat oyster *O. edulis* has disappeared in the wild from much of its historic range in Ireland and the North Sea largely due to overexploitation and habitat degradation from trawling and dredging (Kennedy and Roberts, 2006; Smyth et al., 2009; Thurstan et al., 2013). While not directly targeted as a commercial species, other habitat-forming bivalves in Ireland and in the UK such the flame shell *Limaria hians*, are also known to be sensitive to disruption by MFG and other anthropogenic pressures (Minchin, 1995; Trigg and Moore, 2009).

Our study found a clear hyperbolic relationship between biodiversity and *M. modiolus* density, adding further evidence of its role as a keystone species, cf. Ragnarsson and Burgos (2012). Typical of habitats formed by other keystone taxa (see for example Chapman et al., 2011), this type of relationship suggest a fast decrease in biodiversity under a critical threshold in the numbers of the habitat-forming species, i.e. if individuals are removed or

damaged by trawling. Declines in *M. modiolus* density from historical records of well over 100 mussels⁻² to just under 4 individuals m⁻² in 2010 (this study; Roberts et al., 2011), confirm that, in Strangford Lough, the lower mussel density threshold had been clearly surpassed.

Although evidence of trawling impact on the Strangford Lough *M. modiolus* beds was apparent well before the introduction of the total fishing ban, by 2010 the make-up of the associated biotic assemblage had dramatically changed. Erect, sessile epifaunal taxa including hydroids, sponges, bryozoans and tunicates were worst affected by the scallop fishery, being found in lower abundances or not recorded at all. Example species include the sponges *Lophon hyndmani* and *Mycale* cf. *costarensis*, and the holothurian *Thyonidium drumondii*, all of which have typically been associated with *M. modiolus* in Strangford Lough (Goodwin et al., 2011). These findings are consistent with predictions of wholesale ecological damage by MFG on benthic communities dominated by epifauna, and also with long-term studies showing significant declines in hydroids and other erect taxa (Kaiser et al., 1998; Watling and Norse, 1998).

The scallops *A. opercularis* and *C. varia*, also characteristic of the habitat, were either absent or present in much lower abundances compared with the observations from 2003 (see photographs in Appendix A, Figs. A1 A and B). The declines in the whelk *B. undatum* and decapods (mirroring the findings of Strain et al., 2012), along with the disappearance of queen scallops from areas closed-off to mobile gears, strongly suggest *M. modiolus* beds are essential habitat for a number of commercially important species, as demonstrated by Kent et al. (2016) for a whelk fishery in Wales (UK).

Besides direct removal and abrasion, the pass of MFG over the seafloor resuspends and deposits large quantities of silt (Erftemeijer et al., 2012; Fosså et al., 2002; Jones, 1992), causing further habitat degradation (Depestele et al., 2014). Accumulated resuspended silt can bury and smother epibenthic taxa, including *M. modiolus* (Hutchison et al., 2016) and also drive change in benthic communities. For example, the explosion in numbers of tubificid oligochaetes recorded in some sites and increases in abundance of cirratulids and capitellid polychaetes, amphipods, and infaunal bivalves are signs of degraded benthic habitats (Borja et al., 2000; Collie et al., 2000; Hughes et al., 2014). In Strangford Lough, increased sediment loads have previously been reported during and after the use of MFG, especially in the north basin (Magorrian, 1995; Strong and Service, 2008) where significant decreases in community diversity and evenness were recorded in 2010.

Several factors can affect recoverability of benthic habitats following direct physical disturbance by MFG, but for stressed populations of bivalves, low reproductive output and recruitment failure are one of the most critical (Beck et al., 2009; Gillies et al., 2017; Peterson et al., 1996). *Modiolus modiolus* is a k-strategist with an erratic reproductive cycle and generally low natural recruitment due to high predation pressure of the juvenile stages. As the pediveliger stage prefers to settle amongst conspecifics (Brown and Seed, 1976; Fariñas-Franco et al., 2013), the removal, abrasion and burial of the mussel clumps by repeated passes of a trawl or a dredge will reduce the availability of suitable substrata for larval settlement. Furthermore, physical disruption by MFG also leads to a critical reduction in the size of the reproductive stock and, as a result, damage the fitness of the population due to density-related 'Allee effects' (Amarasekare, 1998; Stephens et al., 1999). Considering that Strangford Lough is also largely closed from external larval sources (Elsässer et al., 2013), reductions of over 50% of the available broodstock (Strong et al., 2016) have probably brought the habitat to an impacted alternate state (Beisner et al., 2003) from which natural recovery is unlikely.

Several factors, other than trawling disturbance, might also be influencing the observed lack of natural recovery, e.g. natural variability, lack of effective fisheries policing, or anthropogenic impacts not linked to demersal fishing. The role of natural variability in the observed declines can be regarded as low, as the physical structure of well established *M. modiolus* beds (and the faunal assemblages associated with them) are known to be stable with time in the absence of anthropogenic pressures (Fariñas-Franco et al., 2014; Holt et al., 1998). In fact, significant shifts in community composition and decreases in biodiversity can be apparent very quickly following disturbance from MFG, e.g. soon after one pass of a scallop dredge (Cook et al., 2013). The damage that MFG cause on *M. modiolus* beds is also known to be long lasting, with numerous examples of damage well after fishing has finished e.g. in Europe (Dinesen and Morton, 2014; Wiborg, 1946) and Canada (Kenchington et al., 2007).

Since the ban on the use of mobile fishing gears was implemented in 2003 DARDNI, through the Inshore Fisheries Branch, was responsible for policing duties. However, fishing pressure from other activities such as pot fishing, not only continued (Strain et al., 2012) but increased because of the ban on MFG (see Appendix 4 in NIAO, 2015). 'No fishing zones' were only implemented in 2011 and 2013, after the present study was conducted, and thus direct or indirect disturbance by potting in certain areas within the remaining *M. modiolus* beds could have played a role in the decline of an already stressed population.

Finally, it should also be considered that *M. modiolus* is a boreal species, known to preferentially spawn at low water temperatures (Fariñas-Franco and Roberts, in press). The Strangford Lough metapopulation is in the southernmost fringe of its distributional range in Europe. Therefore, it could be hypothesised that, similarly to other cold-water species like herring, ocean warming may prevent natural recovery of impacted and stressed *M. modiolus* populations (Hiscock et al., 2004). Furthermore, statistical models have predicted a regression of the existing *M. modiolus* habitats towards higher latitudes under future climate scenarios, eventually disappearing from their current range in the Irish Sea (Gormley et al., 2013).

5. Conclusion

The 'do-nothing' approach to restoration relies on the potential of degraded habitats to recover naturally without further intervention if the stressors are removed, e.g. following the creation of Fishing Exclusion Zones in areas damaged by trawling and dredging (see Table 3 in Elliott et al., 2007). This might be the case for seabed habitats of low sensitivity to MFG, e.g. well-sorted sand (Kaiser et al., 2000; Queirós et al., 2006) and some temperate rocky reefs (see Sheehan et al., 2013). However, for most benthic habitats, especially those of biogenic origin, natural recovery from MFG impacts is generally slow or non-existent as these benthic habitats experience long-term changes in ecosystem function and community composition (Buhl-Mortensen et al., 2016; Kaiser et al., 2000; this study).

The findings of the present study strongly suggest that declines in the density and condition of the keystone species (e.g. *M. modiolus*) are linked to historical damage by demersal fishing. Despite the introduction of fishing bans, these lingering impacts have driven the habitat to an impacted alternate stable state that could further deteriorate if those rates of decline continue. Under this scenario it can be predicted that knock-on effects from MFG will eventually drive *M. modiolus* (the species and the habitat it creates) towards local extinction in Strangford Lough.

Using Strangford Lough as a case study, we conclude that protection alone is not sufficient to promote natural recovery of biogenic reefs that are already too degraded, even if the threat is eliminated and policing is implemented (Conversi et al., 2015; Imeson and van den Bergh, 2006; Yates et al., 2013). In line with current steer in European and international conservation legislation towards habitat restoration, we recommend contemporary surveys to establish the current condition of the habitat followed by environmental restoration using translocation of adult *M. modiolus* (Fariñas-Franco and Roberts, 2014 and references therein). This proactive intervention strategy is straightforward, amenable to experimental

manipulation and likely to be successful in a relatively short period of time if properly planned.

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Figure captions

Fig. 1 Distribution of *M. modiolus* in Strangford Lough (Northern Ireland, UK) in 2010. Black dots are positive records obtained from contemporary ROV surveys (Roberts et al. 2011). Names refer to sampling stations and geographic features mentioned in the main text.

Fig. 2 Temporal decline of *M. modiolus* across its distributional range in Strangford Lough. (A) Number of 0.5 x 0.5 km map grid squares with positive records according to published sources. The historical distribution was retrospectively calculated based on the assumption that a record at a site and at any time forms part of its historical range; (B) Cumulative changes in mean estimated density ($\pm$ SE) from 1970 to 2010 (years). The number of quadrats varied through time (1975 $n = 17$; 2003 $n = 26$; 2010 $n = 30$); (C) Boxplots for *M. modiolus* density in each of the basins surveyed in 2003 and 2010.

Fig. 3 Changes in biodiversity indices in biological communities associated with *M. modiolus* sampled before (2003) and after (2010) the ban on MFG: (A) Total number of individuals (N); (B) Margalef's richness (d); (C) Shannon-Wiener's diversity (H'); and (D) Pielou's evenness (J).

Fig. 4. (A) Abundance of *M. modiolus* recorded across Strangford Lough plotted against the corresponding total number of associated taxa (S) showing fitted hyperbolic curve with 95% confidence intervals; (B) Changes in faunal community classified according to lifestyle (crevice, infauna, sessile, vagile) in the north and south basins of Strangford Lough in 2010 compared to 2003.

Fig. 5. Changes in percentage abundance of major taxonomic groups associated with impacted *M. modiolus* communities before and after the 2003 fishing ban. The boxes represent the inter-quartile range for total number of taxa, with a line indicating the median and whiskers extending to the maximum and minimum observed values (dots represent outlier data).

Fig. 6. nMDS plot of *M. modiolus* faunal samples based on a Bray-Curtis similarity matrix of fourth root transformed macrofaunal abundance data.

773 **Tables**

774 **Table1** Summary results for best fit generalized linear mixed models (GLMM) for changes in *M.*
775 *modiolus* abundance (mussels m⁻²), total macrofaunal abundance (N) and biodiversity and evenness
776 indices in remnant *M. modiolus* habitats studied in Strangford Lough. Factors (levels): Time (2003;
777 2010); Basin (north and south). Random effects: Quadrat (n=42) nested within Site (n=5). Estimate
778 includes ± standard deviation (sd). Significance at α=0.05

Response	Random effects	Intercept	<i>M. modiolus</i> abundance	Year	Basin	Year x Basin	
<i>M. modiolus</i> Abundance	σ quadrat:site=3.65 σ residual=1.37	Estimate t-value p-value	20±1.77 11.27 <0.001	Not included -16.60±2.50 -6.62 <0.001	-3.83±2.40 -1.60 0.12	3.43±3.43 0.99 0.33	
Total abundance of macrofauna (N)	σ quadrat:site=0.51 σ residual=0.01	Estimate t-value p-value	3.55±0.36 9.77 <0.001	0.03±0.02 2.00 0.01	0.98±0.36 -0.29±0.24 -1.20 0.35	-0.66±0.35 -1.93 0.06	
Margalef's richness (d)	σ quadrat:site=0.92 σ residual=0.01	Estimate t-value p-value	5.28±0.65 8.18 <0.001	0.05±0.03 1.82 0.08	-0.77±0.64 -1.20 0.24	-0.46±0.43 -1.06 0.40	3.69±0.61 6.00 <0.001
Shannon- Wiener's diversity (H')	σ quadrat:site=0.25 σ residual=0.10	Estimate t-value p-value	2.65±0.22 12.16 <0.001	-0.005±0.008 -0.67 0.50	-0.90±0.19 -4.81 <0.001	0.02±0.20 0.12 0.91	1.17±0.18 6.45 <0.001
Pielou's evenness (J)	σ quadrat: site=0.07 σ residual=0.09	Estimate t-value p-value	0.78±0.06 12.71 <0.001	-0.003±0.002 -1.31 0.20	-0.25±0.06 -4.37 <0.001	0.03±0.05 0.53 0.65	0.24±0.05 4.33 <0.001

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784 **Table 2** Two-way PERMANOVA model results for differences in faunal community composition
 785 between *M. modiolus* assemblages in the north and south basins of Strangford Lough, sampled just
 786 before the introduction of a total fishing ban in 2003 and seven years later. Significant P values are
 787 indicated in bold. Total unique permutations = 999.

Source	d.f.	SS	MS	Pseudo-F	P
Year (2003, 2010)	1	19451	19451	18.76	0.001
Basin (north/south)	1	7464.4	7464.4	7.20	0.001
Year x Basin	1	5404.7	5404.7	5.21	0.001
Residual	38	39398	1036.8		
Total	41	71372			

788 *d.f.* = degrees of freedom; *SS* = Sums of squares; *MS* = Mean square.

0 0.3 0.6 1.2 Kilometers

Transform: Fourth root

Resemblance: S17 Bray Curtis similarity (+d)

2D Stress: 0.13

a

b

Figure A.1. Underwater video captures showing *Modiolus modiolus* communities in Strangford Lough. The site surveyed is the Hadd Rock area, in the north basin of the Lough (see Fig. 1). (a) The association between the scallop *Chlamys varia* and the horse mussel *M. modiolus* was still present in 2003. (b) In 2010 the scallops have disappeared while reef elevation and complexity have been substantially reduced, with re-suspended mud and empty *M. modiolus* shells dominating the seabed. Photos: SLECI (a) and MRRP (b).

Table A.2. Full results of SIMPER analysis for *Modiolus modiolus* habitats in Strangford Lough. The table shows average abundance and similarity of fourth root transformed abundances of faunal taxa contributing to 70% of the total similarity within *M. modiolus* assemblages in the north basin (a, b) and south basin (d, e), and 40% of the dissimilarity before (2003) and after (2010) the fishing ban introduced in Strangford Lough (c; f).

(a) 2003 (Pre ban) & North Basin: Average similarity: 62.84			
Species	Average abundance	Average similarity	Contribution %
<i>Pisidia longicornis</i>	2.86	5.35	8.51
<i>Ophiotrix fragilis</i>	2.48	4.50	7.15
<i>Nucula nucleus</i>	2.42	4.18	6.65
<i>Modiolus modiolus</i>	2.11	4.07	6.48
<i>Mimachlamys varia</i>	1.86	3.30	5.24
<i>Pododesmus patelliformis</i>	1.82	3.19	5.07
<i>Abra alba</i>	1.81	3.10	4.80
<i>Pherusa plumosa</i>	1.41	7.66	3.91
<i>Lepidonotus squamatus</i>	1.48	2.32	3.70
<i>Amphipholis squamata</i>	1.26	2.22	3.53
<i>Mytilus edulis</i>	1.44	1.66	3.43
<i>Antedon bifida</i>	1.42	1.87	3.39
<i>Alcyonidium diaphanum</i>	1.33	2.03	3.23
<i>Musculus subpictus</i>	1.11	1.88	2.99
<i>Terebellides stroemi</i>	1.22	1.71	2.72
(b) 2010 (Post-ban) & North Basin: Average similarity: 48.41			
Species	Average abundance	Average similarity	Contribution %
<i>Nucula nucleus</i>	2.64	6.35	13.12
<i>Abra alba</i>	2.49	6.15	12.71
<i>Ophiotrix fragilis</i>	2.02	3.71	7.67
<i>Pisidia longicornis</i>	2.32	3.11	6.43
<i>Thyasira flexuosa</i>	1.13	2.45	5.06
<i>Ophiocomina nigra</i>	1.17	2.42	4.99
<i>Pherusa plumosa</i>	1.16	2.32	4.80
<i>Antedon bifida</i>	1.17	1.78	3.67
<i>Notomastus latericeus</i>	1.09	1.74	3.58
<i>Pholoe inornata</i>	1.07	1.72	3.56
<i>Fimbriosthenelais zetlandica</i>	0.91	1.68	3.46
<i>Sphaerodorum gracilis</i>	0.90	1.52	3.13
(c) Community change 2003 vs 2010 North Basin			
Average dissimilarity = 66.05			
Species	Group 2003	Group 2010	Contribution%
	Average abundance	Average abundance	
<i>Mimachlamys varia</i>	1.86	0.00	3.22
<i>Modiolus modiolus</i>	2.11	0.64	2.76
<i>Pododesmus patelliformis</i>	1.82	0.33	2.69

<i>Pisidia longicornis</i>	2.86	2.32	2.65
<i>Mytilus edulis</i>	1.44	0.00	2.51
<i>Amphipholis squamata</i>	1.26	0.00	2.17
<i>Alcyonidium diaphanum</i>	1.33	0.20	2.15
<i>Asciidiella aspersa</i>	1.10	1.49	2.13
<i>Lepidonotus squamatus</i>	1.12	0.42	2.12
<i>Buccinum undatum</i>	2.48	0.00	1.95
<i>Ophiotrix fragilis</i>	0.00	2.02	1.94
<i>Notomastus latericeus</i>	1.11	1.09	1.77
<i>Musculus subpictus</i>	0.20	0.20	1.69
<i>Thyasira flexuosa</i>	0.97	1.13	1.67
<i>Nassarius reticulatus</i>	0.92	0.00	1.64
<i>Sthenelais boa</i>	0.99	0.00	1.64
<i>Hiatella arctica</i>	0.20	0.10	1.61
<i>Pholoe inornata</i>	0.00	1.07	1.61
<i>Sphaerodorum gracilis</i>	0.00	0.90	1.59
<i>Fimbriosthenelais zetlandica</i>	0.00	0.91	1.54

(d) 2003 (Pre ban) & South Basin: Average similarity: 60.49

Species	Average abundance	Average similarity	Contribution %
<i>Nucula nucleus</i>	2.06	4.73	7.82
Cirratulidae	2.15	4.69	7.76
<i>Pisidia longicornis</i>	2.12	4.68	7.74
<i>Modiolus modiolus</i>	1.96	4.54	7.50
<i>Ophiotrix fragilis</i>	1.93	4.18	6.90
<i>Abra alba</i>	1.91	3.99	6.60
<i>Pododesmus patelliformis</i>	1.47	3.36	5.55
<i>Antedon bifida</i>	1.48	3.03	5.01
<i>Lepidonotus squamatus</i>	1.16	2.70	4.46
<i>Amphipholis squamata</i>	1.08	2.32	3.83
<i>Terebellides stroemi</i>	1.14	2.16	3.57
<i>Pherusa plumosa</i>	1.13	1.96	3.24

(e) 2010 (Post-ban) & South Basin: Average similarity: 52

Species	Average abundance	Average similarity	Contribution %
<i>Asciidiella aspersa</i>	2.22	3.24	6.69
<i>Scalibregma inflatum</i>	1.52	2.43	5.22
<i>Terebellides stroemi</i>	1.53	2.24	4.82
<i>Owenia fusiformis</i>	1.33	2.16	4.65
<i>Nucula nucleus</i>	1.40	2.15	4.63
<i>Pisidia longicornis</i>	1.58	2.07	4.46
<i>Thyasira flexuosa</i>	1.13	1.83	3.94
<i>Pholoe inornata</i>	1.11	1.78	3.83
<i>Lumbrinereis latreilli</i>	1.25	1.72	3.70
<i>Melinna palmata</i>	1.01	1.68	3.61
<i>Modiolus modiolus</i>	1.08	1.44	3.10

<i>Notomastus latericeus</i>	1.04	1.40	3.01
<i>Fimbrosthenelais zetlandica</i>	0.91	1.28	2.75
<i>Pherusa plumosa</i>	1.04	1.11	2.39
<i>Nephtys hystrix</i>	0.81	1.05	2.27
<i>Timoclea ovate</i>	0.80	0.97	2.09
<i>Abra alba</i>	0.98	0.94	2.03
<i>Pista cristata</i>	0.74	0.93	2.00
Cirratulidae	0.84	0.92	1.97
<i>Lysianassa ceratina</i>	0.93	0.79	1.70
<i>Ampelisca typica</i>	0.73	0.74	1.59

(f) Community change 2003 vs 2010 South Basin

Average dissimilarity = 66.72

Species	Group 2003	Group 2010	Contribution%
	Average abundance	Average abundance	
<i>Ascidella aspersa</i>	1.13	2.22	2.36
<i>Ophiotrix fragilis</i>	1.93	0.53	2.34
Cirratulidae	2.15	0.84	2.26
<i>Lumbrineris latreilli</i>	0.00	1.25	2.20
<i>Abra alba</i>	1.91	0.98	1.83
<i>Amphipholis squamata</i>	1.08	0.00	1.82
<i>Musculus subpictus</i>	0.90	0.78	1.79
<i>Notomastus latericeus</i>	0.00	1.04	1.72
<i>Melinna palmata</i>	0.00	1.01	1.71
<i>Scalibregma inflatum</i>	0.68	1.52	1.70
<i>Antedon bifida</i>	1.48	0.79	1.68
<i>Leptasterias muelleri</i>	0.96	0.00	1.61
<i>Modiolus modiolus</i>	1.96	1.08	1.57
<i>Fimbriosthenelais zetlandica</i>	0.00	0.91	1.51
<i>Pisidia longicornis</i>	2.12	1.58	1.48
<i>Lysianassa ceratina</i>	0.00	0.93	1.46
<i>Mya truncata</i>	0.87	0.00	1.44
<i>Nephtys hystrix</i>	0.00	0.81	1.41
<i>Sthenelais boa</i>	0.84	0.00	1.38
<i>Nephtys incisa</i>	0.93	0.35	1.36
<i>Pododesmus patelliformis</i>	1.47	0.74	1.35
<i>Ophiocomina nigra</i>	0.81	0.10	1.31
<i>Hiatella arctica</i>	0.94	0.32	1.30
<i>Ampelisca typica</i>	0.00	0.73	1.27