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ESTIMATING THE HISTORICAL DISTRIBUTION, ABUNDANCE AND ECOLOGICAL CONTRIBUTION OF *MODIOLUS MODIOLUS* IN STRANGFORD LOUGH, NORTHERN IRELAND

James Asa Strong, Matthew Service and Heather Moore

James Asa Strong (corresponding author; email: J.Strong@hull.ac.uk), Institute of Estuarine and Coastal Studies, University of Hull, Cottingham Road, Hull, HU6 7RX, UK, and Agrifood and Biosciences Institute, Newforge Lane, Belfast BT9 5PX, Northern Ireland; Matthew Service, Agri-Food and Biosciences Institute, Newforge Lane, Belfast, BT9 5PX, Northern Ireland; and Heather Moore, Agri-Food and Biosciences Institute, Newforge Lane, Belfast, BT9 5PX, Northern Ireland.

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ABSTRACT

Strangford Lough is a large sheltered marine inlet in Northern Ireland. It is also a designated Special Area of Conservation based partially on the presence of an extensive area of *Modiolus modiolus* (Linnaeus, 1758) biogenic reef. However, this feature is believed to have declined substantially over the last 40 years. The objective of the study was to estimate the size of this decline both in terms of extent and abundance. This study combined (i) new survey data (a dedicated multibeam echo-sounder survey of the Lough), (ii) a habitat suitability model for *M. modiolus* with (iii) historical diver surveys to estimate the extent and abundance before 1985 (before the suspected period of greatest decline), 2003 (during the introduction of a ban on mobile fishing gear in the Lough) and 2007 (the most recent diver survey available).

Estimations indicate that the extent reduced from approximately 12.6km^2 in 1986 to just 5.7km^2 by 2007 and the abundance declined by 87% in the same period. The decline has implications both for the remaining population of *M. modiolus* and ecosystem functionality within the Lough, which are both discussed in detail.

INTRODUCTION

Until recently, Strangford Lough (Northern Ireland) contained an extensive area of biogenic reef created by *M. modiolus* (Roberts *et al*., 2004). Although *M. modiolus* is present on many coarse substrata along the Atlantic coasts of North America and northern Europe (Holt *et al*., 1998), the biogenic structures in Strangford Lough were on soft sediment substrata in a sheltered environment (Roberts, 1975), making the reef habitat uniquely important within the Lough and regionally unusual. The biogenic reef created by *M. modiolus* in Strangford Lough is associated with rich and abundant epifaunal and infaunal communities (Magorrian and Service, 1998). Very high levels of species richness have also been reported for other beds of *M. modiolus*, e.g. 230 taxa from just seven small cores from the Pen Llŷn *M. modiolus* reef (north-west Wales) (Rees *et al*., 2008) and 270 taxa associated with the reef near the Isle of Man (unpublished data reported in Holt *et al*., 1998). In view of the biodiversity associated with *M. modiolus* and international concern regarding the status of this species, it has been included on the OSPAR 'threatened and/or declining species and habitats' list in 2008 (OSPAR, 2009). Within the UK, beds of *M. modiolus* have a specific Biodiversity Action Plan that details the management necessary for the conservation of this species (as required by the Convention on Biological Diversity).

Suspension feeding bivalves are of considerable importance as primary consumers in many marine systems and play a significant role in energy transfer between pelagic and benthic realms (Peterson and Black, 1987; Newell, 2004), and between trophic levels (Navarro and Thompson 1996). This is also apparent for *M. modiolus* as high densities have been observed to deplete seston (Wildish and Kristmanson, 1984). Based on the historical abundance *of M. modiolus* within the Lough (Roberts, 1975), it is likely that this species was highly abundant in the Lough and contributed greatly to the character and functioning of the local ecosystem (Roberts *et al*., 2004).

In light of the biodiversity associated with *M. modiolus* and the contribution of the reef to ecological functionality in Strangford Lough, it was listed as a conservation 'feature' when the Lough was designated a Special Area of Conservation (SAC) under the 1992 EC Habitats Directive in 1999. As a SAC, the EC Habitats Directive requires that Strangford Lough is managed to maintain the specified features in a 'favourable conservation status', ensuring that deterioration of the habitats and/or species for which the Lough was designated is avoided. The condition and distribution of the *M. modiolus* in Strangford Lough has been the source of considerable interest recently following numerous reports that the biogenic reef has decreased substantially in extent and density. This decline was probably initiated by a peak in demersal fishing effort in the 1980s (Service and Magorrian, 1997; Roberts *et al*., 2004; Roberts *et al*., 2011; Strain *et al*., 2012) followed by super-abundant densities of the predator starfish, *Asteria rubens*, and a competitive solitary tunicate, *Ascidella aspersa* (J.A Strong *pers. obs*. 2004). Speculation about the magnitude of the decline varies greatly due to the multiplicity of methods used to study *M. modiolus* in the Lough historically and the absence of dedicated efforts to combine historical data into maps of distribution.

The debate regarding the historical and current distribution and status of *M. modiolus* reef has now reached a point where solid scientific evidence is required to (i) progress the appropriate management of the remaining population, (ii) understand the ecological implications of the decline for Strangford Lough and (iii) judge the applicability of restoration and, if appropriate, set restoration targets. Point three has had profound implications for the management of the Lough as the setting of unrealistic targets for restoration may exacerbate several of the existing management failures within the Lough reported by the NIAO (2015). The main aim of this work was to estimate the distribution of *M. modiolus* in Strangford Lough at three points in time. The first time point, before 1986 (actually a composite of diver observations from 1968 to 1985), was presumed to reflect the distribution before a substantial peak in fishing effort in the Lough in the mid-1980s (Roberts *et al*., 2004) and therefore before the period of greatest decline. As demersal fishing was occurring before 1986, this year cannot be assumed to represent a pristine distribution but rather the earliest available baseline from before the period of greatest fishing activity. In 2003 (the second time point), a diver survey suggested that the distribution of *M. modiolus* had undergone a significant but unquantified contraction (Roberts *et al*., 2004) and marks the point where a ban on trawling and dredging within the Lough was imposed to protect the remaining *M. modiolus*. It was suspected that the population of *M. modiolus* may still be declining (Roberts *et al*., 2011). The most recent diver survey, undertaken in 2007 (third time point), was used to estimate the distribution and examine this suggestion. Based on this, the primary objectives of this investigation are to:

1. predict the distribution of the *M. modiolus* biogenic reef before 1986 (before the period of greatest pressure), in 2003 (implementation of ban on mobile fishing gear) and in 2007 (most recent survey data) through the interpolation of point data;
2. generate a generic habitat suitability model to refine the boundaries of the interpolated distributions;
3. examine the distribution and temporal change of *M. modiolus* in relation to the predicted broad-scale substrata and physical seabed features;
4. combine the refined distributions with historical density data to estimate population size at the three points in time; and
5. explore the contribution of *M. modiolus* over time to the ecological functioning of the Lough.

MATERIALS AND METHODS

STUDY SITE

Strangford Lough is a marine inlet situated in the south-east of Northern Ireland (UK). The Lough is approximately 31km long and varies in width from 4 to 7km. It opens into the Irish Sea by a narrow channel known as the Narrows. It is a complex area of islands, shoalings, large areas of intertidal shoreline and subtidal areas down to a depth of 70m. The Lough has a wide range of habitats due to the glacial history and complex hydrography of the area.

APPROACH TO THE ANALYSIS

Other than for the first time period (i.e. the distribution in 1968–85 that is presumed to predate a substantial peak in demersal fishing effort), the distribution of *M. modiolus* in Strangford Lough has been modified greatly by biological and anthropogenic factors. The appropriate information to reflect these factors as predictor variables was not available. As such, the use of a standard predictive habitat mapping technique was not suitable for this analysis. An alternative approach for estimating the distribution, used for this study, combined the interpolation of diver observations (presence/absence data) with a habitat suitability model for *M. modiolus* in Strangford Lough. The entire approach, including the assessment of habitat occupation and abundance, followed five methodological steps, namely:

1. interpolation of diver observations within each of the three time periods to produce coarse presence/absence maps (objective 1);
2. modelling habitat suitability for *M. modiolus* in Strangford Lough (objective 2);
3. refining the boundary of the interpolated presence/absence map of *M. modiolus* (product of step 1) with the habitat suitability map (product of step 2) for each time period;
4. modelling the broad-scale habitat and seabed features to examine the relationship between these features and the refined distribution of *M. modiolus* (product of step 3) over time (objective 3); and
5. multiplying the values of extent from the refined maps (product of step 3) by the observed density values of *M. modiolus* to obtain estimations of total abundance within the Lough for the three time periods (objective 4).

Step 1: Interpolation of diver observations to produce presence/absence maps

Three diver-based surveys of *M. modiolus* occurred in 1968–85 (termed as '<1986' from this point forward), 2003 and 2007—the number and source of the diver records used for the three predictions are shown in Table 1 and their spatial distribution in Figure 2. These years were the only years associated with large diving surveys (> 100 stations distributed throughout the Lough) and therefore represented the best years for analysis. It has been assumed that the observations from before 1986 are reflective of an 'unimpacted' state. This is because Strangford Lough was extensively observed by diver surveys as part of the Northern Irish Sublittoral Survey (Erwin *et al*., 1986). This detailed examination of the Lough reported that the *M. modiolus* reef was in good condition and no decline was apparent. As such, the observations from before 1986 have been combined into one block of observations.

It is also noteworthy that the total number of dive stations in 2007 was about twice that of previous observation periods. Furthermore, over 400 Remotely Operated Vehicle (ROV) stations were taken before the 2007 dive survey to stratify the dives into suspected presence areas. This has increased the relative number of presence observations in 2007 but they can be seen to fall in a much smaller area than that of previous surveys.

All diving surveys were conducted by trained marine biologists. Dive entry positions were recorded with DECCA before 1984 and GPS in 2003 and 2007. Diver logs from <1986, 2003 and 2007 were summarised to presence/absence records for *M. modiolus*.

Before undertaking any analysis, a random selection of 10% of the presence/absence observations was removed from each of the <1986, 2003 and 2007 datasets. These subsets were reserved for use as validation datasets within confusion matrices. Cohen's kappa and classification accuracy were calculated for the habitat suitability model (using the <1986 presence and absence validation dataset) and the individual distributions (using the specific validation subset relevant for each distribution).

The presence/absence observations from <1986 were used for the production of the <1986 interpolation surface. For the 2003 interpolation surface, the following observations were combined: (i) presence/absence observations from 2003 and (ii) presence observations from 2007. Finally, the 2007 interpolation surface used only the presence/absence observations from 2007. The justification for combining presence observations from 2007 with the 2003 dataset is that *M. modiolus* is a long-lived species and if it was observed as adults in 2007, it would have almost certainly been present at the same location in 2003.

For the production of interpolated surfaces, the presence/absence point data were converted into a raster surface with a 2 metre grid size with a transverse Mercator projection. The 'Euclidean allocation' tool within ArcMap version 10.1 (ESRI 380 New York Street, Redlands, CA 92373-8100, USA) attributed each raster cell with a presence or absence probably based on the Euclidean distance. Probabilities of presence greater than 0.5 were classed as presence for *M. modiolus* and absent for probability less than 0.5.

Step 2: Modelling habitat suitability for M. modiolus

A habitat suitability model was produced for *M. modiolus* in Strangford Lough to refine the presence/absence maps generated by step 1. The model used three sources of information: (i) a recent multibeam bathymetry survey of the Lough, (ii) an existing hydrodynamic model and (iii) diver-based presence/absence observations from the three periods to train the model. These three sources of information were combined within (iv) a Maximum Likelihood model.

(i) Multibeam echo-sounder survey of Strangford Lough

Multibeam Echo Sounder data were collected aboard the Department of Agriculture and Rural Development fisheries protection vessel Banríon Uladh in December 2012. Multibeam echo-sounder depth soundings were collected with a Kongsberg EM3002 in a dual head configuration (Kirkegårdsveien 45, NO-3616 Kongsberg, Norway), attitude and navigation with a Kongsberg Seapath 200 and GPS height with a Hemisphere R320 GPS (8444 N 90th Street, Suite 120, Scottsdale, AZ, USA). Sound velocity profiles were collected with an YSI Castaway CTD (1700/1725 Brannum Lane, Yellow Springs, Ohio 45387-1107, USA).

Multibeam echo-sounder depth soundings were processed in CARIS (115 Waggoners Lane, Fredericton, New Brunswick, Canada). Precise Point Positioning in POSPac (Applanix, 85 Leek Crescent Richmond Hill Ontario L4B 3B3 Canada) was used to refine the GPS height. The vertical offshore reference frame model, provided by the United Kingdom Hydrographic Office, was used to reduce all GPS heights to Chart Datum. Bathymetry was exported from CARIS into ArcMap as a grid with 2m spatial resolution. Seabed slope and aspect (easting and northing) were derived from the imported bathymetry grid in ArcMap using the 'Slope' and 'Aspect' tools respectively.

(ii) Hydrographic model

Hydrodynamic information was derived from Ferreira *et al*. (2007). The model generated predicted values for the flood and ebb tidal direction and speed for a 1km x 1km grid. Although eight equidistant depth layers were available, only the surface layer was used and exported to ArcMap. The grid was then interpolated using the 'Kriging' tool to produce a raster surface with the same extent and grid size as the bathymetry data. It is acknowledged that the original grid size was substantially larger than the bathymetry grid (2m x 2m) and represents a very high level of interpolation. Adjustment of the bathymetry grid to match the hydrodynamic grid was considered but represented a substantial loss of information from multiple important variables and a disconnection in scale between the predictor variables and the presence/absence training data (a 90% subset of the total dataset).

(iii) Presence/absence data for <u>M. modiolus</u>

The modelling of habitat suitability combined the diver observations from all three time periods into one database (Table 1 and Figure 1). However, absence records from 2003 and 2007 were excluded from the training data set for the habitat suitability modelling as it was not known whether *M. modiolus* were absent because of a lack of habitat suitability or an excess of anthropogenic pressure. The absence observations in the <1986 dataset were used in the creation of the habitat suitability model. It has been assumed that the observations from before 1986 are reflective of an 'unimpacted' state. As such, the observations reporting an absence of *M. modiolus* from before 1986 are believed to relate to habitat suitability rather than anthropogenically-induced loss, hence their inclusion in the training of the model used for the prediction of suitable habitat.

(iv) Maximum Likelihood Classification

Habitat suitability for *M. modiolus* in Strangford Lough was modelled using Maximum Likelihood Classification, which is widely accepted as the most appropriate method (Bailey and Gatrell, 1995; Eastman, 1997). The input predictor variables used were (i) bathymetry (Figure 3b), (ii) slope (Figure 3f), (iii) aspect (northing and easting) (Figure 3a), (iv) flood tide speed and direction (northing and easting) (Figure 3c) and (v) 'hardness' (Figure 3d) and 'roughness' (Figure 3e) surfaces from a RoxAnn survey undertaken in 2003. Backscatter data, obtained during the MBES survey, is typically influenced by the nature of the superficial sediments and can be variable over time and may be different to that observed in the 1980s. As such, backscatter data were excluded from the analysis. However, several RoxAnn surveys have been carried out within the Lough undertaken by the Agri-Food and Biosciences Institute. In the absence of extensive ground truthing it is not possible to separate the acoustic signatures of live *M. modiolus* from dead shell accumulations, hence it was not possible to use these datasets to directly classify the presence/absence of *M. modiolus*. However, a RoxAnn survey undertaken in 2003 may provide early indicators of the hardness and roughness of the seabed. These parameters are likely to be useful indicators of substratum type and were therefore also included as predictor variables in the habitat suitability model. All of the predictor variables were gridded at 2 metres and a subtidal analysis mask restricted the model output to areas to below MLWS.

Signatures (i.e. the typical values for the predictor variables associated with areas of 'presence' and 'absence') were based on the intersection of presence/absence point data and the underlying predictor layers and generated with ESRI's 'Create Signatures' tool. The 'Maximum Likelihood Classification' tool then assesses the predictor variable values for each pixel and uses a probability function, associated with the signatures, to allocate them to either presence or absence (Eastman, 1997).

Step 3: Refinement of the interpolations with the habitat suitability tool

The interpolated raster maps for <1986, 2003 and 2007 generated in step 1 provided coarse and simplistic representations of the distribution of *M. modiolus*. To provide a more realistic distribution, the interpolated surfaces were 'clipped' by the habitat suitability model (i.e. any 'presence' area within the interpolation that overlapped with habitat predicted to be unsuitable by the model output was deleted). Based on the absence of suitable predictor variables, this was considered the most appropriate approach for estimating the distribution of this species.

Step 4: Modelling broad-scale benthic habitats and seabed features in Strangford Lough

The (i) broad-scale substrata and (ii) physical seabed features were modelled to understand the relationship between these features and the distribution of *M. modiolus* over time. The resulting habitat and seabed feature surfaces were then clipped by the <1986, 2003 and 2007 distributions to extract the habitat occupation by *M. modiolus* over time in Strangford Lough.

(i) Broad-scale substrata

The predictor variables used to model the broad-scale substrata were (i) bathymetry, (ii) aspect (northing and easting represented separately), (iii) slope, (iv) rugosity, (v) hydrodynamics (flood speed and direction) (northing and easting represented separately) and (vi) 'hardness' and 'roughness' surfaces from a RoxAnn survey undertaken in 2003. As the multibeam survey and ground-truthing observations were separated by over 40 years, it was not considered appropriate to use backscatter information (reflective of the character of the surficial sediments) as it may have changed significantly in the intervening years.

Substrata records used for training the classification signatures were provided by the Northern Ireland Sublittoral Survey (Erwin, 1986). The dataset was selected as the best time point for modelling the broad-scale substrata based on it being the earliest available habitat survey (predating much of the period of decline) with a high number of observations spread throughout the Lough. Each diver record was classified into one of five broad-scale substrata.

The five broad-scale substrata for Strangford Lough were again modelled using the 'Create Signatures' and 'Maximum Likelihood Classification' tools in ArcMap. Signatures (i.e. the typical values for each predictor variable associated with each of the five classes) were then generated based on the intersection of habitat point data and the underlying predictor layers with ESRI's 'Create Signatures' tool. The Maximum Likelihood classification tool then used the signatures to allocate each pixel to one of the five substratum classes.

(ii) Seabed features

Benthic Terrain Modeler tools (Wright *et al.*, 2005) installed in ArcMap and were used to calculate the benthic positional index (BPI) at 1-5 (fine BPI) and 25-250 (broad BPI). Rather than using the classification dictionary, both layers were combined into five classes using the ESRI ArcMap 'Isocluster' tool. The resulting classes related to (i) trough basin, (ii) trough slopes, (iii) flat plain, (iv) ridge slope and (v) ridge tops.

Step 5: Estimations of abundance

Estimations of the historical abundance of *M. modiolus* in Strangford Lough were based on the combination of the refined distributions with historical density values from the literature (Table 2). These published densities were specific for particular areas within the Lough. The predicted distributions produced within this study were split into these specific areas and the density values located within these areas used for the calculation of abundance. There was a sizeable level of variation associated with the historical density values from some sites and it is acknowledged that the calculation of total abundance can only provide an indication of population size and the absolute values are highly uncertain.

Step 6: Estimations of the contribution of M. modiolus to ecosystem functions within Strangford Lough

To measure the ecological importance of *M. modiolus* in Strangford Lough, estimations of the abundance were combined with observations of body weight values (Roberts *et al*., 2011) and literature values on (i) clearance rate (PML, 2010) for filtration capacity and (ii) biodeposit and waste production (Navarro and Thompson, 1996; Navarro and Thompson, 1997 respectively) for the cycling of suspended matter and nutrients. Navarro and Thompson (1997) examined the biodeposit production over a range of chlorophyll concentrations during a phytoplankton bloom. The two experiments with the chlorophyll values closest to the mean winter and summer chlorophyll concentrations reported for Strangford Lough by Service *et al*. (1996) were selected and scaled-up (values averaged). It is acknowledged that these estimates will be associated with a high level of uncertainty and have been produced to provide an approximation of functional contribution and some ecological context for the decline.

Step 7: Estimation of model and map accuracy

The accuracy of the habitat suitability model and the predicted distributions was assessed using the validation dataset (not used to generate the signatures) within a confusion matrix and Cohen's kappa calculated.

RESULTS

SUITABLE HABITAT FOR *M. MODIOLUS* IN STRANGFORD LOUGH

Much of the suitable habitat was concentrated in the moderate to deep water regions running along the mid longitudinal section of the Lough (Figure 4c). Habitat predicted to be suitable for *M. modious* was broadly reflective of the available substrata in the Lough though sandy mud with shell and sandy mud contained proportionally more suitable habitat (Figure 4a). In relative terms, mud and fine mud areas were predicted to be less suitable for *M. modiolus* (Table 3). The majority of the suitable habitat was estimated to occur on the flat planar seabed with trough slope areas also being proportionally more suitable (Figure 4b). Ridge flats and sloped areas were considered less suitable as habitat for *M. modiolus*.

Validation of the prediction for suitable habitat was associated with a high rate of false positives and a low Kappa score suggesting a poor level agreement between the predicted and known distribution (Table 4). Possible reasons for this discrepancy are provided in the discussion. The habitat suitability model was subsequently used to refine the interpolated distributions (detailed below).

Refined distribution and habitat occupation of M. modiolus between 1968 and 1985
The distribution (interpolated <1986 data refined with the habitat suitability model) indicates that the realised habitat for *M. modiolus* before the suspected period of greatest decline was mostly concentrated longitudinally in the middle of the Lough and in deeper water (Figure 4d). Small patches of *M. modiolus* were also found in the north of the Lough. The total area occupied in 1986 was estimated to be 12.6km^2, or approximately 70% of the area predicted as suitable habitat for *M. modiolus* (Table 3). Most of the *M. modiolus* was distributed on muddy sand, mud and fine mud substrata on flat plains and the sloping seabed (Figures 4a and 4b). The accuracy and Kappa values for this distribution were high and suggest that the predicted distribution is reflective of the actual distribution (Table 4).

Refined distribution and habitat occupation of M. modiolus in 2003
The distribution (interpolated 2003 data refined with the habitat suitability model) had declined substantially to just three large patches in the central section of the Lough (Figure 4e). The modelled extent had reduced by approximately 38% to 7.9km^2 (Table 3). The remaining *M. modiolus* mostly occupied muddy sand and coarse sediment and was spread more evenly between flat plains and the sloping seabed (Figures 4a and 4b). The greatest decline is predicted to have occurred on mud substrata in flat plain areas. The accuracy and Kappa values for this distribution were high and suggest that the predicted distribution is reflective of the actual distribution (Table 4).

Refined distribution and habitat occupation of M. modiolus in 2007
The distribution (interpolated 2007 data refined with the habitat suitability model) was estimated to have remained in the same area occupied in 2003 (Figure 4f), although the overall coverage had again declined to 5.4km^2 (Table 3). The underlying character of the seabed occupied remained broadly similar to that in 2003, although relative occupation of mud substrata declined marginally (Figures 4a and 4b). The accuracy and Kappa values for this distribution were high and suggest that the predicted distribution is reflective of the actual distribution (Table 4).

THE ESTIMATED ABUNDANCE OF *M. MODIOLUS* IN STRANGFORD LOUGH IN <1986, 2003 AND 2007
The population was estimated to have declined by 77% from ~905 million individuals to ~210 million individuals between <1986 and 2003 (Figure 5). This decrease in the abundance stemmed from both a reduction in extent and a decrease in average density values between Roberts (1975), Brown (1976) and Roberts *et al*., 2004. The population between 2003 and 2007 continued to decline to ~115 million individuals (87% loss of the original population), again driven by both decreases in extent and density (Roberts *et al*., 2011).

THE ESTIMATED CONTRIBUTION OF *M. MODIOLUS* TO ECOSYSTEM FUNCTIONS WITHIN STRANGFORD LOUGH

Extrapolation of the clearance rates for *M. modiolus* suggest that the volume of seawater in Strangford Lough could have been turned-over (the entire volume filtered through the resident *M. modiolus*) within approximately ~255 days before 1986 (Table 5). With the decline in both distribution and density observed by other researchers, the turn-over rate is estimated to decline to about ~2,000 days in 2007.

Before 1986, *M. modiolus* in Strangford Lough were estimated to produce ~120,000kg of biodeposits per day (~680kg of particulate organic nitrogen) and excrete ~470kg of ammonia per day (Table 5). Between 1986 and 2007, rates declined by approximately an order of magnitude, i.e. to just ~15,250kg of biodeposits per day (86kg of particulate organic nitrogen) and ~60kg of ammonia per day.

DISCUSSION

Predictions suggest that *M. modiolus* was a significant biotic component in Strangford Lough, with a population of over 905 million individuals covering 12.6km^2 of subtidal seabed. The area occupied by *M. modiolus* biogenic reef declined by 37% from <1986 to 2003 and the population size shrank by 77% during the same period. A further 17% reduction in the area covered was also apparent between 2003 and 2007, clearly indicating that the process of biogenic reef loss from the Lough continued during this period. During the period of decline, it can be seen that habitat occupation has been modified, with the *M. modiolus* on shallow muddy plains declining, leaving proportionally more individuals in deeper, sandier areas. Outside the Lough *M. modiolus* are usually found on coarser, deeper seabeds, e.g. Pen Llŷn, north-west Wales (Lindenbaum *et al.*, 2008), the Isle of Man (Holt *et al.*, 1998) and in Icelandic waters (Ragnarsson and Burgos, 2012). Previous analysis of the *M. modiolus* in Strangford Lough by Mitchell *et al*. (2004), based on Acoustic Ground Discrimination System data (RoxAnn), estimated the extent to be 10.05km^2 in 1986, 6.4km^2 in 1995 and 3.75km^2 in 2003. These estimates are close to the values generated here and confirm the size and trajectory of the decline before 2003.

POSSIBLE REASONS FOR THE DECLINE OF *M. MODIOLUS* IN STRANGFORD LOUGH

It is apparent that *M. modiolus* has undergone a substantial decline in Strangford Lough. This research has concentrated on describing the decline rather than investigating the reasons for the decline. Roberts *et al*., (2004, 2011) suggest that this decline has been driven by the physical disturbance induced by fishing activities in the Lough, especially during the mid- to late 1980s. This period saw a substantial increase in inshore fishing effort, and especially trawling for queen scallops (*Aequipecten opercularis*) within the Lough (Roberts *et al*., 2004).
Predatory and competitive processes may have also affected the population of *M. modiolus*. Research during the SLECI project (Roberts *et al*., 2004) observed super-abundant densities of the common starfish (*Asteria rubens*) and a solitary tunicate (*Ascidella aspersa*) within the Lough between 2000 and 2003. *Asterias rubens* is known to predate upon *M. modiolus* and may have also contributed to poor recruitment and high adult mortality, especially following the physical damage of the protective ‘clumped’ structure of the biogenic reef by dredging (e.g. as observed by Cook *et al*., 2013). The bloom of the large filter-feeding solitary tunicate *A.*

aspersa is likely to be linked to the greater availability of seabed for colonisation and suspended particulate matter following the decline of *M. modiolus*. Diver observations noted high sedimentation associated with beds of *A. aspersa* within areas historically occupied by *M. modiolus* (J.A Strong *pers. obs*. 2004). The source of the extra sediment may also have been from the resuspension of historical biodeposits following the loss of the protective crust provided by the biogenic reef of *M. modiolus*. As yet, the cause(s) for the continued decline of *M. modiolus* in Strangford Lough remain uncertain. Successful recovery of any feature will require that the sources of the decline have been identified, prioritised and reduced. With this, restoration efforts are likely to encounter significant and unknown sources that undermine recovery efforts.

The documented decline has three important ramifications. First, the loss of ecosystem functions provided by the diminished population of *M. modiolus* and species associated with the biogenic reef. Second, the long-term viability of *M. modiolus* population within the Lough and third, the ability of managers of the Lough to maintain a designation feature at a 'favorable conservation status'. These issues are discussed below.

THE ESTIMATED CONTRIBUTION OF *M. MODIOLUS* TO ECOSYSTEM FUNCTIONS WITHIN STRANGFORD LOUGH

The biogenic habitat generated by reef building bivalves is often associated with high biodiversity (Cranfield *et al*., 2004; Koivisto and Westerbom 2010) and significant provision of important ecosystem functionality (Newell, 2004). When densely aggregated as biogenic reef, this process concentrates large amounts of suspended particulate matter and transfers much of this material to the benthos through secondary production and rejection of biodeposits (faeces and pseudofaeces). This material accumulates within these biogenic structures and provides a favourable environment for a rich and abundant assemblage of infaunal and epifaunal deposit feeders. These biogenic structures are also colonised by surface suspension feeders that benefit from the lowered, yet turbulent, current conditions generated by the rugosity of the epifaunal reef structure provided by *M. modiolus* (Wildish and Kristmanson, 1984). The structural complexity of the biogenic habitat also provides important refuges from predation and physical disturbance for many species (Coen *et al*., 2007).

As a filter feeding species, *M. modiolus* is functionally important for the removal of suspended material and hence water clarity, light penetration and the distribution of primary production within the water column (Newell, 2004). It is possible to measure the importance of *M. modiolus* by combining estimations of the abundance generated here with literature values on clearance rate (PML, 2010) and biodeposit and waste production (Navarro and Thompson, 1996; Navarro and Thompson, 1997 respectively). Extrapolation of the clearance rates for *M. modiolus* suggest that the volume of seawater in Strangford Lough could have been turned-over (the entire volume filtered through the resident *M. modiolus*) within approximately ~250 days before 1986 although after the decline this period has increased to over 2,000 days.

A natural consequence of their prestigious filtration capacity would be the significant transfer of pelagic material to the benthic realm via faeces, pseudo-faeces and biomass conversion. The quantities of biodeposits and ammonia produced by *M. modiolus* were examined by Navarro and Thompson (1997) and Navarro and Thompson (1996) respectively. Before 1986, *M. modiolus* in Strangford Lough were estimated to produce ~120,000kg of biodeposits per day and excrete ~470kg of ammonia per day (based on values from Navarro and Thompson (1997)). Between 1986 and 2007, rates declined to just ~15,250kg of biodeposits per day and ~60kg of ammonia per day.

The total pool of nitrogen in Strangford Lough was taken from Service *et al*. (1996). In 1986, the daily input of N from biodeposits and excreted ammonia represented approximately 1.71% of the total N pool in the Lough. This contribution had declined to just 0.40% in 2003 and 0.22% in 2007. Service *et al.* (1996) also quantified the combined nitrogenous input from sewage treatment works, run-off and small riverine inputs as being 5,430kg per day. The 1986 population generated an additional N input approximately 30% of the size of the anthropogenic and fluvial input. Between 1986 and 2007, the daily N contribution declined to less than 4% of the daily inputs.

Although the nutrient recycling values calculated here for *M. modiolus* are only a rudimentary approximation, these values indicate the value and probable ecosystem importance of *M. modiolus* in Strangford Lough for nutrient regeneration. Furthermore, as a water body considered to be nitrogen-limited throughout much of the year (Service *et al*., 1996), the reduction in abundance and proportional loss of nutrient regeneration from *M. modiolus* is likely to have significant implications for local primary production and consequently other trophic levels. Benthic invertebrates also contribute to denitrification processes (Pelegri and Blackburn, 1995). It is likely that both the reduced abundance of *M. modiolus* and a shift in dominance to other species (e.g. polychaetes or ascideans) may change the dynamics of the process and the availability of nitrogen in the Lough.

The filtration and nutrient recycling values reported here provide a broad approximation of the ecological contribution of *M. modiolus* in Strangford Lough. It was not possible to estimate the uncertainty associated with these values but it is assumed to be very high. It must be stressed that the absolute values associated with these estimates are likely to be inaccurate—the purpose of their calculation was to provide relative comparisons to other processes reported in the scientific literature.

VIABILITY OF THE REMAINING POPULATION OF *M. MODIOLUS* IN STRANGFORD LOUGH

Although regionally abundant, individual beds of *M. modiolus* in Northern Ireland are thought to be beyond the dispersal range of other large populations within the Irish Sea (Gormley *et al*., 2015). This can effectively isolate sub-populations, thereby reducing recruitment between source and sink populations (Elsäßer *et al.*, 2013), and lead to distinct genetic differences (as documented for the Northern Irish population by Gormley *et al*., 2015). The remaining population (brood stock) then becomes the sole local source of gametes. Heavily depleted populations often experience Allee effects (Allee, 1931). It is likely that the population of *M. modiolus* in Strangford Lough is experiencing cumulative, density-dependent Allee effects (Fariñas-Franco *et al.*, 2013). The mechanisms driving these Allee effects may include the use of a trickle spawning strategy by *M. modiolus* in Strangford Lough (Seed and Brown, 1975) that will lead to reduced fertilisation rates in diminished populations of adults. The spat of *M. modiolus* are gregarious (i.e. the settlement of larvae that have been attracted to members of their own species) during settlement (Roberts, 1975; Rees *et al.*, 2008). Depleted populations are thus also likely to lead to a decrease in the availability of optimum substrata for settlement and consequently elevated post-settlement mortality. The recruitment success in populations of

M. *modiolus* is generally reported to be very low (Seed and Brown, 1978), even when compared to levels of bivalve recruitment generally. Furthermore, Gormley *et al*. (2013) predict that sea temperature increases, caused by climate change, will contribute to a substantial retreat northerly and overall decline in the extent of *M. modiolus* in British waters over time. These factors may contribute to the further decline of the remaining population and hamper restoration activities.

MODELLING APPROACH USED TO HIND CAST THE DISTRIBUTION OF *M. MODIOLUS* IN STRANGFORD LOUGH

It is probable that the distribution of *M. modiolus* in Strangford Lough is or has been heavily influenced by 1) environmental variables (e.g. temperature, depth, current speed and food availability), which in turn affect the suitability of the habitat, 2) biotic pressures, such as heavy predation from the common starfish, *A. rubens*, and competition from an abundant solitary tunicate, *A. aspersa*, and most importantly, 3) anthropogenic pressures (physical impacts of demersal fishing). As there is no information available on the intensity and spatial distribution of the biotic or anthropogenic pressures at the same resolution as the required map outputs, it was not possible to incorporate these factors as a predictor variable in modelled distributions for *M. modiolus*. As it is not possible to include the main driving factors that dictate distribution of this species within a modelling approach, the use of standard predictive variable mapping techniques were not suitable in this situation.

Gormley *et al*. (2013) modelled a baseline distribution of *M. modiolus* in British waters using temperature, depth, substratum, water movement and salinity to define an environmental envelope for this species (i.e. a set of environments within which it is believed that the species can persist). As anthropogenic factors are known to have influenced the actual distribution of *M. modiolus* in Strangford, these predictor variables are insufficient for the objectives of this study. Furthermore, at the spatial scale of the Lough (~4 -20km), variables such as temperature and salinity do not vary as much as they do regionally.

The approach for estimating the distribution undertaken here combined the interpolation of direct observations of *M. modulus* with a habitat suitability model to refine the interpolation boundaries. Habitat suitability models reflect niche theory and generate a spatial distribution of the known environmental preferences for a species (Hirzel and Le Lay, 2008). However, they tend to differ from maps of distribution as it is known that there are significant differences between the suitability of a habitat and the realised occupation of this area. This can be due to biological influences that may prevent a species from occupying a suitable area (defined using only environmental variables) such as recruitment, competition or predation factors. This may explain why there was a high level of false positive predictions associated with the habitat suitability model and a low kappa score. Future development of the habitat suitability model should seek to improve the quality of the predictor variables and especially source hydrodynamic information with a finer resolution. In addition, other modelling approaches, such as generalised additive modelling, may provide better predictive outcomes than the maximum likelihood model used here. The accuracy and Kappa values for the predicted distributions were high and suggest that the combined use of a habitat suitability model and interpolated observations is effective at estimating the actual distribution in situations with strong anthropogenic drivers.

CONCLUSIONS

There has been a sizeable reduction in both the extent and abundance of *M. modiolus* in Strangford Lough. It is possible that Allee effects may be contributing to a further decline within the remaining population. Further work is urgently needed to understand the mechanisms during the current decline of the remaining population. Dispersal modelling and genetic analysis suggest that the Northern Irish population of *M. modiolus* is isolated and distinct from other populations in the Irish Sea (Gormley *et al*., 2015). The conservation value of *M. modiolus* is related to the biogenic structure generated from extensive areas of mature beds. Considering the magnitude of the observed decline in *M. modiolus* in Strangford Lough, and the fact that this process is still continuing, local policy and conservation bodies face the threat of returning this feature to a 'recovering' or 'favourable' conservation status required by the Habitats Directive. Further work is urgently required to understand the mechanisms underpinning the continued decline and management and realistic restoration activity required to reverse this situation.

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