Horse mussel reef ecosystem services: evidence for a whelk nursery habitat supporting a shellfishery

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ABSTRACT
Demonstrating the benefits that marine ecosystems provide to society can support marine spatial planning and enhance the protection of fragile, biodiverse habitats. However, the importance of ecosystem services provided by such habitats is rarely accounted for in spatial management due to a lack of detailed information. The present study investigated the ‘habitat provision’ ecosystem service delivered by horse mussel (Modiolus modiolus (L.)) reefs, a ‘Priority Marine Habitat’ in the NE Atlantic. By working with local fishers, the abundance and demographics of commercially important whelks (Buccinum undatum) were examined. B. undatum catches were three times higher on reef sites and a greater number of smaller individuals were caught on the reefs compared to off-reef habitats. We therefore show that these productive and physically complex mussel reefs are important feeding and nursery areas for whelks, demonstrating the ‘essential fish habitat’ value of the now rare M. modiolus reefs. The results are discussed in the context of marine spatial planning and the potential for historically more widespread shellfish habitats to have been capable of providing substantial ecosystem services.

1. Introduction

Policy advisors are keen to integrate ecosystem services, that is, ‘the direct and indirect contributions of ecosystems to human wellbeing’ (Kumar 2010), into management frameworks and strategies (Atkins et al. 2011). However, an understanding of the basic ecological processes that underpin ecosystem services provided by marine systems is rare. Jobstvogt et al. (2014) showed the cultural ecosystem service value of biodiversity features in UK marine protected areas (MPAs) and highlight the need for evidence of the ecological benefits of MPAs. Kremen (2005) suggested the identification of ‘ecosystem service providers’ including keystone species, that is, taxa that are disproportionately important relative to their abundance, to prioritise areas for protection. If ecosystem services are not valued or even considered in management decisions, users generally do not take into account the degradation of services in the way that they utilise resources (Corbera et al. 2007).

While terrestrial ecosystem services have been well mapped, valued and analysed (Brauman et al. 2007; Naidoo et al. 2008; Tianhong et al. 2010), marine ecosystems present a number of challenges for ecosystem valuation and assessment (Kremen 2005). For example, an extensive forest can be mapped using satellite imagery and studied in situ, whereas marine habitats are far less accessible and few marine habitats can be mapped in this way. Therefore, our understanding of the ecological detail and scale of ecosystem services provided by such habitats is fundamentally restricted and research often requires an alternative approach such as ecosystem modelling (Guerry et al. 2012).

For centuries, marine shellfish reefs have been an important resource for humans worldwide, yet historical overfishing has resulted in a dramatic loss of 85% of these habitats (Beck et al. 2011) and their associated ecological functions (Jackson et al. 2001). European native oyster (Ostrea edulis), for example, are now so scarce in the Northeast Atlantic that they are listed as priority marine habitats (PMHs) on the OSPAR list of threatened and/or declining species and habitats. Although not often targeted directly for consumption, horse mussel (Modiolus modiolus) reefs have seen similar declines (Strain et al. 2012; Thurstan et al. 2013) due to their vulnerability to physical impact (Cook et al. 2013) and slow recovery (Fariñas-Franco et al. 2013; Dinesen & Morton 2014) and are therefore also PMHs.

The importance of shellfish habitats for nutrient cycling, increased fish and shellfish production and benthopelagic coupling are clear (Navarro & Thompson 1997; Peterson et al. 2003; Kellogg et al. 2011); as are the benefits of restored oyster reefs in the USA (Coen et al. 2007). Biogenic habitats formed
The aims of the present study were to investigate the habitat provision ecosystem service provided by the Pen Llŷn horse mussel reef (as an EFH for *B. undatum*, a commercially important species) using catch rate and the proportion of juveniles as indicators of this service. The results will be discussed with regard to the benefits of horse mussel reefs to local fishers and the historical function of such habitats.

2. Methods

2.1. The study area

Common whelks have been harvested using baited pots on the north coast of the Pen Llŷn for the past 25 years (P. Jones pers. comm.). Whelk fishing follows a systematic pattern, moving along the coast in a north-easterly direction throughout the year, over a stretch of coast approximately 40 km long where two protected areas of horse mussel reefs occur (Figure 1). Both reefs are protected under Sea Fisheries Order (2012) no. 2571, which prohibits the use of bottom towed fishing gear within the closed areas. The total reef area is approximately 600 ha; the southern part of the reefs has been mapped and monitored since 1999 (Lindenbaum et al. 2008) and the second smaller section of reef to the north of Porth Dinlle was first recorded by the scientists in 2010 (Figure 1; Lindenbaum pers. com.).

2.2. Sampling *B. undatum*

In June and July 2013, baited pots were deployed at 61 sites off the north coast of Pen Llŷn between 19 m and 30 m below chart datum on the horse mussel reefs and adjacent control sites (Figure 1C). Sites were selected by creating a grid in ArcGIS and using the ‘Create Fishnet’ tool to randomly select positions on the grid in an area of horse mussel reefs and three contrasting areas without horse mussel reefs. Modelled habitat maps were used to assess the habitat at each site (Figure 1C, Robinson et al. 2011) and a drop-down camera was used to ground truth sites (though data are not presented in this paper). Some of the selected sites were logistically impractical or inaccessible to sample and therefore moved to the nearest point on the fishing route. The predicted habitat type at each site is shown in Table S1 (Supplementary information).

Control, non-reef sites were selected in areas to the south (*n* = 14), north (*n* = 15) and north-east (*n* = 15) of the horse mussel area (*n* = 17) to accommodate any variation that might have occurred as a result of bathymetry or tidal flow. In addition to drop-down video data, habitats were cross-checked with local knowledge of seabed types from fishermen, to further verify that sites were either ‘reef’ or a fairly homogeneous ‘off-reef’ habitat (Figure 1C). The more
northern area of the reefs (Figure 1B ‘b’) was used in this study to synchronise with the fishing schedule.

Fishing gear consisted of 25 litre weighted plastic pots (Figure 2B), with a hole in the top covered in net material with a simple draw-string opening, similar to those used by Kideys (1996). Pots were deployed in strings of 20 and one pot from the string was selected at random as a sample from each site to account for variation in catch along the string. The bait used was half a catshark (Scyliorhinus canicula) and half a spider crab (Maja squinado); sourced and prepared by the same person each day to ensure the bait was consistent for each deployment. The sites were visited in the same order as they had been deployed for retrieval approximately 24 hours later. All the whelks in each sample pot were counted and measured.

No specific permissions were required for access to the sites visited for this research. The field studies did not involve damage or collection of endangered or protected species and were conducted as part of licensed fishing activity. The work was conducted in consultation and support from the statutory nature conservation agency, Natural Resources for Wales.

2.3. Statistical analysis

B. undatum count data were assessed for outliers and distribution and modelled using a generalised linear mixed model (GLMM) and the negative binomial family. Model selection followed guidance by Zuur et al. (2009) and overdispersion was assessed using Pearson residuals. Sampling area was included as a fixed effect with four levels (Reef, South Control, North Control and North East Control). Site location and depth were included as random effects to account for spatial autocorrelation (Millar &
Anderson 2004). The significance of the factors considered was determined by maximum likelihood (ML) parameter estimates. Model terms were sequentially tested using a likelihood ratio test and AIC values were used to compare models. Non-significant terms \((p > 0.05)\) were removed. Univariate analyses were carried out in R version 2.9.1 (R Core Development Team 2011) using the glmmADMB package (Bolker et al. 2012).

In order to test the difference in size distribution of \(B. \text{ undatum}\) from the different areas, multivariate analysis was carried out using the PRIMER v6 statistical package with PERMANOVA + add-on (Anderson et al. 2008). A two-way design was created with \(B. \text{ undatum}\) lengths (grouped into 0.5 cm size classes from 1–12 cm) used as the response variables for multivariate analysis (as used by Cosser (1989) and Seiderer and Newell (1999) for grain-size distributions). Area was included as a fixed factor, while depth was a random factor nested within area. Site location was also included in the model design as a source of random variation. The model was tested using a permutation analysis of variance (PERMANOVA) to establish if the \(B. \text{ undatum}\) size structure (using the size classes above) varied significantly between these factors. Data collection in the field resulted in an unbalanced design and therefore tested using Type III sums of squares. Using this technique, each variable was accounted for in a sequential manner. The test was therefore not dependent on sample size (Anderson et al. 2008). Where significant differences were found, pairwise tests between the groups were used to find where these differences occurred.

3. Results

Overall, 3913 whelks \((B. \text{ undatum})\) were caught across the four study areas: 2037 (52%) were from the horse mussel reef area and area was a significant influence on \(B. \text{ undatum}\) catches (GLMM, \(X^2 = 22.15, p = < 0.001)\). There was no evidence to show that depth was a significant influence on \(B. \text{ undatum}\) catch (Table 1). Significantly more \(B. \text{ undatum}\) were caught on the reef than the South Control Area \((z = 2.36, p = 0.018)\), the North Control Area \((z = 4.97, p = 0.001)\) and the North East Control Area \((z = 3.25, p = < 0.001)\) (Figure 3).

Catches of whelk on the reef were double that of the

Table 1. Summarised parameters of the generalised linear mixed effects models to compare \(B. \text{ undatum}\) count per pot (per 24-hour deployment) at the experimental areas with site as a random factor. Significance code \(* * * = < 0.001\).

| Response | Factors | DF | Deviance | AIC |
|----------|---------|----|----------|-----|
| \(B. \text{ undatum}\) count | Null | 3 | 22.154 *** | 636.6 |
| | Area | 1 | 10.222 | 620.5 |

Figure 2. (A) Horse mussel reef habitat; (B) Fishing operations; (C) Whelk, \(Buccinum \text{ undatum}\), on a horse mussel reef; (D) \(B. \text{ undatum}\) catch. Images A and C: Richard Shucksmith, B and D: Flora Kent.
North East and South Control Areas, and four times as high as the counts in the North Control Area. There was high spatial variation of catch rates within areas, especially in the South Control Area, where 183 and one *B. undatum* were caught in two sample sites only 400 m apart. Catch rates on the horse mussel reef were consistently high, reaching a maximum of 320 whelks in one pot. The lowest catch rates were at the South Control Area with fewer than five *B. undatum* caught at four sites.

A PERMANOVA test on the size distribution of *B. undatum* at the reef and three control areas (Table 2) showed that depth was not a significant factor in the model (pseudo-F = 0.91, *p* = 0.538). However, area was a significant factor (pseudo-F = 8.54, *p* = 0.002), and the size of whelks at the reef sites was significantly smaller than those at the North East Control Area (*p* = 0.001), and the North Control Area (*p* = 0.001), as shown in Figure 4. The size distribution of *B. undatum* at the South Control Area was not significantly different to those on the reef (*p* = 0.29).

4. Discussion

4.1. Habitat provision

The aim of the present study was to investigate whether horse mussel reefs are EFH for the common whelk (*B. undatum*). Horse mussel reefs were confirmed as EFH at sites off the Pen Llŷn, where significantly higher catch rates of *B. undatum* and smaller size classes were found on the reefs when compared to off reef control sites. The complex structure of the horse mussel reef probably acts as feeding and nursery grounds, also providing protection from predators. Horse mussel reefs have a wide range of organisms associated with them (Rees et al. 2008; Sanderson et al. 2008), including bivalves and crustaceans, which are known to be utilised by *B. undatum* as a food source (Himmelman & Hamel 1993). In comparison, the seabed type at the North and North East Control Area varied between circalittoral mixed sediment and infralittoral muddy sand (Robinson et al. 2011; Table S1), which would be unlikely to

Table 2. PERMANOVA test to compare *B. undatum* size distribution (0.5 cm length classes, transformation = cumulate) at the experimental areas with site included as a random effect.

| Response | Factors | DF | Pseudo-F | *p*  |
|----------|---------|----|----------|------|
| *B. undatum* size | Area | 3 | 8.54 | 0.002 |
| | Depth | 13 | 0.91 | 0.538 |

Figure 3. Whelk (*Buccinum undatum*) counts at 61 sites over four areas off Pen Llŷn, North Wales. Box plots represent interquartile range, median, maximum and minimum values. Outliers are plotted as points. North East Control (*n* = 15), North Control (*n* = 17), Reef (*n* = 17), South Control (*n* = 14). Areas that share a capital letter are not significantly different at *p* < 0.05.

Figure 4. Size frequency distribution of whelks (*Buccinum undatum*) in the four experimental areas off Pen Llŷn, North Wales. Bars represent total counts for each size class at each area, a = North East Control Area, b = North Control Area, c = Reef, d = South Control Area.
provide protection and food for juvenile B. undatum. Overall, the findings are in keeping with other studies that show structurally complex habitats are often utilised by juvenile fish and shellfish to enhance growth and survival rates (Heck et al. 2003; Bejarano et al. 2011). While the present study was restricted to one reef, diver surveys in Orkney and Shetland also show relatively high counts of B. undatum on M. modiolus reefs (Kent unpubl. data).

The observation that the horse mussel reef is a nursery for B. undatum suggests that it may also be seeding the surrounding area and further investigation into B. undatum migration patterns would be useful. Fish size can often be related to depth or distance offshore (Macpherson & Duarte 1991; Gibson et al. 2002), but in the present study there was no such relationship, suggesting that habitat type was more important in structuring the populations ontogenetically within the limited depth ranges of the present study. Video footage obtained for the South Control Area showed that the habitat included some gravel and cobbles, which could have provided some complexity similar to the reef and therefore some niches for smaller B. undatum. This may help explain why whelks at this area had a similar size range to those on the horse mussel reef, although their catch rate was lower.

Fishing pressure is also likely to influence B. undatum population structure, but information on fishing effort is not available at a resolution appropriate for this study. Nevertheless, fishers asserted that for the past two decades, pot fishing has occurred systematically, moving along the coast throughout the year (P. Jones pers. comm.). It was therefore assumed that pot fishing effort was relatively even across the study area. However, on two out of 12 occasions during the present study, the fishermen discarded undersized (<4.5 cm) whelks that had been collected throughout the day on the return journey to Porth Dinllean; effectively relocating the smaller whelks, and over time, potentially influencing the size distribution at the South Control Area.

Beck et al. (2001) describe a nursery area as a ‘juvenile habitat that contributes disproportionately to the production of individuals that recruit to adult population’. Mangrove forests are often quoted as being important nursery habitats, however, most studies have only addressed occurrence or density of the species of interest and not compared this to other habitats (Sheridan & Hays 2003). In light of this, the finding of the present study that horse mussel reefs support disproportionately higher catch rates of juvenile whelks is crucial, and can be used as an indicator of the provisioning service ‘food’ (cf Van Oudenhoven et al. 2015). Indeed, the use of commercial fishing operations to gather data in this study provides evidence of the habitat provision service as well as ‘simply’ the ecological phenomenon of a habitat for whelks.

### 4.2. Remnant habitats and historical function

The Pen Llŷn horse mussel reefs are remnant habitats that can be traced to Edward Forbes sampling in 1848 (Lindenbaum et al. 2008). The southern reefs are part of the Pen Llŷn a’r Sarnau Special Area of Conservation (SAC) and have been closed to mobile fishing activity since 1998, and the northern reefs were closed in 2012 (marked areas a and b in Figure 1B). Sustained fishing for the past 25 years on the north coast of Pen Llŷn and the high catch rates reported for this area suggest a considerable population of B. undatum. The whelk fishery on the Pen Llŷn supports 12 local fishers and according to the fisherman, loss of the horse mussel habitat would therefore put them out of business (P. Jones pers. com.).

Declines of M. modiolus reefs in Strangford Lough (Northern Ireland) have corresponded with declines in queen scallops (Aequipecten opercularis) (Roberts et al. 2011; Strain et al. 2012), giving another indication of the importance of M. modiolus reefs as EFH for shellfish. In addition, aquarium-based experiments have suggested a potential role for M. modiolus in enhanced benthologic coupling and therefore provision of feeding opportunities for other invertebrates (Navarro & Thompson 1997). The present study provides direct evidence of the ecological function and societal benefits of a horse mussel reef ecosystem through EFH provision. The whelk fishery is important for the Welsh economy, being the second most valuable shellfishery in 2013 (MMO 2014). Whelk fishing occurs throughout the UK, particularly in rural locations, yet the link between fisheries productivity and complex habitats has not been made by coastal managers. The local conditions and fisher behaviour on the Pen Llŷn may not represent other coastal areas where M. modiolus occur and therefore warrants further investigation.

Historical evidence from the NE Atlantic suggests that large areas of shellfish beds have been lost over the past 200 years. Native oyster beds were reported from all around the UK including one covering approximately 4,000,000 ha in the North Sea (Olsen 1883), 20 × 6 mile beds in the Firth of Forth (Thurstan et al. 2013), as well as beds in ‘Oystermouth’ (South Wales) capable of supporting 200 vessels and employing 400 men in the mid-1800s (WWF 2012). Intense dredging during the 1800s has undoubtedly caused dramatic degradation of shellfish habitats throughout the UK and the world (Beck et al. 2011) but the loss of associated ecosystem services is beginning to be recognised (Zu Ermgassen et al. 2013).

The horse mussel reef system described in this study was only discovered by scientists in 2010 and since then, a 385 ha reef has been discovered and mapped in Scotland (Hirst et al. 2012) as has a 200 ha reef in Northern Ireland (Geraldi et al. 2014).
Together, these newly discovered reefs make up three out of the four largest horse mussel reefs known in the UK and illustrate the lack of knowledge of subtidal marine habitats. It is therefore likely that there are more ‘undiscovered’ reefs within UK waters and beyond, providing further ecosystem services that are yet to be recognised in emerging spatial management initiatives including MPAs (cf Directive 2008/56/EC and 2014/89/EU).

UK horse mussel reefs have not been targeted by fisheries in the same way as extirpated oyster reefs but have been incidentally damaged by mobile fishing gear (Strain et al. 2012; Cook et al. 2013). Remnant horse mussel reefs still exist in the NE Atlantic today (albeit threatened and declining: JNCC 2015) and are the closest functional analogues to the widespread subtidal oyster reefs of the past. Therefore, historical shellfish reefs (e.g. those formed by horse mussels and oysters) may well have been capable of supporting many more sustainable livelihoods than the same marine space today through indirect exploitation. Overall, our ability to safeguard biodiversity and associated ecosystem services will depend on appropriately balanced marine spatial planning based on sound scientific evidence that, at present, is scarce.

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