1　Commercially important species associated with horse mussel (*Modiolus*

2　*modiolus*) biogenic reefs: a habitat for biodiversity conservation and

3　fisheries benefits

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5　Flora E. A. Kent[1], James M. Mair[1], Jason Newton[2], Charles Lindenbaum[3], Joanne S. Porter[1],

6　William G. Sanderson[1, 4]

7　*[1]School of Life Sciences, Heriot-Watt University, Edinburgh EH14 4AS, UK*

8　*[2]NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental*

9　*Research Centre, Rankine Avenue, East Kilbride G75 0QF, UK*

10　*[3]Natural Resources Wales, Maes y Ffynnon, Bangor, Gwynedd LL57 2DW*

11　*[4]St Abbs Marine Station, St Abbs, Scottish Borders, TD14 5PW*

12

13　<u>Highlights</u>

14　• Communities of conspicuous megafauna were assessed on *Modiolus modiolus* reefs,

15　sand and cobble habitats.

16　• Tissue samples from reef fauna were subject to stable isotope analysis to investigate

17　trophic structure.

18　• *M. modiolus* reefs support a higher abundance of commercially important shellfish,

19　including *Aequipecten opercularis*, *Buccinum undatum* and *Maja brachydactyla*, than

20　cobble and sand habitats.

21　• Evidence of the commercial value of *M. modiolus* reefs in the UK.

22　<u>Abstract</u>

23　Horse mussel beds (*Modiolus modiolus*) are protected biodiversity hotspots in Marine

24　Protected Areas of the NE Atlantic. In this study, horse mussel beds, cobble habitats and

25　sandy habitats were assessed using underwater visual census and drop-down video techniques

26　in three UK regions. Megafauna were enumerated, differences in community composition

27　and individual species abundances were analysed. Samples of conspicuous megafauna were

28　also collected from horse mussel beds in Orkney for stable isotope analysis.

29　Communities of conspicuous megafauna were different between horse mussel habitats and

30　other habitats throughout their range. Three commercially important species: whelks

31　(*Buccinum undatum*), queen scallops (*Aequipecten opercularis*) and spider crabs (*Maja*

32   *brachydactyla*) were significantly more abundant (by as much as 20 times) on horse mussel

33   beds than elsewhere. Isotopic analysis provided insights into their trophic relationship with

34   the horse mussel bed. Protection of *M. modiolus* habitat can achieve biodiversity conservation

35   objectives whilst benefiting fisheries also.

36

37   Introduction

38   Globally, fish stocks are under threat (Jackson et al., 2001) with the proportion of over-

39   exploited fish stocks at 32% in 2008 (FAO, 2010), leading to calls to halt this trend and

40   restore them (Worm et al., 2009). One method of improving fisheries management has been a

41   shift to 'Ecosystem-Based Management' (EBM) that involves a move from traditional single

42   species based management to a greater understanding of the interactions between habitats and

43   commercially important species. In the NE Atlantic, habitat-forming species such as maerl (a

44   coralline red algae) create a physically complex and biodiverse seabed, which provides a

45   nursery ground for commercially important fish and shellfish (Kamenos et al., 2004a, 2004b).

46   *Modiolus modiolus* (horse mussel) reefs are structurally complex habitats, characterised by

47   high species diversity (Hirst et al., 2012; Rees et al., 2008; Sanderson et al., 2008). The

48   societal benefits of horse mussel reefs for fishermen has been demonstrated (Kent et al 2016);

49   yet the utilisation of horse mussel reefs as a resource for benthic consumers has not been

50   studied.

51

52   In the United States, the Sustainable Fisheries Act (SFA) now requires fisheries managers to

53   identify the 'Essential Fish Habitat' (EFH) for commercially important fish species (Fluharty,

54   2000), i.e. "those waters and substrate necessary to fish spawning, feeding or growth to

55   maturity" (NOAA, 1966). This concept is not confined to describing finfish habitat

56   associations; it has also been used for invertebrates such as conch (Glazer and Kidney, 2004),

57   octopus (Garofalo et al., 2011) and even bottlenose dolphin (Ingram and Rogan, 2002).

58

59   The EBM approach extends the focus of managing resources beyond the target species and

60   includes impacts to non-target species and benthic habitats, supporting ecological processes

61   that are required to sustain harvestable resources (Hughes et al., 2005). With an increasing

62   human population comes an increased demand for ecosystem goods and services, i.e. "the

63   benefits natural ecosystems provide to human society" (de Groot et al., 2002). In the marine

64 environment, there is increasing interest in the relationship between biodiversity and

65 ecosystem services given the wide scale loss of biodiversity in marine ecosystems (Worm et

66 al., 2006). Marine Protected Areas (MPAs) are seen as an important management tool to

67 conserve species and habitats (Tundi Agardy, 1994) and, over time, well managed MPAs can

68 support ecosystem services to provide ecological and societal benefits (Fox et al., 2012).

69

70 Those implementing the Habitats Directive across Europe have rarely evaluated the

71 ecosystem services or the commercial value of the biodiversity that they seek to maintain

72 (Maes et al., 2012). Marine biodiversity conservation is lagging behind the terrestrial

73 equivalent, and increasing uses and demands on the marine environment have led to the

74 development of policy frameworks that integrate human activities as part of the system

75 (Atkins et al., 2011). Historically, biodiversity management and fisheries management

76 have been developed separately due to constraints imposed on sectors and fundamentally

77 different aspirations. Thus, the motivation to identify EFH is not provided through

78 fisheries legislation in Europe or spatial management of marine habitats either. However,

79 recognition of habitat associations and appropriate management of EFH has the potential

80 to provide benefits for both fisheries and nature conservation.

81

82 Identifying a habitat as an EFH is not a simple task, especially for highly mobile species

83 that use a range of habitats throughout their life cycle. With limited resources,

84 conserving or restoring every habitat used by a fish is unrealistic, therefore identifying

85 habitats that are used during sensitive life stages are often prioritised (Levin and Stunz,

86 2005). Relative fish abundance measurements provide an initial insight into which areas

87 are important for fish and shellfish. However, to recognise a habitat as an EFH requires a

88 greater understanding of the functional role of the habitat, i.e. whether it is being used

89 for feeding or reproduction, etc.

90

91 Stable isotope analysis is becoming a popular method for studying food webs (Schaal et

92 al., 2012) . ^{15}N becomes enriched during trophic transfers, with a mean increase (or

93 "trophic enrichment factor", TEF) of 3.4‰ (Minagawa and Wada, 1984; Post, 2002)

94 equivalent to approximately one trophic level, though there are variations, with TEF

95 being larger for herbivorous fish (Mill et al., 2007). The $\delta^{13}C$ from the tissue of an

96 animal is more conservative with trophic transfer, instead reflecting the source(s) of

97   carbon in the food chain. Analysis of $\delta^{15}N$ and $\delta^{13}C$ together can be used to determine

98   the feeding relationships on a biogenic habitat (Grall et al., 2006), bentho-pelagic

99   coupling (McIntyre et al., 2006) and habitat associations (Yeager and Layman, 2011).

100

101   UK biogenic reefs have been recognised as biodiversity hotspots, e.g. *M. modiolus* reefs;

102   (Mair et al., 2000; Moore et al., 2013; Rees, 2009) and mapped for conservation

103   purposes, e.g. Lindenbaum et al. (2008). However, our understanding of habitat

104   associations and the trophic structure of many biogenic reef communities is limited.

105   Underwater Visual Censuses (UVCs) can be used to measure relative megafauna

106   abundance (Kamenos et al., 2004b) and the benefit of using this technique is that it is

107   non-destructive and independent of fishing gear bias. Remotely Operated Vehicles

108   (ROVs) and towed videos have also been used to record the abundance of mobile species

109   associated with coral reefs (Söffker et al., 2011) and gorgonians (De Clippele et al.,

110   2015).

111

112   As structurally complex seabed features, *M. modiolus* reefs are expected to provide a 'habitat

113   provision' ecosystem service that has been shown to be the case for other biogenic structures

114   (De Clippele et al., 2015; Kamenos et al., 2004b; Margiotta et al., 2016). However, *M.*

115   *modiolus* reefs are relatively inaccessible and their ecological function is understudied. The

116   aim of this study is to identify the key megafaunal species (defined as animals greater than 2

117   cm maximum length) associated with three *M. modiolus* reefs in the UK and to investigate

118   the trophic feeding niche structure of a *M. modiolus* reef megafaunal community.

119

120   ## Methods

121   *Megafauna abundance*

122   Underwater Visual Censuses (UVCs) were carried out using SCUBA at twenty-three sites in

123   Shetland and Orkney (Figure 1 B and C) between 15 and 25 m below chart datum. It was

124   impractical to survey at multiple sites at Pen Llŷn (Figure 2 D) due to strong currents and

125   short slack water periods, therefore a Drop Down Video (DDV) camera system was used.

126   Sites in Orkney and Shetland were surveyed in May 2013 and September 2012 respectively.

127   Sites off Pen Llŷn were surveyed between May and June of 2008 and 2010. In all cases,

128   conspicuous megafauna, including fish and commercially important invertebrates such as

129   shellfish, were quantified.

130

131 UVC sites were selected at random using extant video footage and preliminary dive data to
132 stratify sampling to 'horse mussel reef' (8 sites), 'sand' (8 sites) or 'cobble' (7 sites) habitats.
133 Horse mussel reef sites had a density of > 20 *M. modiolus* m^{-2}. All observers were trained in
134 species identification during a pilot study in May 2012 in Orkney and all surveys covered a
135 60 m^2 area delineated by a transect tape deployed from a shot-line. Habitats were verified as
136 cobble, sand or *M. modiolus* reef using photoquadrats and granulometry samples.

137

138 The DDV camera system used was a Sony Model DCR-TRV950 camcorder fitted into a
139 tubular aluminium housing with two HID video lamps and lasers (10cm apart) were used to
140 quantify the seabed area covered. The video surface unit included a labelling system that
141 overlaid GPS position and depth information onto the surface image for recording and
142 viewing. DDV camera tows were approximately 100 m in length, but actual distances were
143 calculated from the GPS start and end points and a section of 4-8 minutes was edited from the
144 video clip for analysis. Video footage that was too fast (>30 m per minute) or with less than 1
145 m visibility was disregarded. Eight *M. modiolus* reef sites were sampled off Pen Llŷn as well
146 as 8 cobble sites and 8 sand sites.

147

148 *Food web analysis*
149 Thirty-seven samples were collected for stable isotope analysis from eleven species across
150 three *M. modiolus* reef sites in Orkney (see Supplementary Table S1 for sampling locations)
151 from the 1st-5th December 2013. *Aequipecten opercularis* (n=6), *Leocarcinus depurator*
152 (n=5), *Asterias rubens* (n=1) and *Buccinum undatum* (n=5) were collected using SCUBA by
153 searching the reef from a central location or on a drift dive. *M. modiolus* (n=14) and
154 polychaetes (n=3) were collected using a 'clump sample' technique where a clump of 3-5 *M.*
155 *modiolus* and associated fauna are placed into a bucket along with the underlying sediment
156 (Mair et al., 2000). *Gadus morhua* (n=1) and *Taurulus bubalis* (n=3) were collected from
157 sites adjacent to the reefs using baited creels.

158

159 White muscle was taken from the fish samples and adductor from the bivalves, while the foot
160 muscle was dissected from the *B. undatum* samples. Gill tissue was taken from the
161 crustaceans and tube feet from *A. rubens*. Samples were freeze-dried and ground to a fine
162 powder using a pestle and mortar. Approximately 1 mg of tissue from each sample was
163 loaded into a 4 x 6 mm tin capsule and combusted in continuous flow isotope ratio mass

164   spectrometer (CF-IRMS). Results are expressed as parts per thousand (‰) deviations from

165   international standards, in delta (δ) notation.

166

167   *Data Analysis*

168   Megafauna counts from the Underwater Visual Censuses (UVCs) and those from the Drop

169   Down Video (DDV) transects were analysed separately due to the different methodology

170   used. For the multivariate analysis, all data were log transformed to down-weigh very

171   abundant species (e.g. *Echinus esculentus* abundance varied by three orders of magnitude).

172   Using Bray-Curtis similarity, Analysis of Similarities (ANOSIM) (Clarke and Gorley, 2006)

173   was used to test for differences in megafaunal communities between *M. modiolus* reef, sand

174   and cobble habitats.

175

176   A SIMPER analysis was used to examine the key species driving the differences in

177   community composition (Clarke and Gorley, 2006). Counts of the three species contributing

178   the most to the difference in megafauna communities at the reef, cobble and sand sites were

179   then analysed using a Kruskal-Wallis test with 'habitat type' as the independent variable.

180   Pairwise Kruskal-Wallis tests were then performed using a chi-squared probability

181   distribution with a Bonferroni correction for multiple comparisons. The stable isotope

182   samples were checked to ensure protein had been analysed: samples with a Carbon/Nitrogen

183   ratio of greater than four were removed as this implies a high lipid content or carbonate in the

184   sample. Samples were averaged for each species where possible and standard deviations

185   calculated. All univariate analyses were carried out in R version 2.9.1 (R Core Development

186   Team, 2011).

187

188   ## Results

189   *Megafauna community analysis*

190   Fifteen megafauna species were recorded from 23 UVC samples in Orkney and Shetland. An

191   ANOSIM shows that the megafaunal community was significantly different amongst habitats

192   (r = 0.45, p = <0.001). Pairwise tests showed that the megafauna counted at the *M. modiolus*

193   reefs were significantly different to those living on the sand habitats (r = 0.45, p=0.003) and

194   the cobble habitats (r = 0.38, p = 0.002). The SIMPER analysis showed that the highest

195   within-group similarity was in the *M. modiolus* reef group (72.68%). The sand habitats were

196   the least similar group, with an average similarity of 19.59%. The high counts of flatfish and

197 dragonets at sand sites contributed 70% of the similarity within the sandy sites. *M. modiolus*

198 reef sites were most dissimilar to the sand sites (90.41% dissimilarity) and 50% of this

199 dissimilarity was attributable to higher densities of *E. esculentus*, *A. opercularis* and *B.*

200 *undatum* on the reefs sites (SIMPER; Figure 3a, b and c).

201

202 *M. modiolus* reef sites had over five times more *A. opercularis* than the cobble sites (x^2

203 =11.011, p=0.001) and more than 20 times as many as the sand sites (x^2 = 12.427, p=<0.001).

204 *B. undatum* were almost twenty times more abundant on reef sites compared to sand sites (x^2

205 = 7.136, p=0.008). However, the counts at the reef sites were not significantly different to the

206 cobble sites at the 0.05 significance level (x^2 =3.84, p=0.050). The most abundant species

207 found on the *M. modiolus* reefs was *E. esculentus* (0.46 m^{-2}), which was significantly greater

208 than the cobble sites (x^2=9.442, p=0.002) and the sand sites (x^2=12.308, p=<0.001).

209

210 On the UVC transects, gobies (*Pomatoschistus pictus* and *Pomatoschistus microps*) were

211 abundant in all habitats, but especially the sand sites (a maximum of 24 *P. pictus* counted on

212 one transect). Juvenile flatfish (*Limanda limanda*) were abundant at two of the sand sites and

213 dragonets (*Callionymus spp*) were present at three out of eight sand sites (16 counted in

214 total). The fish species associated with the *M. modiolus* sites were almost entirely different to

215 those associated with the sand sites (with the exception of *Callionymus* sp. and

216 *Pomatoschistus pictus*, which occurred in both habitats). The cling-fish *Diplecogaster*

217 *bimaculata* occurred at the *M. modiolus* sites but not at the off-reef sites.

218

219 A total of 22 species were identified from the DDV analysis at 23 sites off the Pen Llŷn. The

220 megafaunal community associated with the *M. modiolus* reef was significantly different to

221 the sand and cobble habitats (ANOSIM, r=0.26, p=<0.001). The top three species highlighted

222 in the SIMPER analysis, contributing to the difference in community structure between *M.*

223 *modiolus* reef sites and off-reef sites, were *B. undatum, A. rubens* and *Maja brachydactyla*

224 (previously known as *Maja squinado*: Sotelo et al., 2007). The cumulative contribution of

225 these three species in the difference between habitats was 44.15% between reef and sand

226 habitats, and 44.72% between reef and cobble habitats. Other key species causing differences

227 in the species assemblages were curled octopus (*Eledone cirrhosa*) and butterfish (*Pholis*

228 *gunnelus*), which were only seen at *M. modiolus* reef sites.

229

230   The DDV transects showed that *A. rubens* was the most abundant conspicuous megafaunal

231   species and there were significantly more observed on the reef than the sand ($x^2 = 9.26$,

232   p=<0.001) and cobble habitats ($x^2 = 11.618$, p=0.002). *B. undatum* were rarely seen on the

233   DDV surveys compared to the UVCs (0.01 m^{-2} compared to 0.11 m^{-2} respectively). From the

234   DDV analysis, no *B. undatum* were observed on cobble sites, although they were

235   occasionally seen on the reef (0.02 m^{-2}) and sand sites (0.01 m^{-2}). Ballan wrasse (*Labrus*

236   *bergylta*) occurred on the cobble sites but not on the sand sites. Sea scorpions (*Taurulus*

237   *bubalis*) occurred at the reef sites and the cobble sites but not on the sandy sites, whereas

238   dogfish (*Scyliorhinus canicula*) occurred on the reef sites and the sand sites but not the

239   cobble sites.

240

241   *Foodweb analysis*

242   The *M. modiolus*, *A. opercularis*, and *B. undatum* samples from Orkney showed consistent

243   stable isotope signatures (Figure 4). Even *M. modiolus* samples from different reefs (up to

244   2km apart) showed very similar δ^{13}C and δ^{15}N values. For the megafauna tissue samples

245   analysed, δ^{15}N increases in the following order: *A. opercularis*; *M. modiolus*; *B. undatum* and

246   *Liocarcinus depurator*; *T. bubalis* and *G morhua.* The average δ^{15}N for *M. modiolus* is

247   9.21‰ compared with 11.56‰ for *B. undatum.* The highest δ^{15}N values were from the fish

248   samples, showing that these animals are at the top of the food chain in this study, and

249   possibly feeding on crustaceans and bivalves on the reef. The isotope ratios from *M. modiolus*

250   and *A. opercularis* samples formed two distinct groups with the δ^{15}N of *M. modiolus*

251   approximately 2‰ higher than *A. opercularis* (Figure 4).

252

253   # Discussion

254   Through *in situ* observations, this study provides evidence that *M. modiolus* reefs across the

255   UK support a high abundance of megafaunal species compared to other habitats, including

256   the commercially valuable shellfish, *A. opercularis*, *B. undatum* and *Maja brachydactyla*.

257   These findings are in keeping with other biodiversity hotspots in the UK, such as maerl beds

258   that provide an important habitat for *A. opercularis, A. rubens* and *E. esculentus* (Kamenos et

259   al., 2004b). Structurally complex marine habitats such as oyster beds and seagrass beds also

260   provide a disproportionately important refuge for other species (Bertelli and Unsworth, 2014;

261   Shervette and Gelwick, 2008). However this is the first time that *M. modiolus* reefs have been

262   shown to provide a comparable functional role to these other complex habitats.

263

The stable isotope data also show the range of feeding mechanisms used within the reef community and the different food sources on the reef available for mobile species. This also gives an insight into the ecological function of the *M. modiolus* reefs and for example, shows that *B. undatum* and *L. depurator* are approximately one tropic level higher than *M. modiolus*. When considered in combination with the high abundance of *B. undatum* relative to other 'off-reef' habitats, this suggests that *B. undatum* may be feeding on *M. modiolus*. Although normally considered a scavenger, predation on bivalves by *B. undatum* has been observed in a laboratory setting (Scolding et al., 2007). Habitat heterogeneity is often important for mobile species during different life stages (Kimirei et al., 2011) and *M. modiolus* reef habitats provide a range of physical conditions from fine sediment to large shell gravel and epifauna (Nic Aonghua et al., 2001).

The two survey methods used in this study (UVCs and DDV) together provide a comprehensive method for measuring conspicuous megafauna abundance; a wide range of species were sampled and the area of seabed sampled was easily defined. However, it is likely that cryptic fish species are under-represented in these more complex reef habitats, as indicated by Bozec et al. (2011), and the use of different sampling techniques may be required to fully grasp the different fish species associated with *M. modiolus*. Similarly, the high counts of *B. undatum* on *M. modiolus* reefs in Orkney and Shetland were not mirrored in the DDV transects off Pen Llŷn probably because this is a slow moving semi-cryptic species, which is difficult to identify from DDV footage. Divers on the UVC transects were able to look around objects and check if shellfish were live or dead, which was not possible on the DDV transects. In a parallel study, comparatively high catch rates of *B. undatum* on *M. modiolus* reefs off Pen Llŷn using baited traps (Kent et al., In Review) corroborates the view that DDV is not the best technique for recording this species.

Spider crabs (*Maja brachydactyla*) were highly abundant on the Pen Llŷn *M. modiolus* reef compared to the off-reef sites and this species is harvested throughout Europe, especially in the English Channel and the Mediterranean (Fahy, 2001). Within the UK, *M. brachydactyla* is largely distributed on the south coast of England and Wales; hence the lack of observations on the Orkney and Shetland reef sites, although its distribution may extend further north with rising seawater temperatures (Goodwin et al., 2013). *M. modiolus* reefs often form a mosaic with other biogenic habitat (e.g. maerl in Shetland; Hirst et al., 2013) and it is likely that

297 mobile species benefit from this variety (Buhl‑Mortensen et al., 2010). Further investigations

298 into the diet of the key mobile species identified in this study through stomach content

299 analysis and a more comprehensive stable isotope study would develop understanding of the

300 predator-prey interactions occurring within and between biogenic habitats.

301

302 The Underwater Visual Censuses showed very high densities of *A. operculum* on the

303 *M. modiolus* reefs. Elsewhere, juvenile *A. opercularis* has been shown to attach to hard

304 substrates and use rugose structures such as maerl, which provide a refuge from predators

305 (Kamenos et al., 2004c). It is likely that *A. opercularis* utilise *M. modiolus* shell crevices and

306 associated epibiota (Figure 2) to avoid predation and increase post-recruitment survival.

307 Juvenile *A. opercularis* are able to swim, providing the option to move to a more favourable

308 environment once settled, if a different habitat is required.

309

310 The present study shows that the two filter feeding species *M. modiolus* and *A. opercularis*

311 fill different trophic niches, which is consistent with Yakovis et al. (2012) who found that

312 horse mussels and ascidians growing together have distinct diets and there is no overlap in

313 the origin of their food. Increasing evidence for differential particle selection in bivalves

314 (Kiorboe and Mohlenberg, 1981; Shumway et al., 1985; Ward and Shumway, 2004) provides

315 a possible explanation for how the filter feeding *M. modiolus* and *A. opercularis* can co-occur

316 in high densities together as adults in a reef environment.

317

318 Overall, the high abundance of *A. opercularis, B. undatum* and *M. brachydactyla* on reefs in

319 combination with the tropic structure of the former two (Figure 5), provides strong evidence

320 that *M. modiolus* reefs are 'Essential Fish Habitats' for these species. This highlights the

321 value of horse mussel reefs in providing disproportionately more ecosystem services and

322 corresponding benefits to society than other habitats. However, *M. modiolus* reefs along with

323 other shellfish habitats have declined over the past 100 years (Thurstan et al., 2013) and are

324 vulnerable to physical impacts (Cook et al., 2013). Strangford Lough is a Marine Protected

325 Area that was once home to the UK's largest *M. modiolus* reefs ($> 10km^2$), and the *A.*

326 *opercularis* trawl fishery boomed there in the 1980s (Strain et al., 2012) causing long-term

327 declines in *M. modiolus* and associated megafauna, with little sign of recovery of this long-

328 lived reef forming species (Elsäßer et al., 2013; Fariñas-Franco and Roberts, 2014).

329 Ironically, therefore, the fisheries benefits that *M. modiolus* reefs can deliver to society can

330 lead to their demise. Indeed, given that many coastal habitats provide important functional

331   roles for commercially important fish (e.g. nursery, spawning and feeding grounds), it is

332   unsurprising that destruction results in the consequential decline in associated fish landings

333   (see Seitz et al., 2014).

334

335   In many countries, including the UK, biodiversity conservation and fisheries management

336   have historically been the responsibility of separate government departments or agencies.

337   However, marine conservation management has progressed from imposed, command-and-

338   control 'fortress conservation' approaches to systems that increasingly combine both 'top-

339   down' and 'bottom-up' governance (Jones, 2014; Kelleher, 1993). Indeed, these more

340   balanced approaches are reflected globally, where the Convention on Biological Diversity

341   Aichi 6 arguably brings biodiversity concerns closer to fisheries management and UN

342   Sustainable Development Goals than ever before. Understanding the ecological interaction

343   between habitats and mobile species is required for the identification of EFH in contemporary

344   sustainable fisheries management. Here we present evidence to illustrate that this concept can

345   be usefully implemented in the context of Marine Spatial Planning to prioritise the most

346   valuable areas of the seabed (Crowder and Norse, 2008). Thus, the protection of fragile

347   habitats of biodiversity importance can intersect with sustainable fisheries to achieve

348   ecosystem-based management.

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357

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543 <u>Figures</u>
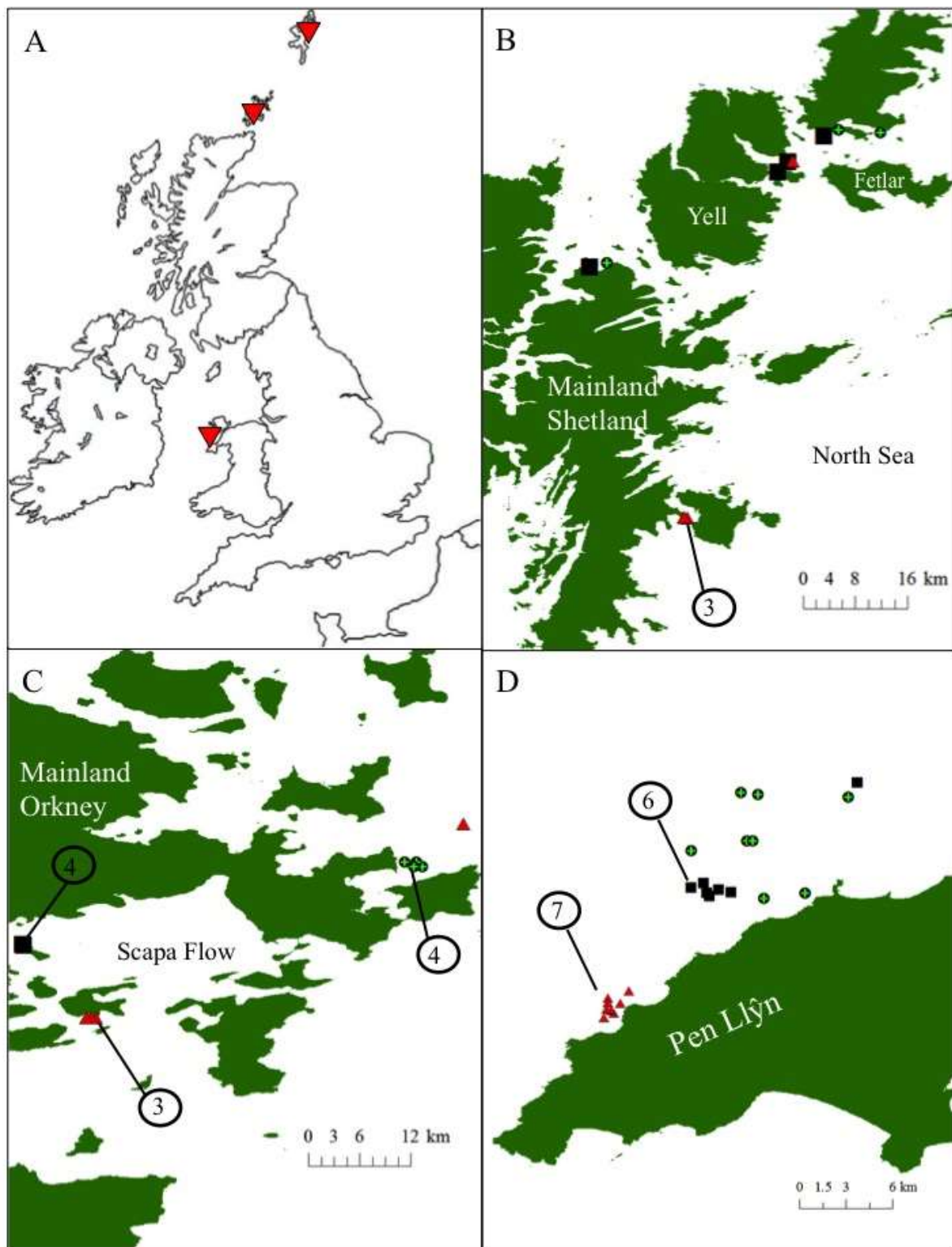
Figure 1. A) *M. modiolus* reefs study regions for megafauna abundance within the UK. B) Survey locations in Shetland (UVC method); C) Orkney (UVC method and stable isotope samples collected); and D) Pen Llŷn (Drop Down Video method). Positions are labelled with the number of sites where markers overlap. Black circle with green cross = sand habitats (16 sites in total); solid square = *M. modiolus* reefs (15 sites in total); red triangle = cobble habitats (15 sites in total).
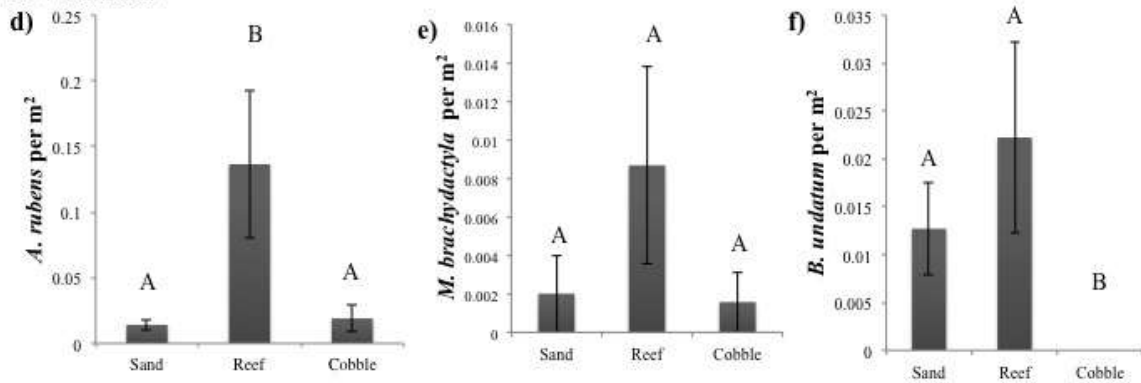
Figure 2. A) UVC transect technique, B) *Aequipecten opercularis*, C) *Pholis gunnelus,* D) *Buccinum undatum,* E) *Echinus esculentus* and *Asterias rubens* and F) *Pomatoschistus pictus*. Images A, B, D, and E: Richard Shucksmith, images C and F: George Stoyle.
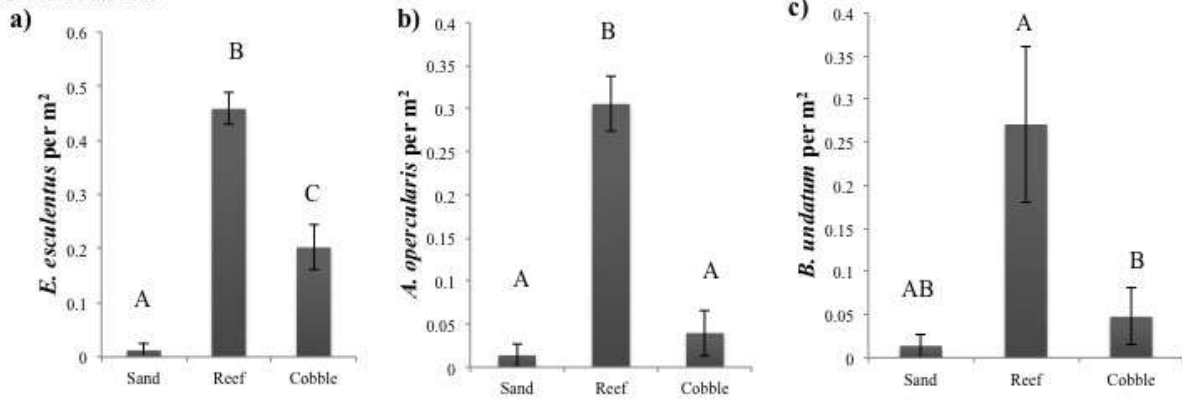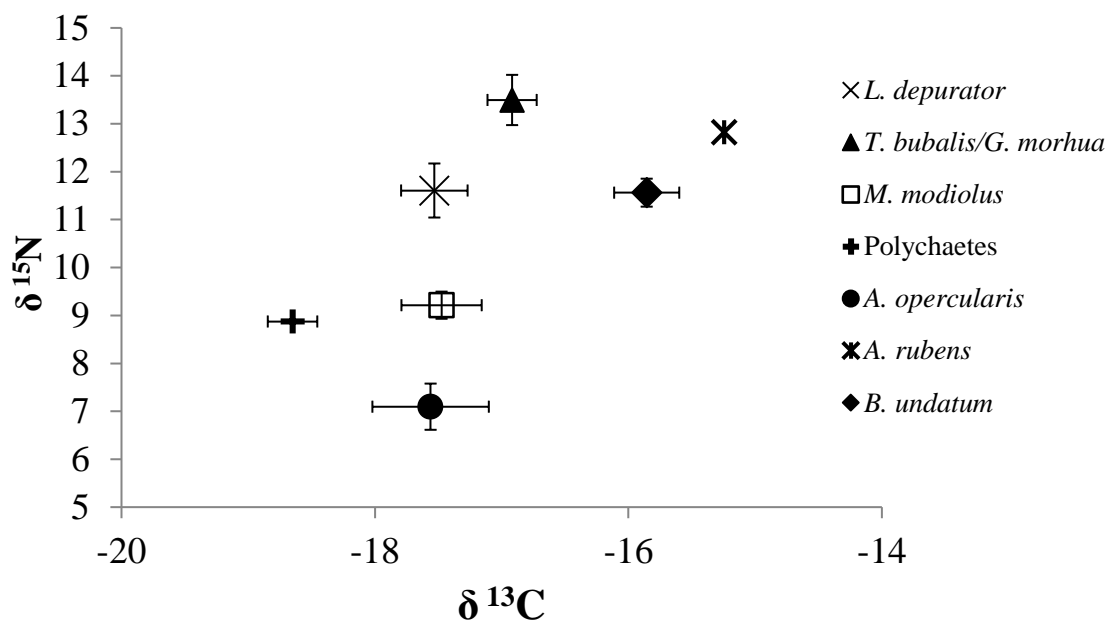
Figure 3. Counts of the key megafauna species from the UVC transects a) b) and c) and the DDV transects d), e) and f). Bars show the mean ± 1SE. Groups that share a capital letter are not significantly different at the 0.017 probability threshold (Bonferroni correction on Kruskal Wallis test).

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Figure 4. Carbon and Nitrogen isotope biplot of the *M. modiolus* reef community in Scapa Flow, Orkney showing average values ± 1 SD.

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Supplementary information

S1. Location of dive sites for stable isotope sample collection in Orkney

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Site	Latitude		Longitude	
West Cava	58	52.718	3	11.458
East Cava	58	50.966	3	11.041
Karlsrhue 1	58	53.357	3	11.394

S2. Underwater Visual Census (UVC) key species pairwise comparisons (Kruskal Wallis tests), Bonferroni correction; significance at $p < 0.016$.

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S3.

Key Species	Habitat comparison	X^2	P value
Buccinum undatum	Reef & Cobble	3.84	0.0500
	Reef & Sand	7.1358	0.0076
	Cobble and Sand	0.686	0.4073
Aequipecten opercularis	Reef & Cobble	11.0112	0.0009
	Cobble & Sand	0.6868	0.4073
	Reef & Sand	12.4272	0.0004
Echinus esculentus	Reef & Cobble	9.422	0.0021
	Cobble & Sand	10.8482	0.0009
	Reef & Sand	12.3077	0.0005

Drop Down Video (DDV)

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585   key species pairwise comparisons (Kruskal Wallis tests), Bonferroni correction; significance at p <
586   0.016.

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Key Species	Habitat comparison	X^2	P value
Buccinum undatum	Reef & Cobble	6.55	0.0100
	Reef & Sand	0.0269	0.8690
	Cobble & Sand	6.5502	0.0100
Maja brachydactyla	Reef & Cobble	2.6042	0.1066
	Reef & Sand	2.6042	0.1066
	Cobble & Sand	0	1.0000
Asterias rubens	Reef & Cobble	9.258	0.0023
	Cobble & Sand	0.0509	0.8214
	Reef & Sand	11.618	0.0007

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