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Aggregations of brittle stars can provide similar ecological roles as mussel reefs.

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Running header: Aggregations of mussels and brittle stars

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1 Abstract

2 Biogenic habitats, such as coral reefs, facilitate diverse communities. In aquatic systems,

3 aggregations of mobile benthic species may play a similar ecological role to that of typically

4 sessile biogenic habitats, however, this has rarely been considered. We quantified the abundance

5 of sessile mussels (*Modiolus modiolus*) and aggregating brittle stars (*Ophiotrix fragilis*) and

6 tested for correlations between the density of mussels (live and dead) and brittle stars each with:

7 1) abundance, biomass, diversity and assemblage structure of associated benthic macrofauna;

8 and 2) percent organic matter of the sediment. We found that the abundance of live *M. modiolus*

9 was positively associated with the abundance and biomass of macrofauna. The positive

10 association between *M. modiolus* and macrofauna abundance was further amplified with an

11 increase in brittle stars and a decrease in dead mussel shells. Macrofauna biomass was lower

12 with more dead mussel shells and macrofauna diversity increased with more live *M. modiolus*

13 and brittle stars. Sediment organic matter was positively related with brittle star density, but not

14 with the abundance of live or dead mussels. The positive relationship between brittle stars and

15 sediment organic matter suggests that brittle stars could enhance rates of benthic-pelagic

16 coupling. Given the importance of understanding the functional role of threatened habitats, it is

17 essential that the underlying community patterns be understood through robust observational

18 studies to then derive testable hypotheses to determine drivers. These findings provide novel

19 insight into the ecological role of aggregations of mobile species, which is essential to prioritize

20 conservation and restoration strategies.

Introduction

21

22 Habitat-forming species, such as corals or trees, are widespread in terrestrial and aquatic

23 ecosystems worldwide. These species create complex biogenic habitats, which are the foundation

24 of communities that do not exist in their absence (Bertness & Callaway 1994, Stachowicz 2001).

25 Increased habitat complexity facilitates increased species richness by reducing predation,

26 competition and disturbance pressure (Stachowicz 2001, Bruno et al. 2003). In aquatic

27 ecosystems, biogenic habitats such as seagrass, saltmarsh, mangroves, and bivalve reefs provide

28 multiple ecosystem services including, the enhanced production of economically important

29 species, reduced erosion rates, and nutrient removal (Costanza et al. 1997, Grabowski &

30 Peterson 2007, Barbier et al. 2011). Unfortunately, these marine species are impacted heavily by

31 human activities and most are reduced to a fraction of their historical abundance globally

32 (Waycott et al. 2009, Beck et al. 2011, De'ath et al. 2012). The loss of biogenic habitats has in

33 some instances negated their ecological roles and severely diminished the benefits they provide

34 to society (Waycott et al. 2009, Ermgassen et al. 2012, 2013).

35 Aggregations of mobile fauna are generally considered deleterious to ecosystems; for

36 example outbreaks of urchins can denude large areas once covered with macroalgae (Steneck et

37 al. 2004). However, aggregations of mobile species can potentially provide similar functions as

38 sedentary, foundation species and create biogenic habitats. For instance, aggregations of urchins

39 can increase biodiversity and provide shelter for prey (Altieri & Witman 2014).

40 Mussel reefs, similar to oyster reefs, have been depleted worldwide (Lotze et al. 2006).

41 The horse mussel, *Modiolus modiolus*, forms reefs in the North Atlantic ocean (Sanderson et al.

42 2008, Wildish et al. 2009) and its abundance has declined most likely from habitat destruction

43 following fishing practices (Magorrian & Service 1998, Strain et al. 2012, Cook et al. 2013) and

44   global warming (Gormley et al. 2013). The complex habitat that *M. modiolus* reefs create is

45   known for its high diversity of organisms (Rees et al. 2008, Ragnarsson & Burgos 2012, Fariñas-

46   Franco et al. 2013). The loss of live mussels can result in a matrix of dead shell. Experimental

47   studies that held shell structure constant found that loss of live blue mussels reduce abundance

48   but not diversity of macrofauna (Norling & Kautsky 2007, Norling et al. 2015), but the loss of

49   live *M. modiolus* on reef ecology in natural settings is unknown.

50   Brittle stars occur in dense aggregations throughout the globe (Fedra 1977, Fratt &

51   Dearborn 1984). In particular, the suspension feeding brittle star, *Ophiothrix fragilis*, exists in

52   dense beds of more than 1,000 individuals m^{-2} around Britain and Ireland (Warner 1971,

53   Aronson 1989, Dauvin et al. 2013). *Ophiothrix fragilis* beds exist in similar environments as *M.*

54   *modiolus* reefs and co-occur in some areas (Sanderson et al. 2008, Ragnarsson & Burgos 2012).

55   Although it was thought that aggregations of *O. fragilis,* which often overlay *M. modiolus reefs,*

56   may have negative effects on benthic macrofauna from smothering and competition effects,

57   many species of macrofauna were recorded beneath brittle star beds (Warner 1971). Brittle stars

58   could facilitate benthic fauna by enhancing deposition of organic material (Warner 1971, Murat

59   et al. 2016) and provide refuge from predators. Dense aggregations of this mobile species could

60   provide ecological benefits similar to sessile reef forming species. In addition, there could be

61   emergent properties when dense aggregations of both sessile and mobile species exist together

62   (Angelini et al. 2011). However, our understanding of ecological roles associated with these two

63   habitats, beds of mobile species and reefs of sessile species, is limited.

64   *Modiolus modiolus* is protected in Europe under Annex I of the EU Habitats Directive

65   (Directive 93/43/EEC) and the OSPAR convention (Rees et al. 2008). Therefore a survey based

66   on benthic grabs was designed to determine the extent and condition of *M. modiolus* reefs in

4

67   Northern Ireland to inform management decisions about their conservation. This intensive survey

68   allowed an unprecedented opportunity to study this heavily protected biogenic habitat and

69   determine ecological patterns which are a necessary precursor to conducting manipulative

70   experiments to pinpoint underlying mechanisms (Underwood et al. 2000). Our aim was to

71   characterize the ecological roles of a declining biogenic-reef forming species, *M. modiolus*, and a

72   common co-occurring benthic species, *O. fragilis*. We quantified how the abundance of live *M.*

73   *modiolus*, *M. modiolus* shell (dead *M. modiolus*) and *O. fragilis* was related with: (i) macro-

74   benthic species abundance, biomass, richness, diversity and assemblage structure; and (ii)

75   sedimentary organic matter. We hypothesized that the abundance of live *M. modiolus* and *O.*

76   *fragilis* would have a similar positive relationship with the abundance, biomass, richness and

77   diversity of the benthic macrofauna, and the sediment organic matter. Moreover, the abundance

78   of *M. modiolus* shell would not have a correlation with the abundance, biomass, richness, and

79   diversity of the benthic macrofauna, and the sediment organic matter because shell has less

80   structural complexity compared to live mussels and does not produce fecal matter (as would be

81   expected in reefs comprised of mainly live animals). Finally, prevalence of live *M. modiolus*, *M.*

82   *modiolus* shell and *O. fragilis* will explain a similar amount of variation in the macrofauna

83   assemblage.

84

85   **Materials and Methods**

86   **Data collection**

87   To quantify the variation in benthic fauna and sediment organic matter related with the

88   abundance of *M. modiolus*, *M. modiolus* shell, and *O. fragilis*, a grab sampler was used to sample

89   53 sites at two locations off the east coast of Northern Ireland at depths of 20-30 m (Fig. 1).

5

90   Sampling sites were dispersed evenly within different acoustic signatures of a single beam sonar

91   survey conducted by Northern Ireland Agri-Food and Biosciences Institute in 2014 (unpub.

92   data). Samples were collected over 5 days between the 9th of September and the 16th of

93   December 2014. The Day grab used in this study removed approximately 0.1 m^2 area of

94   substratum (approximately 2 l of sediment; Appendix S1). Grabs with minimal sediment (< 1 L

95   of sediment) were recorded as misfires and the grab was deployed again. Three replicate grabs

96   were taken at each site unless 3 successive misfires were recorded and no more samples were

97   taken at that site. The environment of these locations made diver surveys impractical (depth and

98   currents) and although larger grab samples would have been optimal, a day grab was used to

99   remove a minimal amount of the protected *M. modiolus* reef. Each sample was photographed and

100   the percentage cover of *M. modiolus* shell, mud, and sand were estimated visually based on the

101   grab surface (Appendix 2). Sediment samples were taken from the top 2 cm of 2 haphazardly

102   chosen grabs from each site. However, sediment was collected from all three samples from 9

103   sites because live *M. modiolus* was present in the grabs. Sediment organic matter was collected

104   from 101 grabs at 46 sites. Sediment samples were freeze dried, sieved through 1 mm mesh, and

105   placed in a combustion oven at 500°C for 6 hours (Dean 1974). The percent organic matter was

106   determined by dividing the difference in mass of the sediment before and after combustion by

107   the mass of the sediment before combustion.

108   Conspicuous macrofauna were quantified from 140 grab samples at 53 sites, which were

109   searched thoroughly on the boat after the grab sample was sieved through 1 mm mesh and all

110   bivalves, crustaceans, echinoderms, fish, gastropod, and polychaetes were collected and frozen.

111   Macrofauna were identified to the lowest practical taxon, counted and wet weight recorded for a

112   total taxon biomass. Macrofauna identification was based on morphological characteristics

113   following guides (Hayward & Ryland 1995). A subset of grab samples (approximately 1 grab

114   from each site) were returned to the laboratory and cryptic species, which were not attached to

115   the substratum, were quantified in addition to the conspicuous macrofauna (Appendix S3).

116   Results of analyses from these samples were consistent with those based on conspicuous fauna

117   thus for clarity we are presenting only the findings for the conspicuous fauna. Animal handling

118   protocols followed the ethical guidelines of Queen's University Belfast.

119   **Data Analysis**

120   We tested effect of substrate type (live *M. modiolus*, *M. modiolus* shell, or *O. fragilis*) on benthic

121   macrofauna abundance, biomass, taxon richness, diversity and assemblage structure.

122   The abundance of *M. modiolus* and *O. fragilis* in grab samples were *a priori* determined as

123   predictor variables and not included as benthic fauna in the analyses. Generalized linear models

124   were used to test for variations in total faunal abundance and taxon richness associated with

125   changes of the three habitat types (*M. modiolus*, *M. modiolus* shell, and *O. fragilis*) with Poisson

126   distributions because data were skewed towards zero. General linear models were used to test for

127   variations in non-integer dependent variables (biomass and diversity) associated with changes in

128   the three habitat types. Diversity for each sample was calculated with the Shannon-Weaver

129   index. Multi-collinearity between predictor variables was tested using the variance inflation

130   factor (VIF) and < 10 indicated minimal multi-collinearity (Hair 2006). Site within location

131   (North or South as shown in Fig. 1) was included as random variables in the model to account

132   for the nested sampling design. All interactions were included in the models and the predictor

133   variables were centred (the mean was subtracted from each value) to reduce multi-collinearity

134   between predictor variables and interactions (Quinn & Keough 2002) and scaled (divided by the

135   standard deviation) to reduce the difference in magnitude among the predictor variables (Bates et

136 al. 2014). All analyses were conducted in R (R Development Core Team 2012). Diversity was

137 calculated using the div function within the v*egan* package (Oksanen et al.). The glmer function

138 within the *lme4* package (Bates et al. 2014 4) was used for both abundance and richness of

139 benthic fauna. Biomass, diversity and organic matter were analysed using lmer function within

140 the *lme4* package to calculate t values, while the Analysis of Variance (ANOVA) function within

141 the *car* package was used to generate p values and test for significance (Fox & Weisberg 2011).

142 Interactions and random variables (site nested in location) were included in the organic matter

143 model. Models were checked to ensure an adequate fit by visually inspecting residuals vs fitted

144 (randomly distributed points) and Q-Q (points were near 1:1 ratio) plots (Crawley 2007).

145 Biomass of macrofauna was log transformed to improve model fit.

146   To quantify the amount of variation in benthic fauna assemblage explained by the

147 abundance of *M. modiolus*, *M. modiolus* shell, and *O. fragilis*, which were all continuous

148 variables, we used Permutational Analysis of Variance (PERMANOVA, McArdle & Anderson

149 2001, Anderson 2001) and redundancy analysis (RDA, Legendre & Anderson 1999).

150 PERMANOVA partitions the variation of a resemblance matrix among sources of variation and

151 fits linear models to test hypotheses and build models without ordination. RDA performs

152 ordination of fitted values to test hypotheses, build models, and create visualizations of the data

153 (Legendre & Anderson 1999). RDA reduces the variance into dimensions, which makes

154 visualizations of the data possible but may reduce the amount of variance explained by predictor

155 variables. However, PERMANOVA analyzes the data without constraining the variance into

156 dimensions so that the relationship between community structure and predictor variables is

157 probably closer to what exists naturally. Histograms of each predictor variable and scatter plots

158 of all combinations of predictor variables were examined to ensure there were no extreme

159   outliers. Linear-based analyses can be biased by multi-collinearity (Legendre & Anderson 1999),

160   we tested for multi-collinearity as previously described using VIF. Multivariate analyses used the

161   *vegan* package version 2.2-0 (Oksanen et al. 2010).

162   Taxon-specific abundances were log-transformed to reduce the influence of abundant

163   taxa in the analyses, and a Bray-Curtis dissimilarity matrix was created (Anderson et al. 2008,

164   Legendre & De Cáceres 2013). The mean of taxon abundance per site was used to remove the

165   possibility of non-independent samples within each site. Interactions were included in the

166   sequential PERMANOVA and predictor variables were centred and scaled to reduce

167   multicollinearity between variables and interactions. A second PERMANOVA was run with

168   taxon-specific biomass following the same procedure described for abundance.

169

170   **Results**

171   *Modiolus modiolus* was present in 45 of the samples and ranged from 1 to 65 individuals per

172   grab (~10 to 650 m^{-2}). *Ophiotrix fragilis* was present in 81 (out of 140) of the samples which

173   ranged from 1-203 individuals per grab (~10 to 2,030 m^{-2}). Fifty-seven different taxa were

174   quantified in the samples (Appendix S3). The substratum of the grabs was primarily *M. modiolus*

175   shell and mud, with sand being less prevalent (Appendix 4). The abundance of live *M. modiolus*

176   and *O. fragilis* had similar patterns with changes in the different types of substratum. The

177   abundance of benthic fauna increased with the number of live *M. modiolus* and there were

178   interactions between *M. modiolus* and *O. fragilis*, and *M. modiolus* and *M. modiolus* shell (Table

179   1; Fig. 2A, D and G; Fig. 3). The interaction between *M. modiolus* and *O. fragilis* resulted from a

180   greater increase in fauna abundance as *M. modiolus* increased when there were more *O. fragilis*

181   (Fig 3A). The opposite trend existed for the interaction between *M. modiolus* and *M. modiolus*

182   shell; there was a greater increase in fauna abundance as *M. modiolus* increased when there was

183   less shell (Fig 3B). Biomass of macrofauna increased with *M. modiolus*, but decreased with *M.*

184   *modiolus* shell (Table 1; Fig 2B and E). The interaction between all predictor variables was also

185   significant for the biomass of macrofauna (Table 1).

186   The three predictor variables did not explain a significant amount of variation in the

187   number of taxon (richness) in a sample and there were no significant interactions (Table 1). *M.*

188   *modiolus* and *O. fragilis* were associated with an increase in the macrofauna diversity (Table 1,

189   Fig 2C and I). *O. fragilis* was positively related with organic matter, while the prevalence of *M.*

190   *modiolus* or *M. modiolus* shell did not explain a significant amount of variation in organic matter

191   (Table 1; Fig. 4A-C). The three-way interaction was significant for organic matter and resulted

192   from a positive relationship between *O. fragilis* and organic matter, which was greatly reduced

193   with an increase in *M. modiolus* abundance and reduced with an increase in *M. modiolus* shell

194   cover (Fig. 4D).

195   The amount of variation in faunal assemblage using abundance explained by *M.*

196   *modiolus*, *O. fragilis*, and *M. modiolus* shell was quantified using a PERMANOVA. *Modiolus*

197   *modiolus* ($F_{1,52} = 3.16$; P<0.001), *O. fragilis* ($F_{1,52} = 5.45$; P<0.001), and *M. modiolus* shell ($F_{1,52}$

198     $= 5.11$; P<0.001) were significant and explained more variation in fauna assemblage than would

199   be expected by random chance. No interactions were significant. *Modiolus modiolus* shell

200   explained the most variation in macrofauna assemblage of the 3 continuous predictor variables

201   ($R^2 = 8.4\%$), followed by *O. fragilis* ($R^2 = 5.7\%$), and *M. modiolus* ($R^2 = 5.2\%$). The RDA

202   represents the relationship between predictor variables and individual taxon. RDA explained

203   10.7% of the variation in fauna assemblage. The first and second axes explained 6.5 and 2.9% of

204   the variation respectively. *Modiolus modiolus* was positively related with axis 1 and *M. modiolus*

205   shell was positively related with axis 2 (Appendix S5). *Ophiocomina nigra* (a brittle star) was

206   positively related with the second axis, and *Ophiura* spp. (a brittle star) and *Timoclea ovata* (a

207   bivalve) were negatively related with the second axis (Appendix S5). The fauna assemblage

208   based on biomass had similar findings as the assemblage using abundance with all three

209   predictor variables explaining a significant amount of variation. *Modiolus modiolus* shell

210   explained the most variation in macrofauna assemblage of the 3 continuous predictor variables

211   ($R^2 = 8.7\%$), followed by *O. fragilis* ($R^2 = 6.3\%$), and *M. modiolus* ($R^2 = 4.1\%$).

212

213   **Discussion**

214   Biogenic habitats composed of aggregations of sessile species, often referred to as

215   meadows or reefs, are touted for their ecological and economic benefits (Anton et al. 2011,

216   Barbier et al. 2011, Firth et al. 2015). On the other hand, dense aggregations of mobile species

217   are generally viewed negatively; however, this study indicates that increasing densities of *O.*

218   *fragilis* were associated with greater macrofauna diversity and organic matter, and had a positive

219   emergent effect on the total abundance of fauna within *M. modiolus* reefs. Although these results

220   are correlations, they could suggest that aggregates of brittle stars enhance diversity of

221   macrofauna and increase sediment organic matter similar to or more than filter feeding bivalves.

222   The ecological effect of a single foundation species on the local community has been

223   extensively studied (Grabowski et al. 2005, Geraldi et al. 2009), however, multiple species often

224   coexist together and little is known about potential interactions among different species

225   (Angelini et al. 2011, Donadi et al. 2015). One study that included multiple ecosystem engineers

226   found that the presence of *Caulerpa taxifolia*, a macroalgae, near *Anadora trapezia*, a clam,

227   increased diversity and abundance of epibiota on the bivalve (Gribben et al. 2009). Most of these

228   studies focused on relatively sessile species and there is the potential for mobile species to also

229   enhance both density and diversity of associated fauna (Altieri & Witman 2014). The abundance

230   of *O. fragilis* was related with enhanced diversity of macrofauna and had a positive emergent

231   effect with *M. modiolus* reefs on the abundance of macrofauna. In addition, minimal

232   multicolinearity among predictor variables indicates that there was no facilitation between *O.*

233   *fragilis* and *M. modiolus*, and that abundances of live and dead *M. modiolus* were independent.

234   Finally, all three habitat types measured had similar influence on the macrofauna assemblage

235   (explained between 5 and 8% of the variation in assemblage).

236   Our conclusions are based on a robust survey, which aimed to identify ecological patterns

237   associated with different dominant species (mussels and/or brittle stars). Experimental

238   manipulation is required to determine the mechanisms driving these differences, which is

239   difficult given the ethical and logistical limitations of manipulating a rare species that primarily

240   exist in areas with high currents and deeper than 20 m. Given our existing knowledge,

241   aggregations of brittle stars and other mobile species appear to share similar roles as some well-

242   described sessile foundation species. For example, positive effects on the macrofauna

243   community associated with aggregations of mobile fauna could result from reduced predation

244   from provision of shelter (Bruno et al. 2003) or from increased food provision via biodeposition

245   (Norling & Kautsky 2007).

246   Understanding how the loss of individual bivalves from reefs affects ecological

247   functioning is important given the prevalence of reef degradation (Beck et al. 2011, Ermgassen et

248   al. 2012). Teasing apart the provision of habitat by the physical structure from the biotic function

249   of bivalve reefs has been studied using experimental reefs. For example, the diversity of

250   macrofauna was similar on blue mussel (*Mytilus edulis*) reefs compared to reefs made of intact

251   shells, while the abundance was greater on live reefs possibly because of resources supplied by

252   biodeposition (Norling & Kautsky 2007). Similarly, another study found that diversity of

253   epibenthic fauna was similar among live and dead experimental reefs of oysters or mussels,

254   while abundance of epibenthic fauna was greatest on oyster shell, moderate on live bivalve reefs

255   and lowest on mussel shell reefs (Norling et al. 2015). We found that the amount of naturally

256   occurring dead shell was not related with the abundance, richness and diversity of benthic

257   macrofauna, and that dead shell cover was negatively related with the biomass of macrofuana.

258   Separating the role of the physical reef structure from associated biotic functioning is necessary

259   to identify ecological mechanisms, and also to predict changes in ecosystem functioning

260   associated to bivalve mortality from direct or indirect anthropogenic impacts.

261   Biodeposition by filter feeding bivalves is an important process in coastal ecosystems

262   because it couples pelagic and benthic communities. Benthic-pelagic coupling may reduce

263   occurrences of hypoxia by directly reducing phytoplankton abundance (Dame & Olenin 2005,

264   Grizzle et al. 2008) and indirectly through nitrogen removal by enhancing denitrification on the

265   sediment because of the high quality resources provided by biodeposits (Kellogg et al. 2013,

266   Smyth et al. 2013, 2015). *Modiolus modiolus* produce nutrient rich biodeposits (Navarro &

267   Thompson 1997), however, we did not identify a relationship between *M. modiolus* density and

268   sediment organic matter content. We did find a positive relationship between brittle star density

269   and organic matter content. This relationship could have resulted from brittle stars preferring

270   benthos with greater organic matter. However, our results indicate that *O. fragilis* and *M.*

271   *modiolus* have similar abundance patterns in shell, mud and sandy substratum suggesting that

272   brittle stars are not preferentially selecting one type of substratum that could be causing this

273   relationship, which is likely driven by benthic-pelagic coupling. A positive relationship between

274 total organic carbon and brittle star density was found in stable environments (Murat et al. 2016)

275 and benthic-pelagic coupling associated with brittle star beds was suggested to reduce

276 eutrophication in coastal bays (Hily 1991). Both *M. modiolus* and *O. fragilis* are suspension

277 feeders but use entirely different mechanisms to collect suspended particles. *M. modiolus* is an

278 active filter feeder while *O. fragilis* passively feeds on phytoplankton (Roushdy & Hansen 1960,

279 Migne et al. 2012, BlanchetAurigny et al. 2015). The stronger association between brittle stars

280 and sediment organic matter compared to *M. modiolus* could result from *O. fragilis* having a low

281 absorption efficiency (Migné & Davoult 1998) or that aggregations reduce water motion and the

282 erosion of biodeposits (Warner 1971) more than mussel reefs. Our findings, that organic matter

283 was positively related with brittle star abundance and not *M. modiolus* density, may suggest that

284 benthic-pelagic coupling in brittle star beds is potentially greater than in bivalve reefs and this

285 should be investigated further.

286   The ecological and economic benefits of marine biogenic habitats, such as coral reefs,

287 salt marshes and bivalve reefs, are well known and are the impetus for their conservation and

288 restoration (Brumbaugh & Coen 2009, Barbier et al. 2011, Geraldi et al. 2013, La Peyre et al.

289 2014). Beds of brittles stars may enhance the diversity of macrofauna and increase benthic-

290 pelagic coupling equal to or greater than bivalve reefs. The carbon budgets associated with

291 biomass production and calcification has been quantified for brittle star beds (Migne et al. 1998,

292 Davoult et al. 2009, Lebrato et al. 2010), however, their potential importance for other rates of

293 ecosystem functioning and associated services is relatively unknown. The ecosystem functions

294 provided by brittle stars are probably context-dependent, but the global functional role of these

295 taxa may be equal to or greater than other sessile foundation species for multiple reasons. First,

296 brittle star beds are prevalent around the globe given that they have been documented from the

297   Arctic (Piepenburg & Schmid 1996, Blicher & Sejr 2011) to the Antarctic (Fratt & Dearborn

298   1984) and throughout the mid-latitudes (Haedrich et al. 1980, Fujita 1990). They are also present

299   at broad depth ranges (Lebrato et al. 2010) and not restricted to estuaries and coasts like

300   traditional biogenic habitats.

301   Determining the ecological functions provided by aggregations of mobile species and

302   comparing these to functions provided by traditional biogenic habits, as well as potential

303   emergent effects between the two are needed to understand the relative importance of these

304   species to broader ecosystem processes and functions. This is of utmost importance as humans

305   are constantly altering the abundance and extent of both sessile and mobile species. The applied

306   implications of these results, if confirmed by manipulative experiments, include assigning

307   aggregates of mobile species similar conservation status as sessile foundation species (Peterson

308   & Lipcius 2003, Byers et al. 2006, Lampert & Hastings 2014).

309

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515   Table 1. Summary of statistical models to assess the relationship between the predictor variables

516   (abundance of *M. modiolus*, *M. modiolus* shell, and *O fragilis*) and the abundance, biomass,

517   richness, and diversity of benthic fauna, and organic matter collected in samples (significant

518   predictor variables and interactions are bold).

Dependent variable	Independent variable	Estimate	Std. Error	z or t value	p value
# of individuals	**M. Modiolus**	**0.981**	**0.111**	**8.81**	**<0.001**
	M. Modiolus shell	0.004	0.066	0.06	0.957
	O. fragilis	-0.083	0.061	-1.35	0.178
	M. Modiolus: M. Modiolus shell	**-0.678**	**0.106**	**-6.38**	**<0.001**
	M. Modiolus: O. fragilis	**0.162**	**0.078**	**2.07**	**0.038**
	M. Modiolus shell: O. fragilis	0.012	0.045	0.27	0.789
	M. Modiolus: M. Modiolus shell: O. fragilis	-0.004	0.075	-0.06	0.954
Biomass	**M. Modiolus**	**0.009**	**0.028**	**0.32**	**<0.001**
	M. Modiolus shell	**-0.008**	**0.003**	**-2.39**	**<0.001**
	O. fragilis	0.002	0.001	1.52	0.214
	M. Modiolus: M. Modiolus shell	0.001	0.001	1.18	0.744
	M. Modiolus: O. fragilis	0.001	0.000	1.67	0.920
	M. Modiolus shell: O. fragilis	0.000	0.000	0.90	0.230
	M. Modiolus: M. Modiolus shell: O. fragilis	**0.000**	**0.000**	**-2.09**	**0.037**
# of species	M. Modiolus	0.090	0.095	0.95	0.344
	M. Modiolus shell	-0.022	0.050	-0.44	0.662
	O. fragilis	0.016	0.040	0.40	0.691
	M. Modiolus: M. Modiolus shell	-0.062	0.093	-0.66	0.508
	M. Modiolus: O. fragilis	0.027	0.084	0.33	0.744
	M. Modiolus shell: O. fragilis	0.003	0.038	0.09	0.928
	M. Modiolus: M. Modiolus shell: O. fragilis	0.029	0.087	0.33	0.739
Diversity	**M. Modiolus**	**0.256**	**0.170**	**1.51**	**0.032**
	M. Modiolus shell	-0.116	0.086	-1.35	0.069
	O. fragilis	**0.129**	**0.068**	**1.90**	**0.021**
	M. Modiolus: M. Modiolus shell	-0.127	0.166	-0.77	0.335
	M. Modiolus: O. fragilis	0.042	0.145	0.29	0.963
	M. Modiolus shell: O. fragilis	0.081	0.066	1.23	0.235
	M. Modiolus: M. Modiolus shell: O. fragilis	-0.055	0.152	-0.36	0.719
Organic matter	M. Modiolus	0.001	0.002	0.61	0.605
	M. Modiolus shell	-0.002	0.001	-1.16	0.636
	O. fragilis	**0.002**	**0.001**	**1.72**	**0.048**
	M. Modiolus: M. Modiolus shell	-0.001	0.002	-0.69	0.928
	M. Modiolus: O. fragilis	-0.005	0.002	-2.95	0.388
	M. Modiolus shell: O. fragilis	-0.002	0.001	-1.36	0.677
	M. Modiolus: M. Modiolus shell: O. fragilis	**0.006**	**0.002**	**3.79**	**<0.001**

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524   Figure legends

525   Fig. 1. Sampling sites near the Outer Ards Peninsula, east coast of Northern Ireland. Three

526   replicate grab samples were taken at each site

527   Fig. 2. The relationship between the abundance (left column), biomass (middle column), and

528   diversity (right column) of benthic fauna quantified in day grabs, and *M. modiolus*, *M. modiolus*

529   shell or *O. fragilis*. Predictor variables that were significant are indicated by black lines (See

530   Table 1 for statistical summary).

531   Fig. 3. The interactions between the abundance of *M. modiolus* and *O. fragilis* (A) and between

532   *M. modiolus* and *M. modious* shell (B) in explaining variation in the abudnance of benthic fauna.

533   The data points and trend lines were catagorized based on abundance of *O. fragilis* (A) or

534   percent shell cover (B).

535   Fig. 4. The relationship between the abundance of *M. modiolus* (A), *M. Modiolus* shell (B), *O.*

536   *fragilis* (C), and the percent organic matter in sediment collected in day grabs. The interaction

537   between all three predictor variables and the percent organic matter (D). *O. fragilis* and the

538   interaction between the three predictor variables explained a significant amount of variation in

539   percent organic matter. Predictor variables that were significant are indicated by black lines (See

540   Table 1 for statistical summary).

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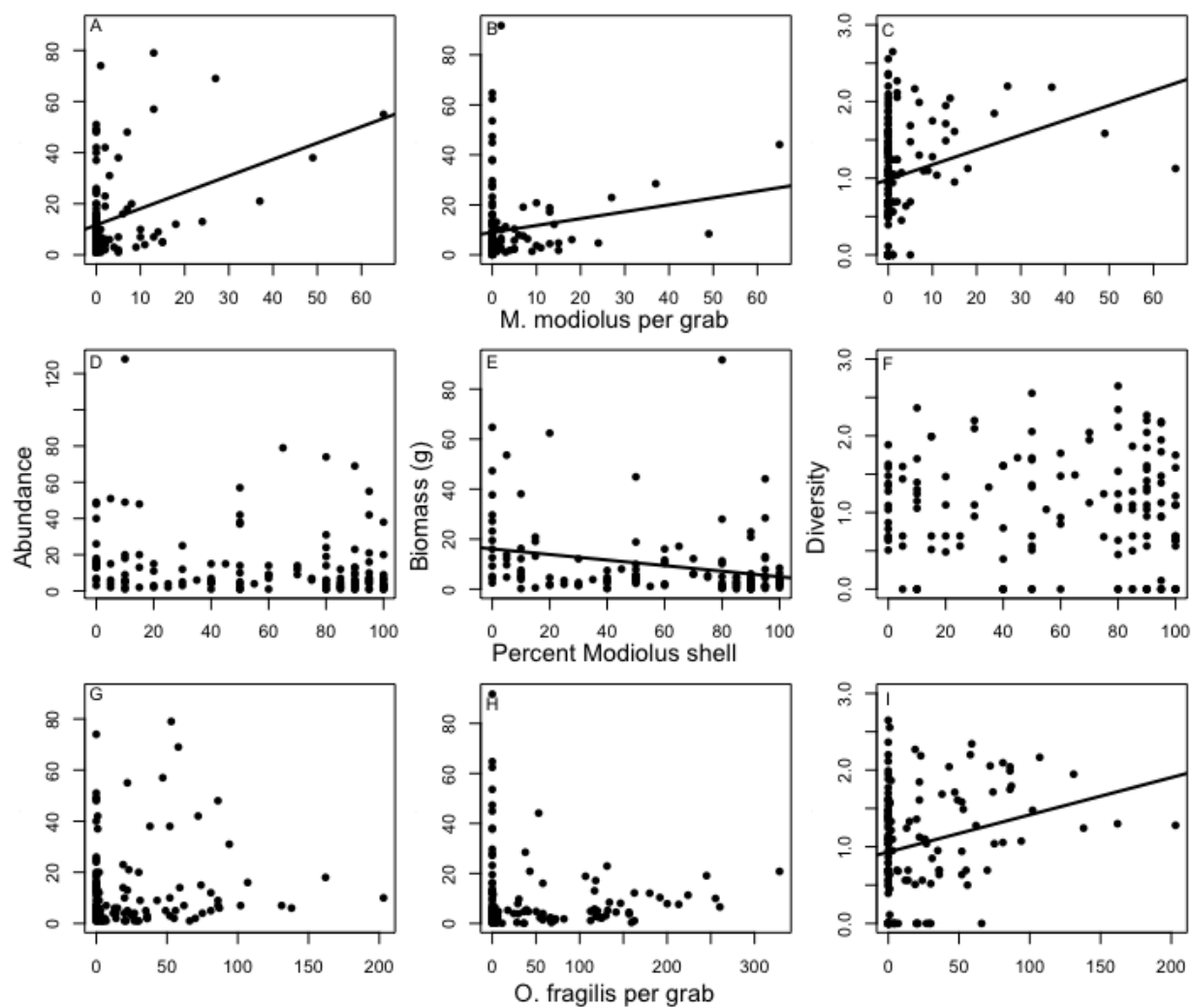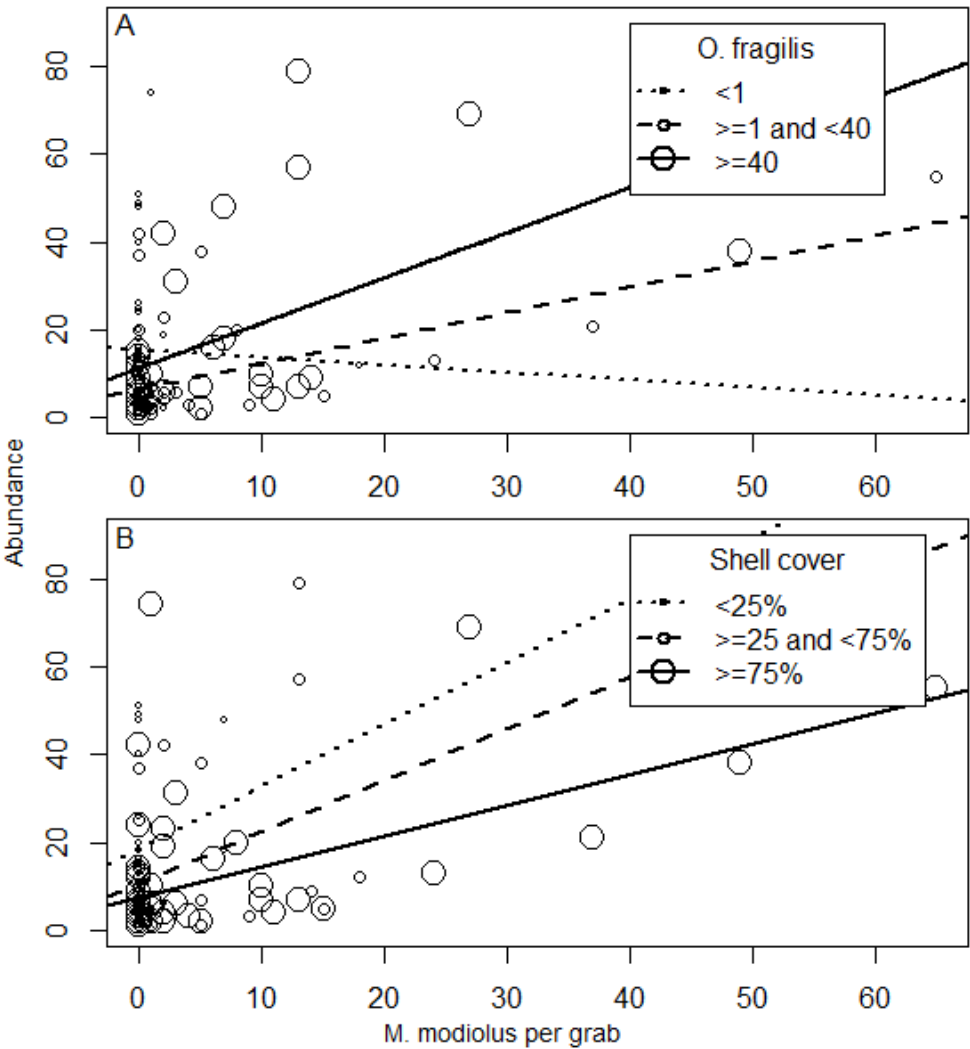542   Fig. 1
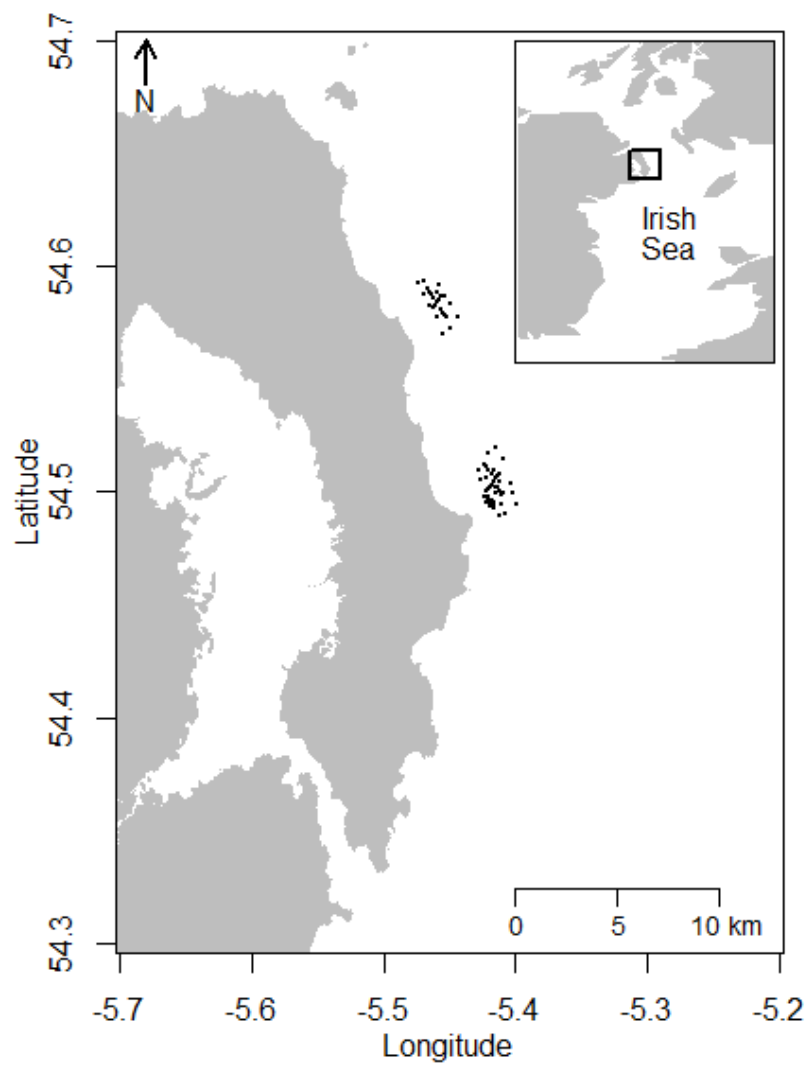
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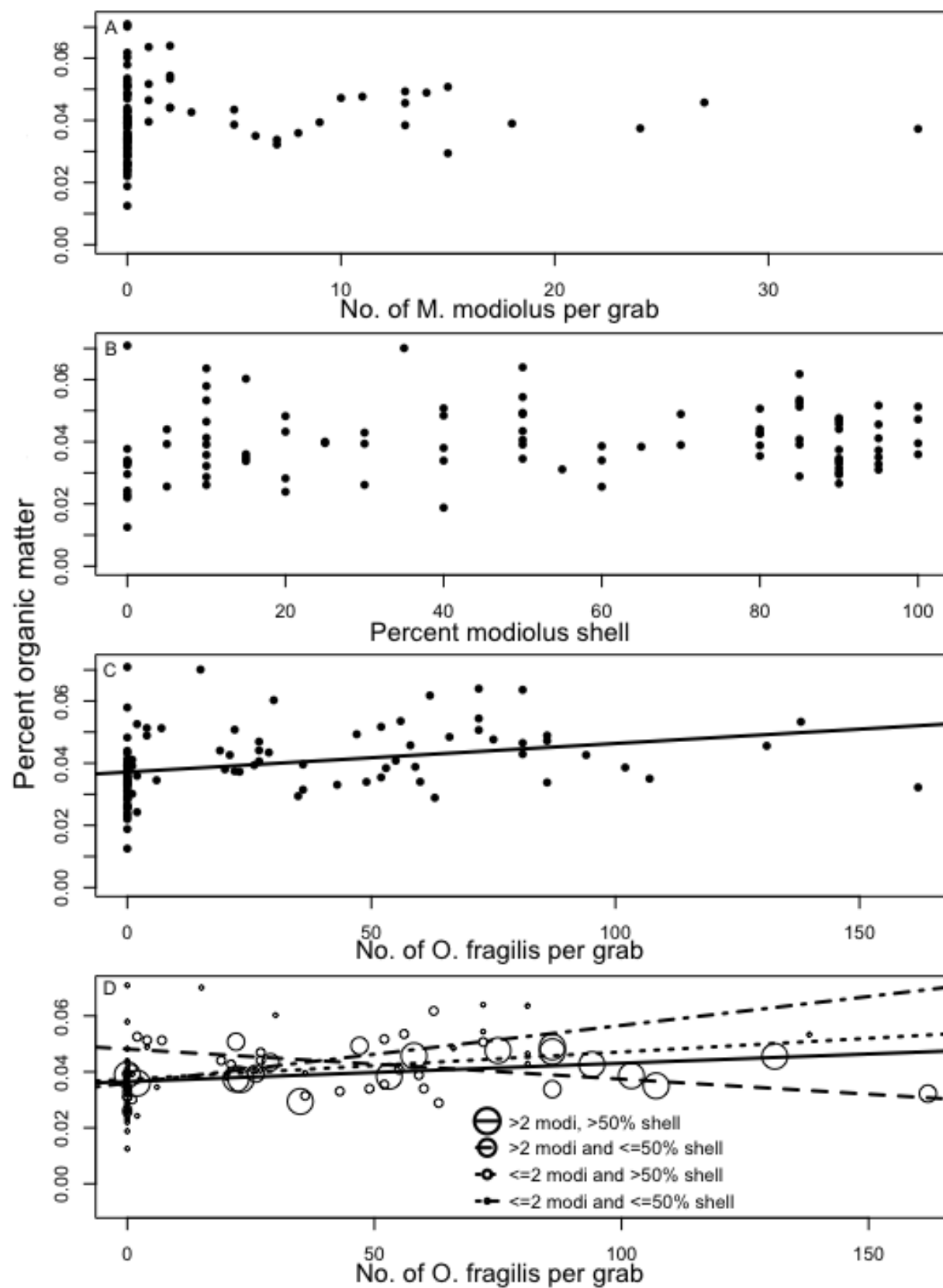546   Fig. 2

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554   Appendices

555   Appendix S1. Picture of the day grab used to sample fauna. Photo credit: C. Bertolini

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557   Appendix S2. Day grabs illustrating typical samples with *M. modiolus* and *O. fragilis* (A), *M.*

558   *modiolus* shell (B), *O. fragilis* (C), and mud (D). The grab sampled 0.1m^2. Photo credits: C.

559   Bertolini and N. Geraldi.

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562 Appendix S3. Taxon and their respective groups quantified in the grab samples. The proportion
563 for each taxon of the total number of individuals for the grabs that had all taxon quantified and
564 for the grabs that only conspicuous taxon were qunatified. Only data from conspicuous taxon
565 were used for all analyses.
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Taxa	Taxa group	Full	Conspicuous
Abra alba	Bivalve	0.248	0.254
Amphipholis squamata	Echinoderm		0.002
Amphiura chiajei	Echinoderm		0.008
Amphiura filiformis	Echinoderm		0.010
Anomiidae	Bivalve	0.018	
Aphrodita aculeata	Polychaete	0.001	0.001
Astarte sulcata	Bivalve	0.033	0.036
Atelecyclus rotundatus	Crustacean		0.001
Buccinum undatum	Gatropod	0.005	0.012
Capitellidae	Polychaete	0.046	
Caprella acanthifera	Crustacean		0.001
Clausinella fasciata	Bivalve	0.009	0.015
Crossaster papposus	Echinoderm		0.003
Diodera graeca	Gatropod		0.001
Ebalia tuberosa	Crustacean		0.003
Echinocardium cordatum	Echinoderm		0.001
Emarginula fissura	Gatropod	0.003	
Eschinus esculentus	Echinoderm	0.003	0.003
Eteone longa	Polychaete	0.004	
Eunereis longissima	Polychaete	0.004	
Eunicidae	Polychaete	0.005	
Euspira nitida	Gatropod	0.002	
Galathea	Crustacean		0.017
Galathowenia oculata	Polychaete	0.002	
Gammaridae	Crustacean		0.008
Gari depressa	Bivalve	0.024	0.021
Gari tellinella	Bivalve	0.027	0.030
Gattyana cirrhosa	Polychaete	0.002	
Gibbula cineraria	Gatropod	0.002	
Glycera spp.	Polychaete	0.004	
Glycimeris glycimeris	Bivalve	0.004	0.003
Gobiesocidae	Fish		0.004
Golfingiidae	Sipunucla	0.005	0.005
Harmothoe	Polychaete	0.014	0.009
Hesionidae	Polychaete	0.002	
Hiatella arctica	Bivalve	0.013	0.010
Hippolytidae	Crustacean		0.017

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Lepidonotus squamatus	Polychaete	0.013	0.010
Leptochiton asellus	Chiton	0.029	0.018
Limaria sp.	Bivalve	0.010	0.007
Liocarcinus spp.	Crustacean		0.004
Lumbrineridae	Polychaete	0.015	
Marthasterias glacialis	Echinoderm		0.008
Mediomastus fragilis	Polychaete	0.002	
Mimachlamys varia	Bivalve	0.018	0.017
Mya arenaria	Bivalve	0.009	0.009
Mya truncata	Bivalve	0.009	0.007
Myrtea spinifera	Bivalve	0.003	
Mytilus edulis	Bivalve		0.006
Nemertea	Nematode	0.001	0.003
Nephtheidae	Polychaete	0.027	0.018
Nereis spp.	Polychaete	0.001	0.001
Nucula nucleus	Bivalve	0.079	0.069
Nuculanidae	Bivalve	0.002	
Oenonidae	Polychaete	0.003	
Onchidoris spp.	Nudibranch	0.001	
Onoba semicostata	Gatropod	0.002	
Ophelina acuminata	Polychaete	0.009	
Ophiocomina nigra	Echinoderm		0.057
Ophiura spp.	Echinoderm		0.062
Orbiniidae	Polychaete	0.003	
Owenia fusiformis	Polychaete	0.013	0.008
Paguridae	Crustacean		0.024
Parvicardium pinnulatum	Bivalve	0.004	
Pecten maximus	Bivalve	0.003	
Pectinariidae	Polychaete	0.004	
Pherusa plumosa	Polychaete	0.058	0.038
Pholas dactylus	Bivalve		0.014
Pilumnus hirtellus	Crustacean		0.003
Pisa spp.	Crustacean		0.009
Pisidia longicornis	Crustacean		0.006
Platyhelminthes	Platyhelminthes	0.001	
Polynoidae	Polychaete	0.016	0.013
Psammechinus miliaris	Echinoderm	0.001	0.002
Sabellidae	Polychaete	0.045	
Scalibregma inflatum	Polychaete	0.011	
Scoloplos armiger	Polychaete	0.004	
Sepiola spp.	Cepholopod	0.001	
Serpulidae	Polychaete	0.005	0.006
Spatangus purpureus	Echinoderm		0.001

Spionidae	Polychaete	0.001	0.001
Talochlamys pusio	Bivalve		0.001
Tapes aureus	Bivalve	0.002	
Tapes rhomboides	Bivalve	0.005	
Terebellidae	Polychaete	0.020	0.017
Timoclea ovata	Bivalve	0.087	0.085
Tritia incrassata	Gatropod	0.001	0.005
Trivia arctica	Gatropod	0.002	
Tubificoides spp.	Polychaete	0.001	
Velutina velutina	Gatropod	0.002	

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569 Appendix S4
570 The abundance of *M. modiolus* (left column) and *O. fragilis* (right column) in grab samples

571 compared to the percent cover of 3 substrate categories. Substrate type was determined from

572 photos of grabs. Fitted lines were determined by the lowess function in R.
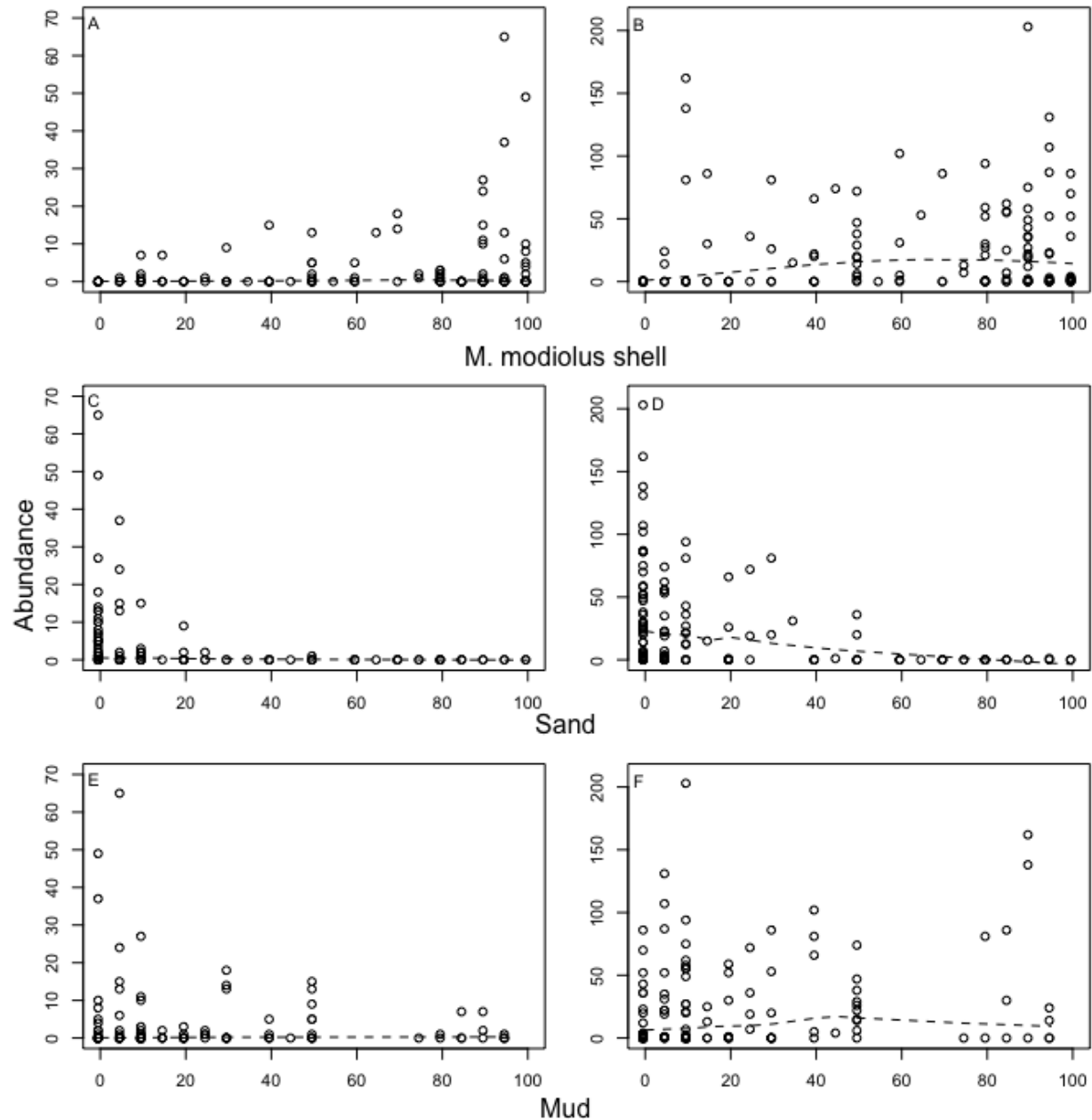
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575   Appendix S5. The first and second axis of RDA of the fauna assemblage in grab samples

576   overlaid with vectors of predictor variables (A) and taxon centroids (B). The first axis explained

577   6.5% and the second explained 2.9% of the variation respectively. To make taxon labels readable

578   and to reduce clutter in B, only the most abundant taxon that did not overlap with other taxon

579   labels are shown. Grey dots represent individual samples and vector length is relative to the

580   variance explained by the variable.

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