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

Nathan R. Geraldi[1,2,3*], Camilla Bertolini[1,2] Mark C. Emmerson[1,2], Dai Roberts[1,2], Julia D. Sigwart[1,2], and Nessa E. O'Connor[1,2]

1 Queen's University Marine Laboratory, 12-13 the Strand, Portaferry, BT22 1PF, Northern Ireland, UK. 2: Institute of Global Food Security, School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road, Belfast, BT9 7BL, Northern Ireland, UK 2). 3:Present address- Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia

*Corresponding author: nathan.r.geraldi@gmail.com,

Running header: Aggregations of mussels and brittle stars

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Abstract

Biogenic habitats, such as coral reefs, facilitate diverse communities. In aquatic systems, aggregations of mobile benthic species may play a similar ecological role to that of typically sessile biogenic habitats, however, this has rarely been considered. We quantified the abundance of sessile mussels (*Modiolus modiolus*) and aggregating brittle stars (*Ophiotrix fragilis*) and tested for correlations between the density of mussels (live and dead) and brittle stars each with: 1) abundance, biomass, diversity and assemblage structure of associated benthic macrofauna; and 2) percent organic matter of the sediment. We found that the abundance of live *M. modiolus* was positively associated with the abundance and biomass of macrofauna. The positive association between *M. modiolus* and macrofauna abundance was further amplified with an increase in brittle stars and a decrease in dead mussel shells. Macrofauna biomass was lower with more dead mussel shells and macrofauna diversity increased with more live *M. modiolus* and brittle stars. Sediment organic matter was positively related with brittle star density, but not with the abundance of live or dead mussels. The positive relationship between brittle stars and sediment organic matter suggests that brittle stars could enhance rates of benthic-pelagic coupling. Given the importance of understanding the functional role of threatened habitats, it is essential that the underlying community patterns be understood through robust observational studies to then derive testable hypotheses to determine drivers. These findings provide novel insight into the ecological role of aggregations of mobile species, which is essential to prioritize conservation and restoration strategies.

Introduction

Habitat-forming species, such as corals or trees, are widespread in terrestrial and aquatic ecosystems worldwide. These species create complex biogenic habitats, which are the foundation of communities that do not exist in their absence (Bertness & Callaway 1994, Stachowicz 2001). Increased habitat complexity facilitates increased species richness by reducing predation, competition and disturbance pressure (Stachowicz 2001, Bruno et al. 2003). In aquatic ecosystems, biogenic habitats such as seagrass, saltmarsh, mangroves, and bivalve reefs provide multiple ecosystem services including, the enhanced production of economically important species, reduced erosion rates, and nutrient removal (Costanza et al. 1997, Grabowski & Peterson 2007, Barbier et al. 2011). Unfortunately, these marine species are impacted heavily by human activities and most are reduced to a fraction of their historical abundance globally (Waycott et al. 2009, Beck et al. 2011, De'ath et al. 2012). The loss of biogenic habitats has in some instances negated their ecological roles and severely diminished the benefits they provide to society (Waycott et al. 2009, Ermgassen et al. 2012, 2013).

Aggregations of mobile fauna are generally considered deleterious to ecosystems; for example outbreaks of urchins can denude large areas once covered with macroalgae (Steneck et al. 2004). However, aggregations of mobile species can potentially provide similar functions as sedentary, foundation species and create biogenic habitats. For instance, aggregations of urchins can increase biodiversity and provide shelter for prey (Altieri & Witman 2014).

Mussel reefs, similar to oyster reefs, have been depleted worldwide (Lotze et al. 2006). The horse mussel, *Modiolus modiolus*, forms reefs in the North Atlantic ocean (Sanderson et al. 2008, Wildish et al. 2009) and its abundance has declined most likely from habitat destruction following fishing practices (Magorrian & Service 1998, Strain et al. 2012, Cook et al. 2013) and global warming (Gormley et al. 2013). The complex habitat that *M. modiolus* reefs create is known for its high diversity of organisms (Rees et al. 2008, Ragnarsson & Burgos 2012, Fariñas-Franco et al. 2013). The loss of live mussels can result in a matrix of dead shell. Experimental studies that held shell structure constant found that loss of live blue mussels reduce abundance but not diversity of macrofauna (Norling & Kautsky 2007, Norling et al. 2015), but the loss of live *M. modiolus* on reef ecology in natural settings is unknown.

Brittle stars occur in dense aggregations throughout the globe (Fedra 1977, Fratt & Dearborn 1984). In particular, the suspension feeding brittle star, *Ophiothrix fragilis*, exists in dense beds of more than 1,000 individuals m^{-2} around Britain and Ireland (Warner 1971, Aronson 1989, Dauvin et al. 2013). *Ophiothrix fragilis* beds exist in similar environments as *M. modiolus* reefs and co-occur in some areas (Sanderson et al. 2008, Ragnarsson & Burgos 2012). Although it was thought that aggregations of *O. fragilis*, which often overlay *M. modiolus reefs,* may have negative effects on benthic macrofauna from smothering and competition effects, many species of macrofauna were recorded beneath brittle star beds (Warner 1971). Brittle stars could facilitate benthic fauna by enhancing deposition of organic material (Warner 1971, Murat et al. 2016) and provide refuge from predators. Dense aggregations of this mobile species could provide ecological benefits similar to sessile reef forming species. In addition, there could be emergent properties when dense aggregations of both sessile and mobile species exist together (Angelini et al. 2011). However, our understanding of ecological roles associated with these two habitats, beds of mobile species and reefs of sessile species, is limited.

Modiolus modiolus is protected in Europe under Annex I of the EU Habitats Directive (Directive 93/43/EEC) and the OSPAR convention (Rees et al. 2008). Therefore a survey based on benthic grabs was designed to determine the extent and condition of *M. modiolus* reefs in

Northern Ireland to inform management decisions about their conservation. This intensive survey allowed an unprecedented opportunity to study this heavily protected biogenic habitat and determine ecological patterns which are a necessary precursor to conducting manipulative experiments to pinpoint underlying mechanisms (Underwood et al. 2000). Our aim was to characterize the ecological roles of a declining biogenic-reef forming species, *M. modiolus*, and a common co-occurring benthic species, *O. fragilis*. We quantified how the abundance of live *M. modiolus*, *M. modiolus* shell (dead *M. modiolus*) and *O. fragilis* was related with: (i) macro-benthic species abundance, biomass, richness, diversity and assemblage structure; and (ii) sedimentary organic matter. We hypothesized that the abundance of live *M. modiolus* and *O. fragilis* would have a similar positive relationship with the abundance, biomass, richness and diversity of the benthic macrofauna, and the sediment organic matter. Moreover, the abundance of *M. modiolus* shell would not have a correlation with the abundance, biomass, richness, and diversity of the benthic macrofauna, and the sediment organic matter because shell has less structural complexity compared to live mussels and does not produce fecal matter (as would be expected in reefs comprised of mainly live animals). Finally, prevalence of live *M. modiolus*, *M. modiolus* shell and *O. fragilis* will explain a similar amount of variation in the macrofauna assemblage.

Materials and Methods

Data collection

To quantify the variation in benthic fauna and sediment organic matter related with the abundance of *M. modiolus, M. modiolus* shell, and *O. fragilis,* a grab sampler was used to sample 53 sites at two locations off the east coast of Northern Ireland at depths of 20-30 m (Fig. 1).

Sampling sites were dispersed evenly within different acoustic signatures of a single beam sonar survey conducted by Northern Ireland Agri-Food and Biosciences Institute in 2014 (unpub. data). Samples were collected over 5 days between the 9th of September and the 16th of December 2014. The Day grab used in this study removed approximately 0.1 m^2 area of substratum (approximately 2 l of sediment; Appendix S1). Grabs with minimal sediment (< 1 L of sediment) were recorded as misfires and the grab was deployed again. Three replicate grabs were taken at each site unless 3 successive misfires were recorded and no more samples were taken at that site. The environment of these locations made diver surveys impractical (depth and currents) and although larger grab samples would have been optimal, a day grab was used to remove a minimal amount of the protected *M. modiolus* reef. Each sample was photographed and the percentage cover of *M. modiolus* shell, mud, and sand were estimated visually based on the grab surface (Appendix 2). Sediment samples were taken from the top 2 cm of 2 haphazardly chosen grabs from each site. However, sediment was collected from all three samples from 9 sites because live *M. modiolus* was present in the grabs. Sediment organic matter was collected from 101 grabs at 46 sites. Sediment samples were freeze dried, sieved through 1 mm mesh, and placed in a combustion oven at 500°C for 6 hours (Dean 1974). The percent organic matter was determined by dividing the difference in mass of the sediment before and after combustion by the mass of the sediment before combustion.

Conspicuous macrofauna were quantified from 140 grab samples at 53 sites, which were searched thoroughly on the boat after the grab sample was sieved through 1 mm mesh and all bivalves, crustaceans, echinoderms, fish, gastropod, and polychaetes were collected and frozen. Macrofauna were identified to the lowest practical taxon, counted and wet weight recorded for a total taxon biomass. Macrofauna identification was based on morphological characteristics following guides (Hayward & Ryland 1995). A subset of grab samples (approximately 1 grab from each site) were returned to the laboratory and cryptic species, which were not attached to the substratum, were quantified in addition to the conspicuous macrofauna (Appendix S3). Results of analyses from these samples were consistent with those based on conspicuous fauna thus for clarity we are presenting only the findings for the conspicuous fauna. Animal handling protocols followed the ethical guidelines of Queen's University Belfast.

Data Analysis

We tested effect of substrate type (live *M. modiolus*, *M. modiolus* shell, or *O. fragilis*) on benthic macrofauna abundance, biomass, taxon richness, diversity and assemblage structure.

The abundance of *M. modiolus* and *O. fragilis* in grab samples were *a priori* determined as predictor variables and not included as benthic fauna in the analyses. Generalized linear models were used to test for variations in total faunal abundance and taxon richness associated with changes of the three habitat types (*M. modiolus*, *M. modiolus* shell, and *O. fragilis*) with Poisson distributions because data were skewed towards zero. General linear models were used to test for variations in non-integer dependent variables (biomass and diversity) associated with changes in the three habitat types. Diversity for each sample was calculated with the Shannon-Weaver index. Multi-collinearity between predictor variables was tested using the variance inflation factor (VIF) and < 10 indicated minimal multi-collinearity (Hair 2006). Site within location (North or South as shown in Fig. 1) was included as random variables in the model to account for the nested sampling design. All interactions were included in the models and the predictor variables were centred (the mean was subtracted from each value) to reduce multi-collinearity between predictor variables and interactions (Quinn & Keough 2002) and scaled (divided by the standard deviation) to reduce the difference in magnitude among the predictor variables (Bates et al. 2014). All analyses were conducted in R (R Development Core Team 2012). Diversity was calculated using the div function within the v*egan* package (Oksanen et al.). The glmer function within the *lme4* package (Bates et al. 2014 4) was used for both abundance and richness of benthic fauna. Biomass, diversity and organic matter were analysed using lmer function within the *lme4* package to calculate *t* values, while the Analysis of Variance (ANOVA) function within the *car* package was used to generate p values and test for significance (Fox & Weisberg 2011). Interactions and random variables (site nested in location) were included in the organic matter model. Models were checked to ensure an adequate fit by visually inspecting residuals vs fitted (randomly distributed points) and Q-Q (points were near 1:1 ratio) plots (Crawley 2007). Biomass of macrofauna was log transformed to improve model fit.

To quantify the amount of variation in benthic fauna assemblage explained by the abundance of *M. modiolus*, *M. modiolus* shell, and *O. fragilis*, which were all continuous variables, we used Permutational Analysis of Variance (PERMANOVA, McArdle & Anderson 2001, Anderson 2001) and redundancy analysis (RDA, Legendre & Anderson 1999). PERMANOVA partitions the variation of a resemblance matrix among sources of variation and fits linear models to test hypotheses and build models without ordination. RDA performs ordination of fitted values to test hypotheses, build models, and create visualizations of the data (Legendre & Anderson 1999). RDA reduces the variance into dimensions, which makes visualizations of the data possible but may reduce the amount of variance explained by predictor variables. However, PERMANOVA analyzes the data without constraining the variance into dimensions so that the relationship between community structure and predictor variables is probably closer to what exists naturally. Histograms of each predictor variable and scatter plots of all combinations of predictor variables were examined to ensure there were no extreme outliers. Linear-based analyses can be biased by multi-collinearity (Legendre & Anderson 1999), we tested for multi-collinearity as previously described using VIF. Multivariate analyses used the *vegan* package version 2.2-0 (Oksanen et al. 2010).

Taxon-specific abundances were log-transformed to reduce the influence of abundant taxa in the analyses, and a Bray-Curtis dissimilarity matrix was created (Anderson et al. 2008, Legendre & De Cáceres 2013). The mean of taxon abundance per site was used to remove the possibility of non-independent samples within each site. Interactions were included in the sequential PERMANOVA and predictor variables were centred and scaled to reduce multicollinearity between variables and interactions. A second PERMANOVA was run with taxon-specific biomass following the same procedure described for abundance.

Results

Modiolus modiolus was present in 45 of the samples and ranged from 1 to 65 individuals per grab (~10 to 650 m^{-2}). *Ophiotrix fragilis* was present in 81 (out of 140) of the samples which ranged from 1-203 individuals per grab (~10 to 2,030 m^{-2}). Fifty-seven different taxa were quantified in the samples (Appendix S3). The substratum of the grabs was primarily *M. modiolus* shell and mud, with sand being less prevalent (Appendix 4). The abundance of live *M. modiolus* and *O. fragilis* had similar patterns with changes in the different types of substratum. The abundance of benthic fauna increased with the number of live *M. modiolus* and there were interactions between *M. modiolus* and *O. fragilis*, and *M. modiolus* and *M. modiolus* shell (Table 1; Fig. 2A, D and G; Fig. 3). The interaction between *M. modiolus* and *O. fragilis* resulted from a greater increase in fauna abundance as *M. modiolus* increased when there were more *O. fragilis* (Fig 3A). The opposite trend existed for the interaction between *M. modiolus* and *M. modiolus* shell; there was a greater increase in fauna abundance as *M. modiolus* increased when there was less shell (Fig 3B). Biomass of macrofauna increased with *M. modiolus*, but decreased with *M. modiolus* shell (Table 1; Fig 2B and E). The interaction between all predictor variables was also significant for the biomass of macrofauna (Table 1).

The three predictor variables did not explain a significant amount of variation in the number of taxon (richness) in a sample and there were no significant interactions (Table 1). *M. modiolus* and *O. fragilis* were associated with an increase in the macrofauna diversity (Table 1, Fig 2C and I). *O. fragilis* was positively related with organic matter, while the prevalence of *M. modiolus* or *M. modiolus* shell did not explain a significant amount of variation in organic matter (Table 1; Fig. 4A-C). The three-way interaction was significant for organic matter and resulted from a positive relationship between *O. fragilis* and organic matter, which was greatly reduced with an increase in *M. modiolus* abundance and reduced with an increase in *M. modiolus* shell cover (Fig. 4D).

The amount of variation in faunal assemblage using abundance explained by *M. modiolus*, *O. fragilis*, and *M. modiolus* shell was quantified using a PERMANOVA. *Modiolus modiolus* ($F_{1,52} = 3.16$; $P<0.001$*)*, *O. fragilis* ($F_{1,52} = 5.45$; $P<0.001$*)*, and *M. modiolus* shell ($F_{1,52} = 5.11$; $P<0.001$) were significant and explained more variation in fauna assemblage than would be expected by random chance. No interactions were significant. *Modiolus modiolus* shell explained the most variation in macrofauna assemblage of the 3 continuous predictor variables ($R^2 = 8.4\%$), followed by *O. fragilis* ($R^2 = 5.7\%$), and *M. modiolus* ($R^2 = 5.2\%$). The RDA represents the relationship between predictor variables and individual taxon. RDA explained 10.7% of the variation in fauna assemblage. The first and second axes explained 6.5 and 2.9% of the variation respectively. *Modiolus modiolus* was positively related with axis 1 and *M. modiolus* shell was positively related with axis 2 (Appendix S5). *Ophiocomina nigra* (a brittle star) was positively related with the second axis, and *Ophiura* spp. (a brittle star) and *Timoclea ovata* (a bivalve) were negatively related with the second axis (Appendix S5). The fauna assemblage based on biomass had similar findings as the assemblage using abundance with all three predictor variables explaining a significant amount of variation. *Modiolus modiolus* shell explained the most variation in macrofauna assemblage of the 3 continuous predictor variables (R^2 = 8.7%), followed by *O. fragilis* (R^2 = 6.3%), and *M. modiolus* (R^2 = 4.1%).

Discussion

Biogenic habitats composed of aggregations of sessile species, often referred to as meadows or reefs, are touted for their ecological and economic benefits (Anton et al. 2011, Barbier et al. 2011, Firth et al. 2015). On the other hand, dense aggregations of mobile species are generally viewed negatively; however, this study indicates that increasing densities of *O. fragilis* were associated with greater macrofauna diversity and organic matter, and had a positive emergent effect on the total abundance of fauna within *M. modiolus* reefs. Although these results are correlations, they could suggest that aggregates of brittle stars enhance diversity of macrofauna and increase sediment organic matter similar to or more than filter feeding bivalves.

The ecological effect of a single foundation species on the local community has been extensively studied (Grabowski et al. 2005, Geraldi et al. 2009), however, multiple species often coexist together and little is known about potential interactions among different species (Angelini et al. 2011, Donadi et al. 2015). One study that included multiple ecosystem engineers found that the presence of *Caulerpa taxifolia*, a macroalgae, near *Anadora trapezia*, a clam, increased diversity and abundance of epibiota on the bivalve (Gribben et al. 2009). Most of these studies focused on relatively sessile species and there is the potential for mobile species to also enhance both density and diversity of associated fauna (Altieri & Witman 2014). The abundance of *O. fragilis* was related with enhanced diversity of macrofauna and had a positive emergent effect with *M. modiolus* reefs on the abundance of macrofauna. In addition, minimal multicolinearity among predictor variables indicates that there was no facilitation between *O. fragilis* and *M. modiolus*, and that abundances of live and dead *M. modiolus* were independent. Finally, all three habitat types measured had similar influence on the macrofauna assemblage (explained between 5 and 8% of the variation in assemblage).

Our conclusions are based on a robust survey, which aimed to identify ecological patterns associated with different dominant species (mussels and/or brittle stars). Experimental manipulation is required to determine the mechanisms driving these differences, which is difficult given the ethical and logistical limitations of manipulating a rare species that primarily exist in areas with high currents and deeper than 20 m. Given our existing knowledge, aggregations of brittle stars and other mobile species appear to share similar roles as some well-described sessile foundation species. For example, positive effects on the macrofauna community associated with aggregations of mobile fauna could result from reduced predation from provision of shelter (Bruno et al. 2003) or from increased food provision via biodeposition (Norling & Kautsky 2007).

Understanding how the loss of individual bivalves from reefs affects ecological functioning is important given the prevalence of reef degradation (Beck et al. 2011, Ermgassen et al. 2012). Teasing apart the provision of habitat by the physical structure from the biotic function of bivalve reefs has been studied using experimental reefs. For example, the diversity of macrofauna was similar on blue mussel (*Mytilus edulis*) reefs compared to reefs made of intact shells, while the abundance was greater on live reefs possibly because of resources supplied by biodeposition (Norling & Kautsky 2007). Similarly, another study found that diversity of epibenthic fauna was similar among live and dead experimental reefs of oysters or mussels, while abundance of epibenthic fauna was greatest on oyster shell, moderate on live bivalve reefs and lowest on mussel shell reefs (Norling et al. 2015). We found that the amount of naturally occurring dead shell was not related with the abundance, richness and diversity of benthic macrofauna, and that dead shell cover was negatively related with the biomass of macrofuana. Separating the role of the physical reef structure from associated biotic functioning is necessary to identify ecological mechanisms, and also to predict changes in ecosystem functioning associated to bivalve mortality from direct or indirect anthropogenic impacts.

Biodeposition by filter feeding bivalves is an important process in coastal ecosystems because it couples pelagic and benthic communities. Benthic-pelagic coupling may reduce occurrences of hypoxia by directly reducing phytoplankton abundance (Dame & Olenin 2005, Grizzle et al. 2008) and indirectly through nitrogen removal by enhancing denitrification on the sediment because of the high quality resources provided by biodeposits (Kellogg et al. 2013, Smyth et al. 2013, 2015). *Modiolus modiolus* produce nutrient rich biodeposits (Navarro & Thompson 1997), however, we did not identify a relationship between *M. modiolus* density and sediment organic matter content. We did find a positive relationship between brittle star density and organic matter content. This relationship could have resulted from brittle stars preferring benthos with greater organic matter. However, our results indicate that *O. fragilis* and *M. modiolus* have similar abundance patterns in shell, mud and sandy substratum suggesting that brittle stars are not preferentially selecting one type of substratum that could be causing this relationship, which is likely driven by benthic-pelagic coupling. A positive relationship between total organic carbon and brittle star density was found in stable environments (Murat et al. 2016) and benthic-pelagic coupling associated with brittle star beds was suggested to reduce eutrophication in coastal bays (Hily 1991). Both *M. modiolus* and *O. fragilis* are suspension feeders but use entirely different mechanisms to collect suspended particles. *M. modiolus* is an active filter feeder while *O. fragilis* passively feeds on phytoplankton (Roushdy & Hansen 1960, Migne et al. 2012, BlanchetAurigny et al. 2015). The stronger association between brittle stars and sediment organic matter compared to *M. modiolus* could result from *O. fragilis* having a low absorption efficiency (Migné & Davoult 1998) or that aggregations reduce water motion and the erosion of biodeposits (Warner 1971) more than mussel reefs. Our findings, that organic matter was positively related with brittle star abundance and not *M. modiolus* density, may suggest that benthic-pelagic coupling in brittle star beds is potentially greater than in bivalve reefs and this should be investigated further.

The ecological and economic benefits of marine biogenic habitats, such as coral reefs, salt marshes and bivalve reefs, are well known and are the impetus for their conservation and restoration (Brumbaugh & Coen 2009, Barbier et al. 2011, Geraldi et al. 2013, La Peyre et al. 2014). Beds of brittles stars may enhance the diversity of macrofauna and increase benthic-pelagic coupling equal to or greater than bivalve reefs. The carbon budgets associated with biomass production and calcification has been quantified for brittle star beds (Migne et al. 1998, Davoult et al. 2009, Lebrato et al. 2010), however, their potential importance for other rates of ecosystem functioning and associated services is relatively unknown. The ecosystem functions provided by brittle stars are probably context-dependent, but the global functional role of these taxa may be equal to or greater than other sessile foundation species for multiple reasons. First, brittle star beds are prevalent around the globe given that they have been documented from the

Arctic (Piepenburg & Schmid 1996, Blicher & Sejr 2011) to the Antarctic (Fratt & Dearborn 1984) and throughout the mid-latitudes (Haedrich et al. 1980, Fujita 1990). They are also present at broad depth ranges (Lebrato et al. 2010) and not restricted to estuaries and coasts like traditional biogenic habitats.

Determining the ecological functions provided by aggregations of mobile species and comparing these to functions provided by traditional biogenic habits, as well as potential emergent effects between the two are needed to understand the relative importance of these species to broader ecosystem processes and functions. This is of utmost importance as humans are constantly altering the abundance and extent of both sessile and mobile species. The applied implications of these results, if confirmed by manipulative experiments, include assigning aggregates of mobile species similar conservation status as sessile foundation species (Peterson & Lipcius 2003, Byers et al. 2006, Lampert & Hastings 2014).

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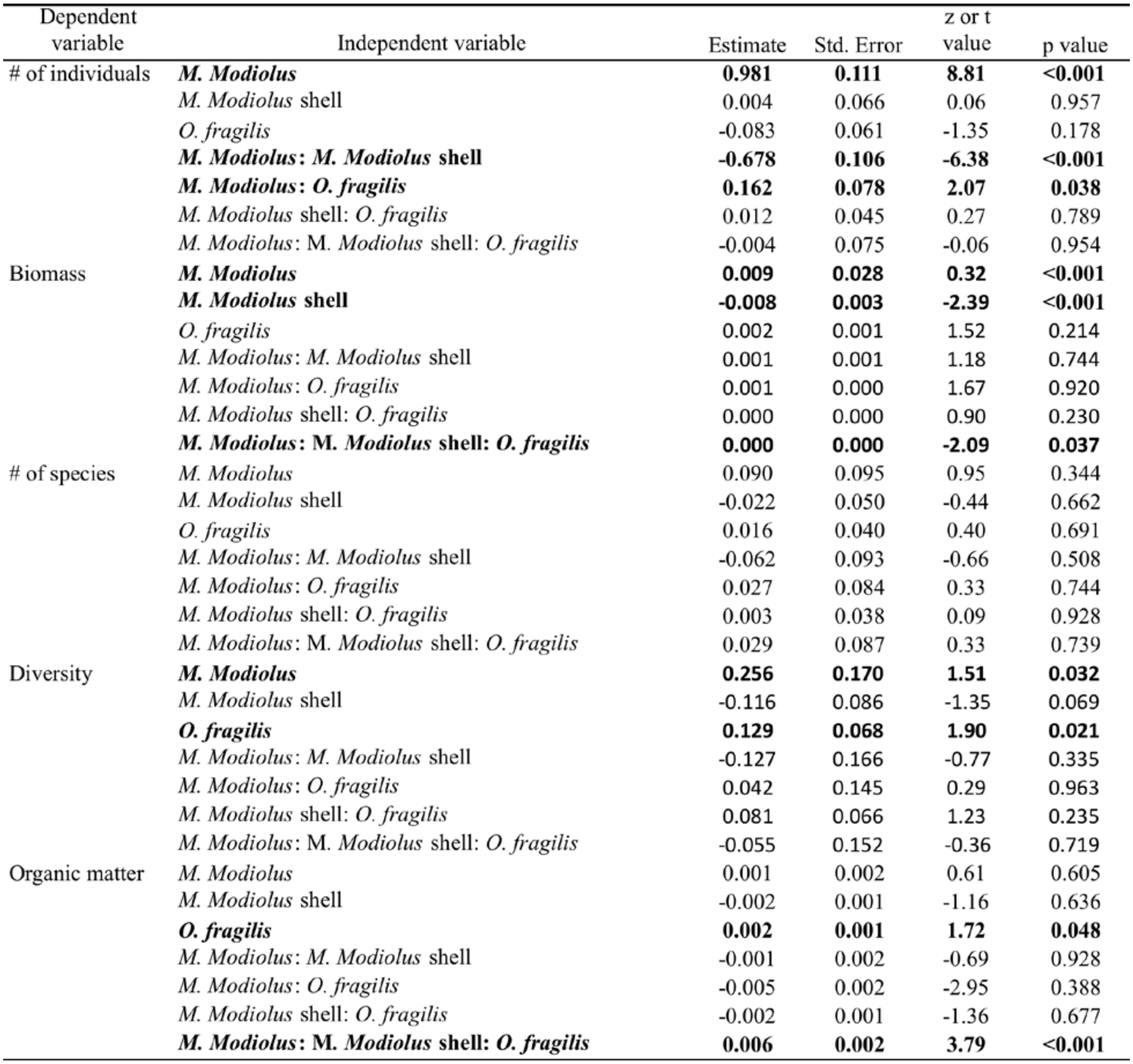
Table 1. Summary of statistical models to assess the relationship between the predictor variables (abundance of *M. modiolus*, *M. modiolus* shell, and *O fragilis*) and the abundance, biomass, richness, and diversity of benthic fauna, and organic matter collected in samples (significant predictor variables 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**

Figure legends

Fig. 1. Sampling sites near the Outer Ards Peninsula, east coast of Northern Ireland. Three replicate grab samples were taken at each site

Fig. 2. The relationship between the abundance (left column), biomass (middle column), and diversity (right column) of benthic fauna quantified in day grabs, and *M. modiolus*, *M. modiolus* shell or *O. fragilis*. Predictor variables that were significant are indicated by black lines (See Table 1 for statistical summary).

Fig. 3. The interactions between the abundance of *M. modiolus* and *O. fragilis* (A) and between *M. modiolus* and *M. modious* shell (B) in explaining variation in the abudnance of benthic fauna. The data points and trend lines were catagorized based on abundance of *O. fragilis* (A) or percent shell cover (B).

Fig. 4. The relationship between the abundance of *M. modiolus* (A), *M. Modiolus* shell (B), *O. fragilis* (C), and the percent organic matter in sediment collected in day grabs. The interaction between all three predictor variables and the percent organic matter (D). *O. fragilis* and the interaction between the three predictor variables explained a significant amount of variation in percent organic matter. Predictor variables that were significant are indicated by black lines (See Table 1 for statistical summary).

Fig. 1

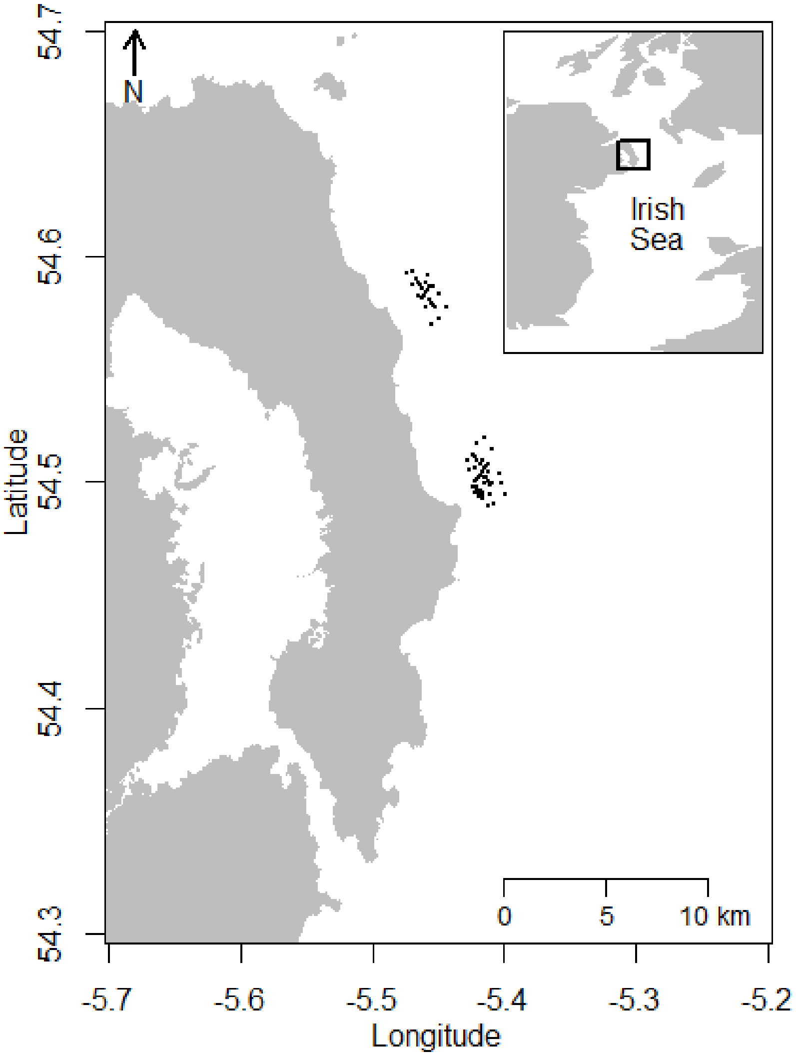

N
Irish
Sea
0
5
10 km
54.7
54.6
54.5
54.4
54.3
Latitude
-5.7
-5.6
-5.5
-5.4
-5.3
-5.2
Longitude

Fig. 2

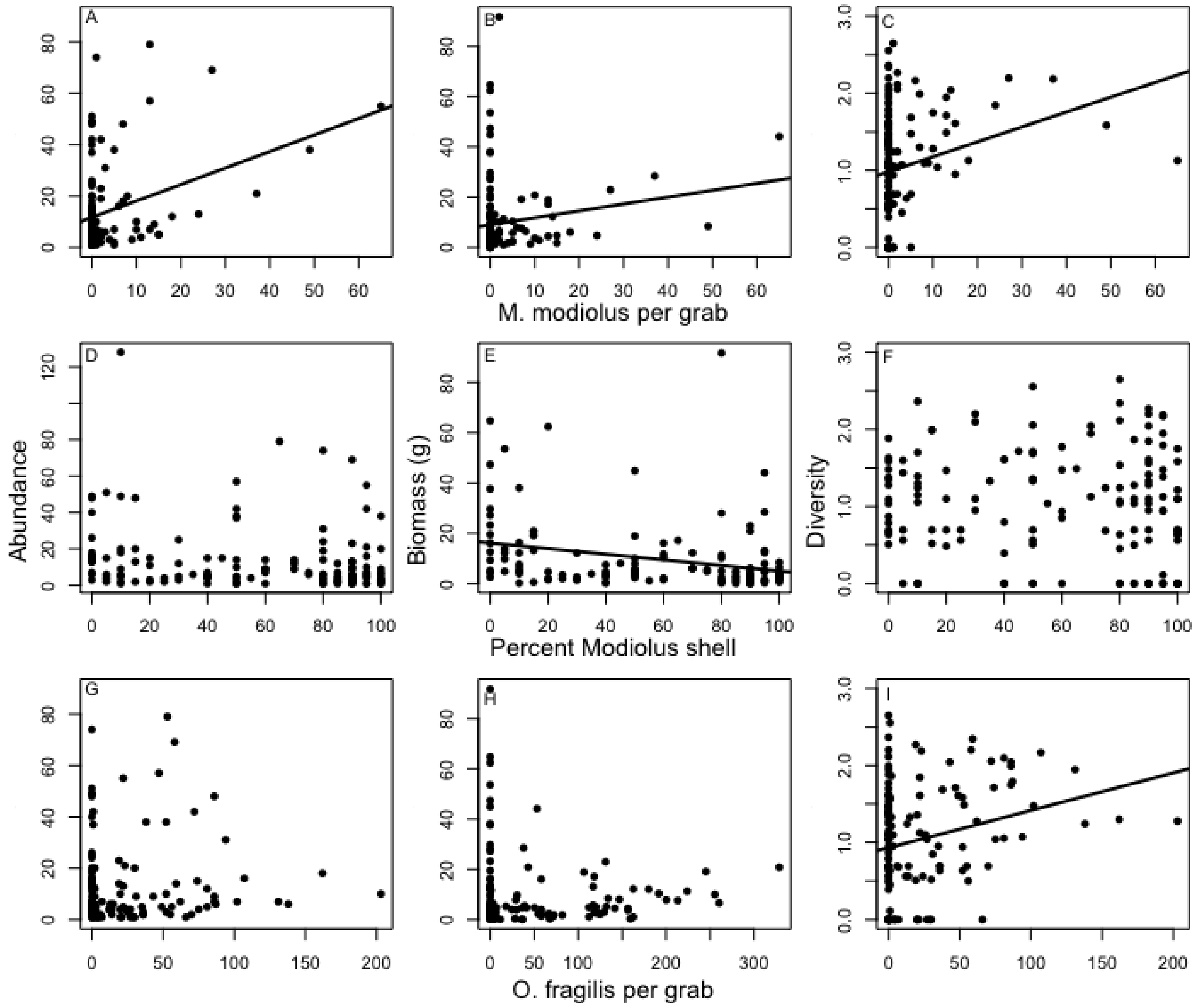

A
B
C
0
20
40
60
80
0.0
1.0
2.0
3.0
0
10
20
30
40
50
60
M. modiolus per grab
D
E
F
Abundance
Biomass (g)
Diversity
120
100
Percent Modiolus shell
G
H
I
150
200
300
O. fragilis per grab

Fig. 3

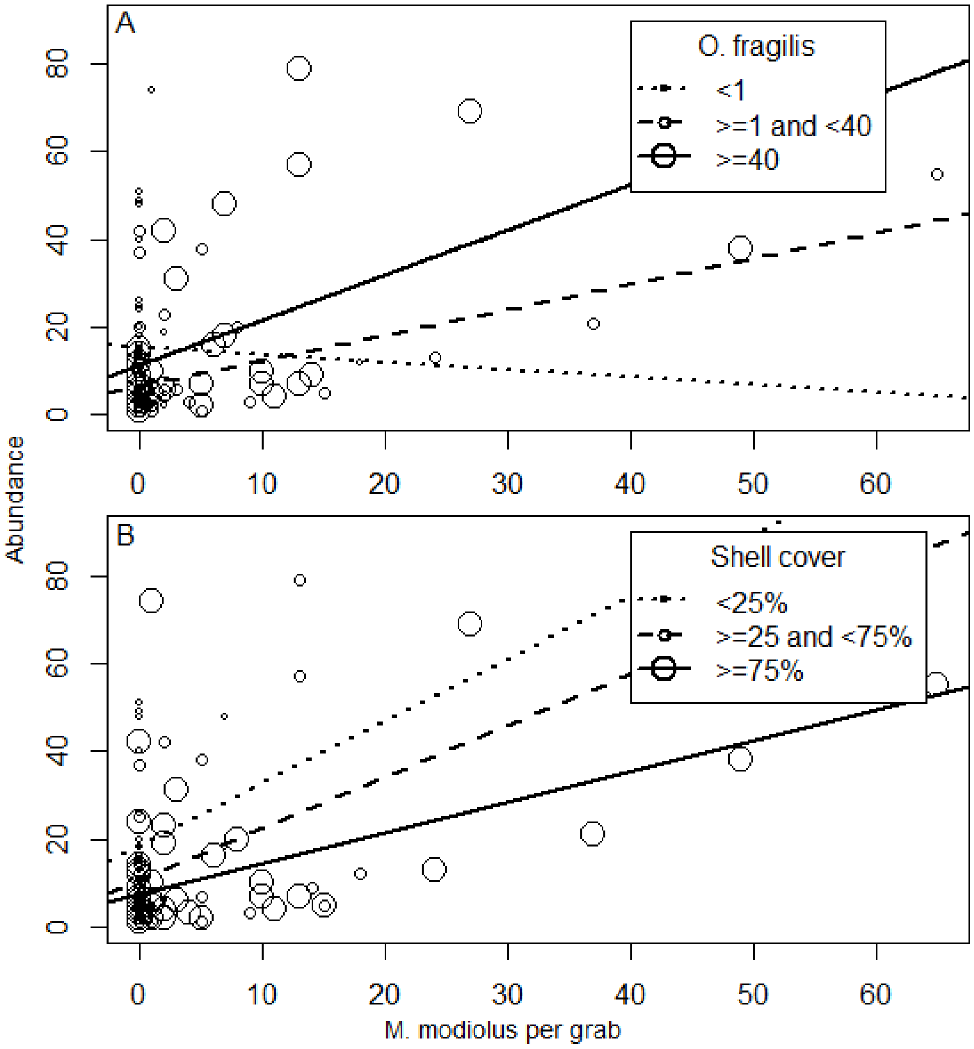
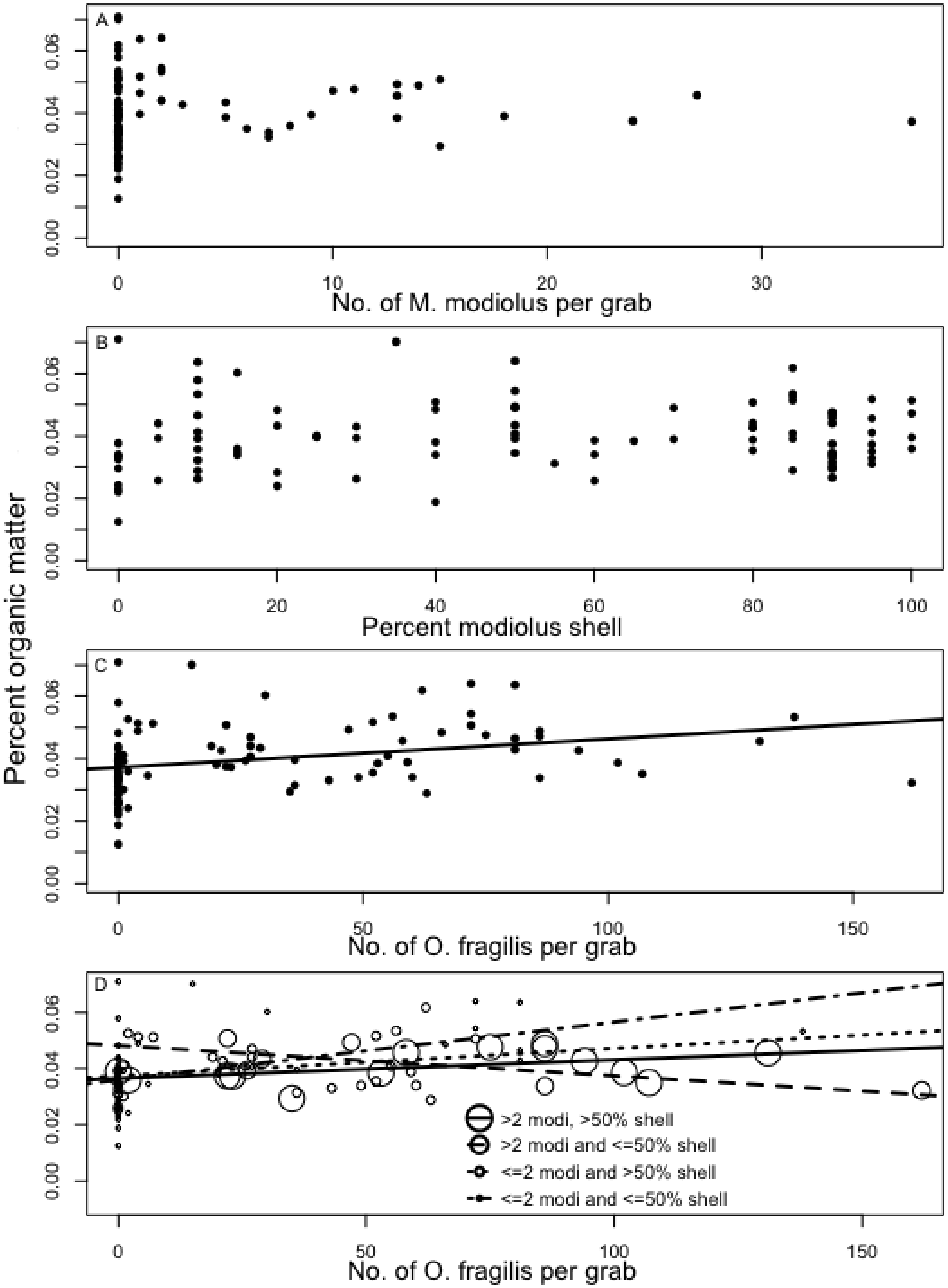

A
O. fragilis
<1
>=1 and <40
>=40
80
60
40
20
0
0
10
20
30
40
50
60
Abundance
B
Shell cover
<25%
>=25 and <75%
>=75%
80
60
40
20
0
0
10
20
30
40
50
60
M. modiolus per grab

Fig. 4


Percent organic matter
A
0.00
0.02
0.04
0.06
0
10
20
30
No. of M. modiolus per grab
B
0
20
40
60
80
100
Percent modiolus shell
C
0
50
100
150
No. of O. fragilis per grab
D
>2 modi, >50% shell
>2 modi and <=50% shell
<=2 modi and >50% shell
<=2 modi and <=50% shell
No. of O. fragilis per grab

Appendices

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

Appendix S2. Day grabs illustrating typical samples with *M. modiolus* and *O. fragilis* (A), *M. modiolus* shell (B), *O. fragilis* (C), and mud (D). The grab sampled 0.1m^2. Photo credits: C. Bertolini and N. Geraldi.

Appendix S3. Taxon and their respective groups quantified in the grab samples. The proportion for each taxon of the total number of individuals for the grabs that had all taxon quantified and for the grabs that only conspicuous taxon were qunatified. Only data from conspicuous taxon were used for all analyses.

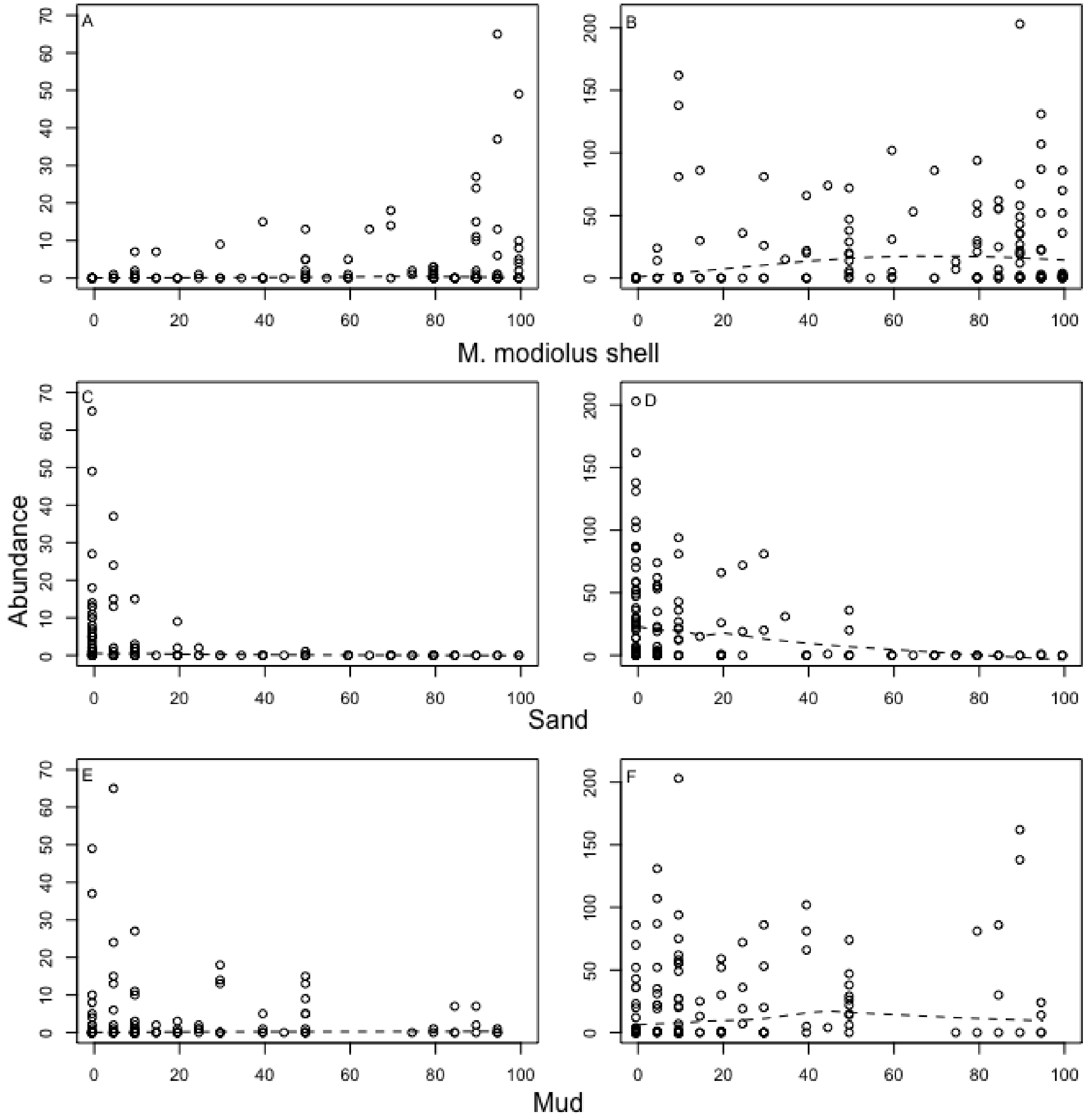
Taxa	Taxa group	Full	Conspicuous
Abra alba	Bivalve	0.248	0.254
Amphipholis squamata	Echinoderm		0.002
Amphiura chiajei	Echinoderm		0.008
Amphiura filiformis	Echinoderm		0.010
Anomiidae	Bivalve	0.018	
Aphrodita aculeata	Polychaete	0.001	0.001
Astarte sulcata	Bivalve	0.033	0.036
Atelecyclus rotundatus	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

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	

Appendix S4

The abundance of *M. modiolus* (left column) and *O. fragilis* (right column) in grab samples compared to the percent cover of 3 substrate categories. Substrate type was determined from photos of grabs. Fitted lines were determined by the lowess function in R.



Appendix S5. The first and second axis of RDA of the fauna assemblage in grab samples overlaid with vectors of predictor variables (A) and taxon centroids (B). The first axis explained 6.5% and the second explained 2.9% of the variation respectively. To make taxon labels readable and to reduce clutter in B, only the most abundant taxon that did not overlap with other taxon labels are shown. Grey dots represent individual samples and vector length is relative to the variance explained by the variable.