Aggregations of brittle stars can perform similar ecological roles as mussel reefs

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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 horse mussels *Modiolus modiolus* and aggregating brittle stars *Ophiothrix 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 macrofaunal abundance was further amplified with an increase in brittle stars and a decrease in dead mussel shells. Macrofaunal biomass was lower with a higher percentage of dead mussel shells, and macrofaunal diversity increased with greater abundances of live *M. modiolus* and brittle stars. Sediment organic matter was positively related to brittle star density, but not to 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.

KEY WORDS: Foundation species · Reef · Benthic–pelagic coupling · Biogenic habitat · Brittle star · Bivalve · Organic matter · Ophiuroids

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 glob-

ally (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, zu 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 shells. Experimental studies that held shell structure constant found that the loss of live blue mussels *Mytilus edulis* reduced the 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 worldwide (Fedra 1977, Fratt & Dearborn 1984). In particular, the suspension-feeding brittle star *Ophiothrix fragilis* exists in dense beds of more than 1000 ind. m^{-2} around Britain and Ireland (Warner 1971, Aronson 1989, Dauvin et al. 2013). *O. 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 2 habitats, viz. beds of mobile species and reefs of sessile species, is limited.

M. 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 abundances of live *M. modiolus*, *M. modiolus* shell (i.e. dead *M. modiolus*), and *O. fragilis* were related to (1) macrobenthic species abundance, biomass, richness, diversity, and assemblage structure; and (2) sedimentary organic matter (OM). 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 with the sediment OM. Moreover, the abundance of *M. modiolus* shell would not show a correlation with the abundance, biomass, richness, and diversity of the benthic macrofauna or the sediment OM because shell has less structural complexity compared to live mussels and does not produce fecal matter (as would be expected in reefs composed of mainly live animals). Finally, we hypothesized that the prevalence of live *M. modiolus*, *M. modiolus* shell, and *O. fragilis* would explain a similar amount of variation in the macrofaunal assemblage.

MATERIALS AND METHODS

Data collection

To quantify the variation in benthic fauna and sediment OM related to the abundance of *Modiolus modiolus*, *M. modiolus* shell, and *Ophiothrix fragilis*, a grab sampler was used to sample 53 sites at 2 locations off the east coast of Northern Ireland at depths of 20 to 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 (unpubl. data). Samples were collected over 5 d between 9 September and 16 December 2014. The day grab used in this study removed approximately 0.1 m^2 area of substratum (approximately 2 l of sediment; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m563p157_supp.pdf). 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 (depth and currents) of these locations made diver surveys impractical, 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 (Fig. S2). Sediment samples were taken from the top 2 cm of 2 haphazardly chosen grabs from each site. However, sediment was collected from all 3 samples from 9 sites because live *M. modiolus* was present in the grabs. Sediment OM 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 h (Dean 1974). The percent OM 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, gastropods, and polychaetes were collected and frozen. Macrofauna were identified to the lowest practical taxon and counted, and wet weight was recorded for a total taxon biomass. Macrofaunal identification was based on morphological characteristics following guides (Hayward & Ryland 1995). A subset of grab samples (approximately 1 grab from each site) was returned to the laboratory, and cryptic species, which were not attached to the substratum, were quantified in addition to the conspicuous macrofauna (Table S1 in the Supplement). 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 the effect of substrate type (live *M. modiolus*, *M. modiolus* shell, or *O. fragilis*) on benthic macrofaunal 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 3 habitat types (*M. modiolus*, *M. modiolus* shell, and *O. fragilis*) with Poisson distributions because data were skewed towards 0. General linear models were used to test for variations in non-integer dependent variables (biomass and diversity) associated with changes in the 3 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), where VIF < 10 indicated minimal multi-collinearity (Hair 2006). Sites within locations (north or south as shown in Fig. 1) were 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
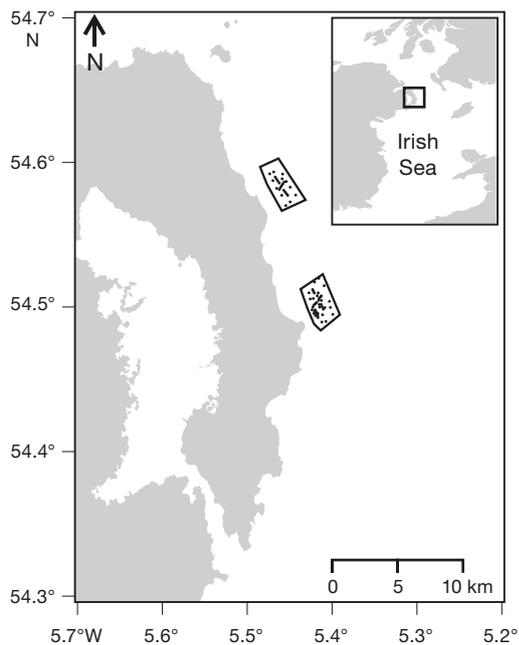

Fig. 1. Sampling sites near the Outer Ards Peninsula, east coast of Northern Ireland. Three replicate grab samples were taken at each site. 'North' and 'south' locations are enclosed in boxes

were centered (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 *vegan* package (Oksanen et al. 2010). The glmer function within the *lme4* package (Bates et al. 2014) was used for both abundance and richness of benthic fauna. Biomass, diversity, and OM were analyzed using the lmer function within the *lme4* package to calculate *t*-values, while the 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 faunal assemblage explained by the abundance of *M. modiolus*, *M. modiolus* shell, and *O. fragilis*, which were all continuous variables, we used permutational ANOVA (PERMANOVA; Anderson 2001, McArdle & 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 that there were no extreme outliers. Linear-based analyses can be biased by multi-collinearity (Legendre & Anderson 1999), so 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 ana-

lyses, 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 centered and scaled to reduce multi-collinearity 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 ind. grab^{-1} (~10 to 650 m^{-2}). *Ophiothrix fragilis* was present in 81 (out of 140) of the samples and ranged from 1 to 203 ind. grab^{-1} (~10 to 2030 m^{-2}). We quantified 57 different taxa in the samples (Table S1). The substratum of the grabs was primarily *M. modiolus* shell and mud, with sand being less prevalent (Fig. S3). 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 between *M. modiolus* and *M. modiolus* shell (Table 1; Figs. 2A,D,G & 3). The interaction between *M. modiolus* and *O. fragilis* resulted from a greater increase in faunal 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 faunal 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,E). The interaction between all predictor variables was also significant for the biomass of macrofauna (Table 1).

The 3 predictor variables did not explain a significant amount of variation in the number of taxa (richness) in a sample, and there were no significant interactions (Table 1). *M. modiolus* and *O. fragilis* were associated with an increase in the macrofaunal diversity (Table 1; Fig. 2C,I). *O. fragilis* was positively related with OM, while the prevalence of *M. modiolus* or *M. modiolus* shell did not explain a significant amount of variation in OM (Table 1; Fig. 4A–C). The 3-way interaction was significant for OM and resulted from a positive relationship between *O.*

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

Dependent variable	Independent variable	Estimate	SE	z or t	p
No. 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**
No. 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**

fragilis and OM, 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 PERM-ANOVA. *M. 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 faunal assemblage than would be expected by random chance. No interactions were significant. *M. modiolus* shell explained the most variation in macrofaunal 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 faunal assemblage. The first and second axes explained 6.5 and 2.9% of the variation, respectively. *M. modiolus* was positively related to axis 1 and *M. modiolus* shell was positively related to axis 2 (Fig. S4). *Ophiocomina nigra* (a brittle star) was positively related to the second axis, and *Ophiura* spp. (brittle stars) and *Timoclea ovata* (a bivalve) were negatively related to the second axis (Fig. S4). The faunal assemblage based on biomass had similar findings as the assemblage using abundance with all 3 predictor variables explaining a significant amount of variation. Of the 3 continuous predictor variables, *M. modiolus* shell explained the most variation in macrofaunal assemblage (R^2 = 8.7%), followed by *O. fragilis* (R^2 = 6.3%) and *M. modiolus* (R^2 = 4.1%).
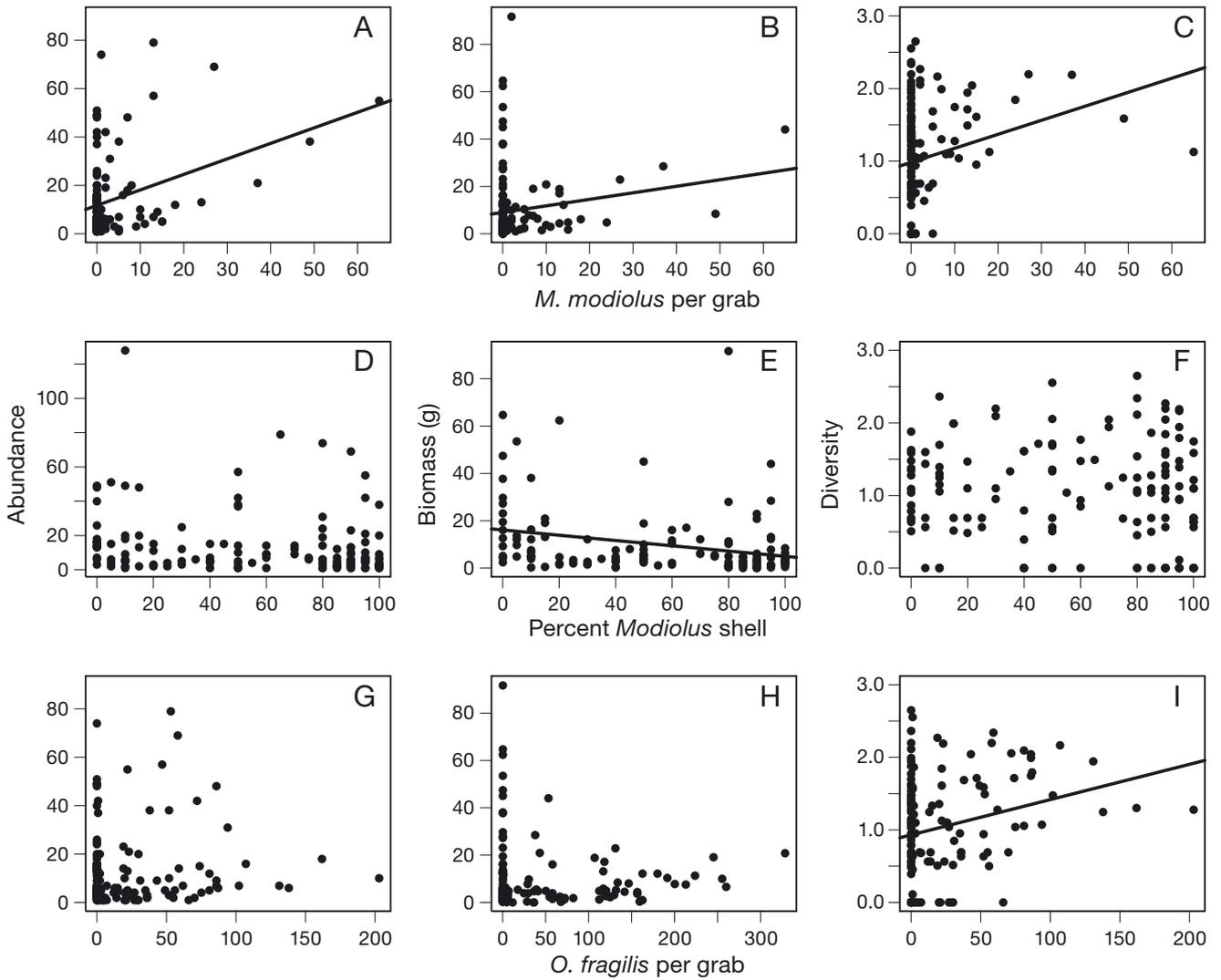
Fig. 2. Relationship between the (A,D,G) abundance, (B,E,H) biomass, and (C,F,I) diversity of benthic fauna quantified in Day grabs, and *Modiolus modiolus*, *M. modiolus* shell, or *Ophiothrix fragilis*. Predictor variables that were significant are indicated by black lines (see Table 1 for statistical summary)
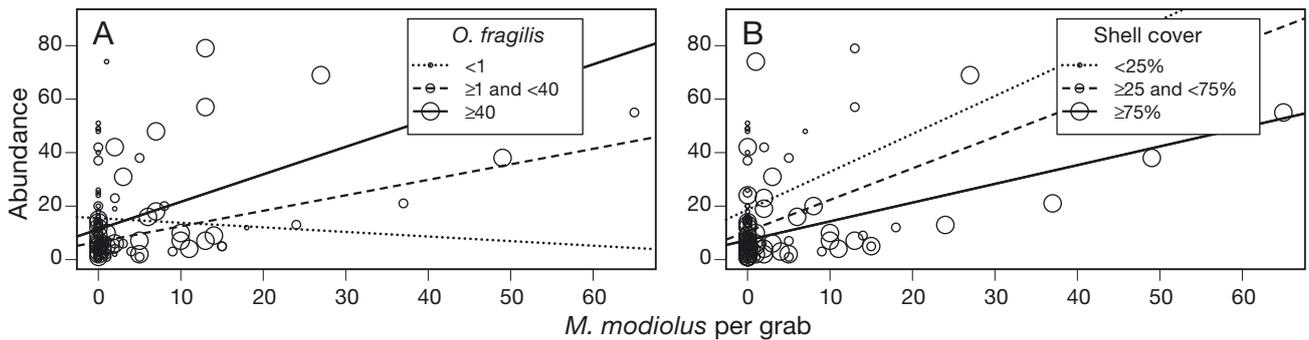

Fig. 3. Interactions between the abundance of (A) *Modiolus modiolus* and *Ophiothrix fragilis* and (B) *M. modiolus* and *M. modiolus* shell in explaining variation in the abundance of benthic fauna. Data points and trend lines were categorized based on the abundance of (A) *O. fragilis* or (B) percent shell cover
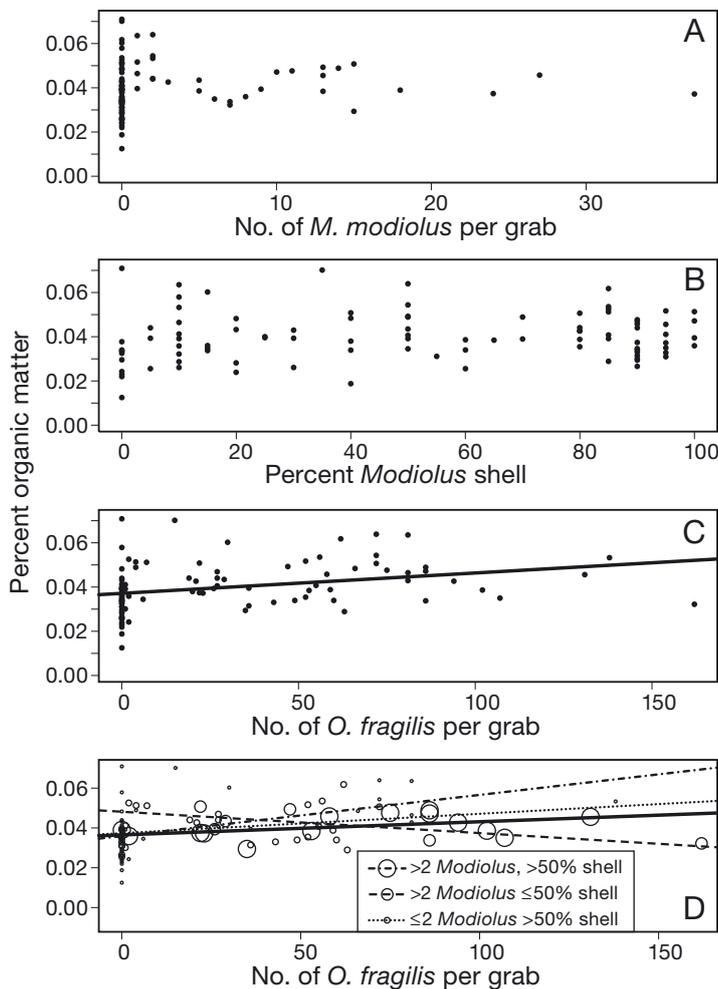
Fig. 4. Relationships between the percent organic matter in sediment collected in Day grabs and (A) the abundance of *Modiolus modiolus*, (B) the percent *M. modiolus* shell, and (C) the abundance of *Ophiothrix fragilis*. (D) Interaction between all 3 predictor variables and the percent organic matter. *O. fragilis* and the interaction between the 3 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)

DISCUSSION

Biogenic habitats composed of aggregations of sessile species, often referred to as meadows or reefs, are touted for their ecological and economic benefits (Antón 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, our study indicates that increasing densities of *Ophiothrix fragilis* were associated with greater macrofaunal diversity and OM, and had a positive emergent effect on the total abundance of fauna within *Modiolus modiolus* reefs. Although

these results are correlations, they could suggest that aggregates of brittle stars enhance diversity of macrofauna and increase sediment OM 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 macroalga, 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 to enhanced diversity of macrofauna and had a positive emergent effect with *M. modiolus* reefs on the abundance of macrofauna. In addition, minimal multi-collinearity among predictor variables indicates no facilitation between *O. fragilis* and *M. modiolus*, and that abundances of live and dead *M. modiolus* were independent. Finally, all 3 habitat types measured had a similar influence on the macrofaunal 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 exists 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 macrofaunal community associated with aggregations of mobile fauna could result from reduced predation as a result of increased availability of shelter (Bruno et al. 2003) or from increased food provisioning 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, zu 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 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 to the abundance, richness, or diversity of benthic macrofauna, and that dead shell cover was negatively related to the biomass of macrofauna. 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 with 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). *M. modiolus* produces nutrient-rich biodeposits (Navarro & Thompson 1997); however, we did not identify a relationship between *M. modiolus* density and sediment OM content. We did find a positive relationship between brittle star density and OM content. This relationship could have resulted from brittle stars preferring benthos with greater OM. 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 1 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, Migné et al. 2012, Blanchet-Aurigny et al. 2015). The stronger association between brittle stars and sediment OM 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 finding that OM was positively related to 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; 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 have been quantified for brittle star beds (Migné 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; 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 & Ohta 1990). They are also present over broad depth ranges (Lebrato et al. 2010) and are 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 2, 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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