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Benthic assemblages associated with native and non-native oysters are similar

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Abstract

Invasive species can impact native species and alter assemblage structure, which affects associated ecosystem functioning. The pervasive Pacific oyster, *Crassostrea gigas*, has been shown to affect the diversity and composition of many host ecosystems. We tested for effects of the presence of the invasive *C. gigas* on native assemblages by comparing them directly to assemblages associated with the declining native European oyster, *Ostrea edulis.* The presence of both oyster species was manipulated in intertidal and subtidal habitats and reefs were constructed at horizontal and vertical orientation to the substratum. After 12 months, species diversity and benthic assemblage structure between assemblages with *C. gigas* and *O. edulis* were similar, but differed between habitats and orientation, suggesting that both oyster species were functionally similar in terms of biodiversity facilitation. These findings support evidence, that non-native species could play an important role in maintaining biodiversity in systems with declining populations of native species.

Highlights

- We manipulated the presence of *Ostrea edulis* and *Crassostrea gigas* in the field
- After 12 months assemblages associated with both oyster species were similar
- Supported taxa diversity was also not different between both oyster species
- *C. gigas* may replace the functional role of *O. edulis* and stabilize diversity

Introduction

Invasive species, non-native species which generate a negative impact on the local ecosystem, are thought to be a major contributor to global biodiversity loss and threaten native biological diversity (IUCN, 2000; Millennium Ecosystem Assessment, 2005). Some invasive species that are considered ecosystem engineers (sensu Jones et al., 1997), however may provide structure and shelter for other species, which can occasionally lead to increased

local species diversity (Crooks, 2002; Rodriguez, 2006). The zebra mussel *Dreissena polymorpha*, for example, an invasive ecosystem engineer in fresh water and estuarine habitat increases the diversity of other associated benthic consumers and primary producers, albeit by altering plankton communities (Higgins and Vander Zanden, 2015). Many previous studies examining the impacts of invasive ecosystem engineers, have examined the arrival of a novel functional group to the recipient community and identified positive as well as negative effects on diversity (Gribben et al., 2013; Lejart and Hily, 2011; Levin et al., 2006). Such invaders, which are taxonomically distinct and differ functionally from local species, are more likely to cause a greater impact on the recipient community (Ricciardi and Atkinson, 2004). It remains unclear whether such species, termed invasive on the basis of their impact on ecosystems lacking similar functional groups, have a strong, or any, impact on communities where functionally similar native species are also present. Comparison of benthic macrofaunal communities associated with an invasive and a native habitat-forming cord grass, for example, showed no difference in assemblages, demonstrating that both species are functionally similar in terms of biodiversity facilitation (Neira et al., 2005).

The Pacific oyster, *Crassostrea gigas,* is a reef-forming ecosystem engineer, which is native to East Asia and has been introduced globally for aquaculture, which has led to the spread and establishment of wild populations in many regions of its introduction (Ruesink et al., 2005). *C. gigas* has spread to Atlantic coasts in Europe and regions such as the Wadden Sea, where benthic assemblages associated with *C. gigas* differ and are more diverse than those of native mussel, *Mytilus edulis,* beds and surrounding substratum (Kochmann et al., 2008; Markert et al., 2009). These different assemblages may be driven by differences in the structural properties of native mussel beds compared to the invasive oyster reefs (Lenihan, 1999; Lintas and Seed, 1994; Markert et al., 2009). Further, comparison of communities with *C. gigas* to the structurally similar Sydney rock oyster, *Saccostrea glomerata,* in Australia showed that effects of the invasive oyster on local assemblages was limited to the low shore, where environmental conditions are considered more benign (Wilkie et al., 2012). The importance of facilitative effects of biogenic structure is thought to be greater in harsh environmental conditions (Bruno et al., 2003). Here the abundance of complex structure, such as oyster reefs may help to increase diversity by mitigating physical stress (Bruno et al., 2003; Lejart and Hily, 2011).

The native European oyster, *Ostrea edulis,* is an economically important species and an ecosystem engineer, which increases diversity at a local scale (Smyth et al., 2009). It has been eradicated throughout much of its native range (Laing et al., 2006; Lockwood, 2001). Remaining populations in the UK, Ireland and Scandinavia may be threatened by the introduction of the invasive *C. gigas* (Zwerschke et al, in review).Until recently it was assumed that *C. gigas* and *O. edulis* occupy intertidal and subtidal habitats respectively, but not overlapping habitats. More recent surveys show, however, that in Ireland *O. edulis* has always and still is, albeit at reduced densities, present in both intertidal and subtidal habitats (Kennedy and Roberts, 1999; Smyth et al., 2009; personal observation). Further concerns have been raised when *C. gigas* has been found on existing subtidal *O. edulis* populations (Tully and Clarke, 2012; personal observation). *C. gigas* has been found to affect *O. edulis* adversely and thus may displace the native species, potentially also altering associated diversity and functioning (Beck et al., 2011; Ruesink et al., 2005; Smyth and Roberts, 2010; Zwerschke et al., in review).

To make better informed management decisions and to improve predictions of the impacts of invasive species it is important to understand how impacts of invasive species compare to similar (equivalent!) native species. Although *O. edulis* and *C. gigas* co-occur occasionally, the composition of their associated communities is poorly understood. This study therefore examined differences in diversity and assemblage structure of benthic communities which developed over 12 months in association with the native oyster, *O. edulis,* and the non-native oyster, *C. gigas* to predict how the spread of *C. gigas* might affect species diversity in *O. edulis* communities. The underpinning aim was to test the hypothesis that seemingly morphologically similar species can be considered as functionally inter-changeable across different habitats (intertidal, subtidal) and at different orientations of attachment substratum (vertical and horizontal).

Methods

An experiment was conducted on a sheltered rocky shore at Ballyhenry Bay, Strangford Lough, Northern Ireland (54°29.945'N 5°35.294'W), where recently increasing wild

populations of *C. gigas* have been found and local *O. edulis* populations are in decline (Kennedy and Roberts, 1999; Smyth et al., 2009). Experimental treatments were established in the intertidal and the adjacent subtidal habitat at 12 m depth. During the experiment, temperature was estimated with HOBO® Pendant® temperature loggers (Onset Computer Corporation, Bourne, USA) and ranged from -1°C to 34.5°C (mean ± S. D. = 11.48°C ± 3.57) in the intertidal and from 6.5°C to 15.1°C (11.01°C ± 2.48) in the subtidal habitat.

Experimental design

The factorial experiment had three fixed factors: (i) oyster treatment (three levels: only *C. gigas* present, only *O. edulis* present, and both species present); (ii) habitat (two levels: intertidal and subtidal); and (iii) oyster orientation (two levels: vertical and horizontal). Each treatment was replicated five times and the experiment ran for 12 months from September 2013.

Populations of *C. gigas* and *O. edulis* are not sufficiently abundant at Strangford Lough to collect the required amount of oysters with similar morphological features without potentially impacting these populations. To ensure consistent bivalve morphology within experimental treatments, juvenile oysters were obtained from local hatcheries. Using juvenile *C. gigas* (mean length ± S. D. = 14.10 mm ± 0.15 mm) and *O. edulis* (15.10 mm ± 0.18 mm) also increased scope for settlement and growth of other associated species as more space for settlement was available (Dayton, 1971). The density of oysters was selected to mimic their presence in the field (Zwerschke et al., in review).To establish experimental treatments, juvenile oysters were fixed to perspex plates (15 x 15 cm) using Milliput© (Dolgellau, UK) and Gorilla Super Glue© (Euxton, UK), to mimic hard bottom substratum which closely resembles natural conditions and provide a removable experimental unit (McGuinness, 1989). Each plate had ten individual oysters, which were either, all *C. gigas*, or all *O. edulis,* or a mixture of five *C. gigas* and five *O. edulis* placed randomly on each plate. The use of experimental plates, rather than manipulating oyster abundance directly on bedrock, was unavoidable for sampling thus, care should be taken when interpreting results according to general methodological caveats (Kennelly, 1983; Lathlean and Minchinton, 2012; Nozawa et al., 2011). Although we did not have plates without any oysters attached to compare to

natural rock we can compare directly for effects of experimental treatments within similar experimental conditions. The plates were placed inside cages (mesh size: 0.5 cm) to limit predation on juvenile oysters during the experiment. Experimental treatments were allocated randomly to plates. Orientation of substratum can affect epibiotic assemblages, which may be further altered by the presence of biogenic structure (Fraser et al., 2014; Glasby and Connell, 2001).Therefore intertidal plates were bolted directly on to boulders, randomly chosen in the mid to low intertidal zone, in a horizontal or vertical orientation, and all were at least 1 m apart. The subtidal plates were attached, either horizontally or vertically, to five steel frames (180 cm x 130 cm x 50 cm) placed on the seafloor. Each of the frames, which were 10 m apart, housed six plates. All plates were photographed immediately before the deconstruction of the experiment to account for the possible loss of any species during the disassembling process. Destructive samples were taken at the end of the experiment and all benthic taxa on each plate were identified to the highest taxonomic resolution practicable (Hayward and Ryland, 2008; Hayward et al., 2007; WoRMS, 2015). The abundance of all taxa was quantified by estimating %-cover on each plate.

Statistical analysis

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) was used to test for differences in assemblage structure among experimental treatments. Multivariate analyses were based on Bray-Curtis similarity matrices calculated from un-transformed and fourth-root transformed data to distinguish between the effects of rare and dominant species (Clarke and Warwick, 2001) and were done with 9999 permutations of the residuals under a reduced model. The presence of *O. edulis* and *C. gigas* was not included as response variable for multivariate analyses to avoid confounding independent (manipulated) and dependent (response) variables (Huston, 1997). Analyses were carried out on all taxa initially and subsequently data were also classified into taxonomical groups (class, order) and re-analyzed, to test for general effects on functional diversity based on taxonomically distinct groups. A dummy species was added to each sample to correct for the erratic behavior of the Bray Curtis coefficient with zero inflated data (Clarke et al., 2006), because a number of species were found in low percentages. Similarity of Percentage (SIMPER) analysis was used to identify the most important taxa driving differences between significant treatments. A 50% cut-off was used for the cumulative

dissimilarity between groups, because, thereafter, remaining taxa individually contributed to less than two percent of overall differences in assemblage structure.

Simpson's diversity index (C) was estimated, for all taxa, because this metric is less likely to over- or under-estimate diversity when samples have a low number of individuals (Lepretre and Mouillot, 1999). Simpson's diversity index was tested for normality, homogeneity of variance and collinearity of co-variates. Analysis of co-variance (ANCOVA) was used to test for differences among experimental treatments (oyster species treatment, habitat and orientation). A linear regression showed a significant increase of diversity with increasing percentage cover of oysters ($F_{1, 54} = 10.63$, $R^2 = 0.17$, $P = 0.002$), thus total oyster percentage cover was added as a covariate in the analysis, to account for any differences in oyster cover which could affect diversity and could have been confounded in treatments (where different combinations of oysters grew faster during the experiment; Table 1). PERMANOVA was performed with PRIMER, version 6 (Clarke and Warwick, 2001) and all other data analyses were completed using R 3.1.2 (R Core Team 2014).

Results

A total of 181 taxa were identified, including 86 taxa from the intertidal habitat and 144 from the subtidal habitat (Supplementary material 1). There were no significant interactions among any of the factors in the analyses. Benthic assemblage structure did not differ among oyster treatments ($F_{2, 42} = 0.92$, $P = 0.64$; Figure 1). Assemblages differed, however, between subtidal and intertidal habitats ($F_{1, 42} = 27.53$, $P < 0.001$) and between horizontal and vertical orientation ($F_{1, 42} = 1.54$, $P = 0.05$; Figure 1). When taxa were grouped based on taxonomic similarity (e.g. order, class) to test for functional group effects, the results were generally consistent with analysis based on species-level (or highest practicable) identification for oyster treatments and between habitats (order [oyster treatment: $F_{2, 54} = 0.856$, $P = 0.76$; habitat: $F_{1, 54} = 17.03$, $P < 0.001$] and class [oyster treatment: $F_{2, 54} = 0.87$, $P = 0.73$; habitat: $F_{1, 54} = 17.03$, $P < 0.001$]). However, in contrast to results based on species-level taxonomic resolution, oyster orientation was no longer significant when species were classed into functional groups (order: $F_{1, 54} = 1.92$, $P = 0.39$, class: $F_{1, 54} = 1.9$, $P = 0.39$). Analyses were performed on untransformed and fourth-root-transformed data and following the latter the

difference between inter- and subtidal habitats assemblages remained, which suggests that this shift was driven by the presence of less common species. SIMPER analysis results also show that whole assemblages shifted, rather than the abundance of few dominant species. Differences in assemblages between subtidal and intertidal habitats were driven mainly by the increased abundance of scallops (*Aequipecten opercularis*), sea squirts (*Ascdiella aspersa, Ascidia conchilega*) and saddle oysters (*Monia squama*) in the subtidal zone and the presence of encrusting calcareous red algae (*Lithothamnion* sp.) in the intertidal zone (Table 2 a). Differences between horizontal and vertical assemblages can be attributed to a greater abundance of bivalves, such as scallops, *Aequipecten opercularis* and blue mussels*, Mytilus edulis* and sea squirts, such as *Ascdiella aspersa* and *Ascidia conchilega* on reefs at vertical orientation compared to a relatively greater abundance of algae *Lithothamnion* sp. and *Ulva lactuca* at horizontal orientation in both habitats (Table 2 b).

Taxa diversity increased with oyster percentage cover ($F_{1, 53} = 6.57$, $P < 0.01$) but was not affected by oyster treatments ($F_{1, 53} = 0.60$, $P = 0.55$; Figure 2). Taxa diversity was greater in the subtidal than intertidal habitat ($F_{1, 53} = 14.18$, $P < 0.01$, Figure 2), yet was not affected by orientation ($F_{1, 53} = 2.91$, $P = 0.10$, Figure 2).

Discussion

Our findings show that the benthic assemblages and taxonomic diversity associated with each oyster species (*C. gigas* and *O. edulis*) were similar, irrespectively of whether they occurred separately or together. Differences in assemblage structure were identified between intertidal and subtidal habitats and between horizontal and vertical orientations. The additional hard substratum provided by both oyster species appeared to be the driving mechanism behind increasing diversity at this early successional stage (1 year). Other functional traits, such as abundance of prey and provision of nutrients, would influence diversity in later successional stages particularly if these involved greater reef formation (Dame and Patten, 1981; Grabowski, 2004).

Our findings contrast with some previous studies that examined the impact of invasive species on native biodiversity (Kochmann et al., 2008; Markert et al., 2009; e. g. Smaal et al., 2005; Trimble et al., 2009). This is most likely because previous studies did not always compare invaded assemblages with those of structurally similar native ecosystem engineers. Communities supported by ecosystem engineers are typically specific to the created habitat, such as mussel or kelp beds, oyster reefs and seagrass meadows, because of the innate differences between the foundation species (Buschbaum et al., 2006; Hosack et al., 2006). The present study indicates that *C. gigas* and *O. edulis* provide similar physical structures, which facilitate other species consistently, suggesting that both species are functionally similar or inter-changeable supporting our original hypothesis. These findings may lead to reconsideration of the broad ecological status of *C. gigas* within Europe. At present *C. gigas* is classified as invasive species in several regions, for example in the Wadden Sea where it has established extensive reefs with different effects (Diederich, 2006; Eschweiler and Christensen, 2011; Fey et al., 2009; Global Invasive Species Database, 2015; Lang and Buschbaum, 2010; Nehls and Büttger, 2007). Historically, however, these regions would have supported widespread populations of *O. edulis* (Reise et al., 1989; Riesen and Reise, 1982). Increasing *C. gigas* populations may counteract the consequences of species loss associated with declining *O. edulis* populations.

Differences in reef-forming potential of both oyster species may cause problems following the replacement of *O. edulis* with *C. gigas*; the latter can form dense oyster reefs over a relatively short period (three to five years; Diederich 2006; Troost 2010) whereas although *O. edulis* may have formed massive reefs in historic periods (Todorova et al., 2009) there are no contemporary records of it forming reefs. Species diversity is related to habitat heterogeneity, generally following a unimodal curve, with greatest diversity usually in habitats with intermediate levels of heterogeneity (Allouche et al., 2012; Dittmann, 1990; Snover and Commito, 1998). Although no decrease of diversity was associated with increasing oyster cover in the present study, previous studies have shown lower species richness in experimental plots with high oyster cover compared to those with low oyster abundance (Green and Crowe, 2013). In fact, high densities of two different structurally complex habitat engineers seems to cause a significant decline in diversity (Green and Crowe, 2014). Presently, seawater temperature is thought to limit the range and density of wild *C. gigas*

populations in cooler temperate regions. Climate-driven ocean warming, however, may lead to a more detrimental impact of *C. gigas* on species diversity by establishing high density populations, thus reducing associated species diversity (Cognie et al., 2006; Syvret et al., 2008).

This study focused on the facilitative role of oysters on hard substrate communities, where both species typically occur and it is possible that small differences in physical attributes of *O. edulis* and *C. gigas* shells would play a more important role in soft sediment habitats (Lejart and Hily, 2011). Similarly, it may be possible that later successional stages of assemblages may differ between the two species, which we were unable to detect, owing to time constraints. However, this seems unlikely since other studies detected differences in assemblage structure between *C. gigas* and other habitat engineers within a similar timeframe (Green and Crowe, 2014; Kochmann et al., 2008; Markert et al., 2009). Meanwhile, our findings showed clearly that *C. gigas* and *O. edulis* are functionally similar with regard to species facilitation. We conclude that the presence of *C. gigas* may not have a negative effect on species diversity and assemblage structure on temperate rocky shores and could replace the key functions of declining *O. edulis* populations, by supporting local diversity.

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Table 1

	Mean (± SD) % oyster abundance	
	Intertidal	Subtidal
Crassostrea gigas	32 .0 (22.82)	39.67 (31.53)
Ostrea edulis	15.44 (13.3)	30.0 (20.18)
Both species present	32 .0 (18.51)	37.05 (20.18)

Table 2

	Average abundance		Diss/SD	Average %Contribution
a)	intertidal	subtidal		
Aequipecten opercularis	0.00	11.29	0.83	12.26
Ascdiella aspersa	0.00	8.90	0.53	9.39
Ascidia conchilega	0.00	4.63	0.80	6.18
Monia squama	0.09	2.83	1.09	4.94
Mytilus edulis	1.04	1.95	0.94	3.35
Lithothamnion	1.60	0.00	0.70	2.93
Anomia ephippium	0.01	1.88	0.93	2.85
Patella vulgata	1.37	0.00	0.71	2.68
Schizoporella unicornis	0.16	1.78	0.90	2.49
Hydroides elegans	0.00	1.13	0.64	2.25
b)	horizontal	vertical		
Aequipecten opercularis	5.16	6.13	0.71	9.21
Ascdiella aspersa	3.17	5.73	0.50	7.82
Ascidia conchilega	1.81	2.81	0.66	4.54
Mytilus edulis	1.08	1.91	0.79	4.25
Lithothamnion	1.32	0.29	0.62	3.43
Monia squama	1.26	1.67	0.87	3.33
Patella vulgata	0.83	0.54	0.64	3.13
Ulva lactuca	0.70	0.29	0.37	2.30
Elminius modestus	0.43	0.60	0.54	2.21
Schizoporella unicornis	0.54	1.40	0.76	2.16
Anomia ephippium	0.66	1.23	0.75	2.05

Table 1: Mean (± SD) percentage cover of oysters in the different treatments in intertidal and subtidal habitats, after 12 month of submersion.

Table 2: SIMPER (similarity of percentages) analysis of taxa contributing to differences between a) intertidal and subtidal and b) between horizontal and vertical assemblages.. These taxa account for > 50% of the dissimilarity between the two habitats. A 50% cut-off was used, because, thereafter, remaining taxa individually contributed to less than two percent of overall differences in assemblage structure. Average abundance = average percentage cover of species, Diss/SD = ratio of dissimilarity and standard variation, Average percentage contribution = percentage contribution to the overall Bray-Curtis dissimilarity between the assemblages in both habitats. N = 5
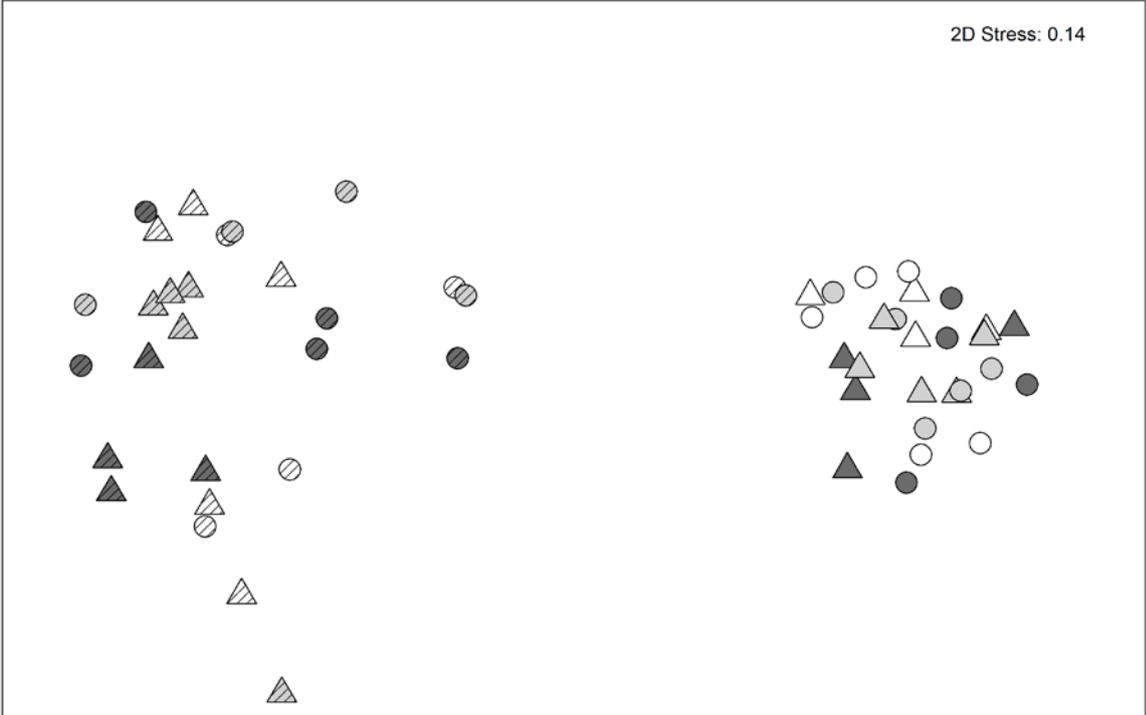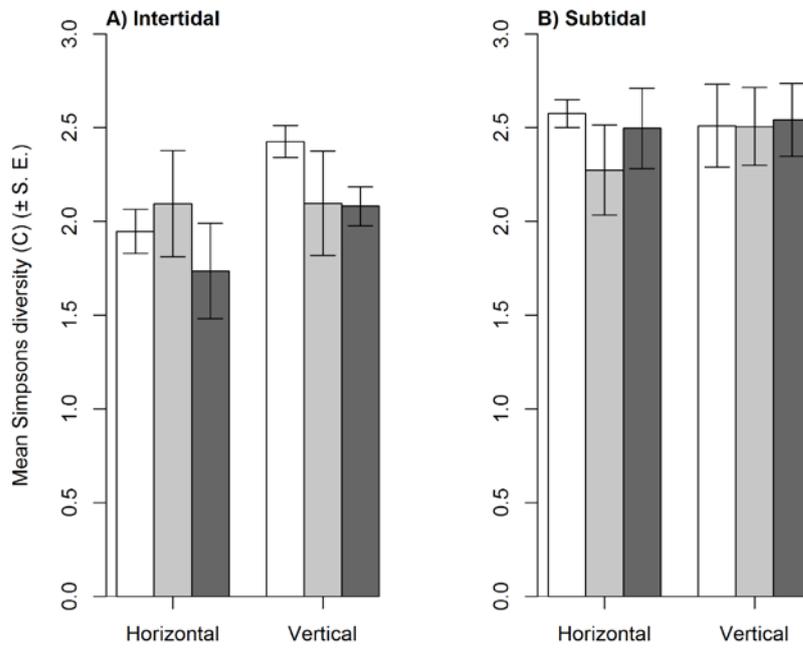
Figure 1

Figure 2

Figure 1: MDS (multi-dimensional scaling) plot of benthic assemblages in experimental treatments with only *C. gigas* (white), only *O. edulis* (dark grey) and both species present (light grey). Circles represent vertical orientated assemblages and triangles horizontally orientated assemblages. Open symbols represent subtidal assemblages and striped symbols represent intertidal assemblages. Data were fourth root transformed. N=5

Figure 2: Mean Simpson's Diversity Index (C) (± S. E.) of oyster treatments (*C. gigas* – white; both species – light grey, *O. edulis* – dark grey) in (A) intertidal and (B) subtidal habitats at horizontal and vertical orientation.