

Physical and biological effects of introduced oysters on biodiversity in an intertidal boulder field

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ABSTRACT: Invasive species have been identified as a serious threat to biodiversity, particularly in protected habitats. The Pacific oyster *Crassostrea gigas*, which is invasive in many parts of the world, can form very dense populations affecting the abundance and distribution of native organisms. We experimentally separated the effects of the cover and state (physical structure or biological activities) of *C. gigas* on the development of invertebrate and macroalgal assemblages. Living (biologically active) and dead (physical structure only) oysters were glued in increasing cover to the tops of cleaned boulders and deployed within an intertidal boulder field. After 14 mo, diversity, evenness and assemblage structure of invertebrates and algae were affected by *C. gigas*, and results varied depending on the cover and state of oysters. Interestingly, boulders with the lowest cover of living *C. gigas* supported the most diverse assemblages. Differences in assemblage structure were driven by changes in the establishment of several key species including *Fucus vesiculosus* and *Littorina littorea*, which were facilitated by oysters and the honeycomb worm *Sabellaria alveolata*, which was inhibited by oysters. *S. alveolata*, an ecosystem engineer that can generate reefs protected by the European Union Habitats directive, mainly established on the underside of boulders but was nonetheless greatly reduced by increasing cover of dead or living oysters on the topside. This work highlights the importance of understanding the direct and indirect mechanisms by which invasive species alter biodiversity and how effects vary as invaders increase in abundance.

KEY WORDS: Invasive species · Biodiversity · Protected habitats · Ecosystem engineer · Density dependent · *Crassostrea gigas* · *Sabellaria alveolata*

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INTRODUCTION

Non-native invasive species can strongly impact native biodiversity and ecosystem functioning (Simberloff 2005, Molnar et al. 2008). Invasive species which are also ecosystem engineers (Jones et al. 1994, 1997) can have far reaching effects on the abundance and distribution of associated organisms over time and space through multiple direct and indirect mechanisms (Crooks 2002). Many species of algae (Kelaher 2002) and invertebrates (Reimer 1976, Khaitov et al. 1999) form biogenic habitats, providing a physical structure which other organisms can attach to or shelter within. These habitats, and the

organisms that occupy them, may differ depending on the identity, size and density of the ecosystem engineer that forms them (Stewart et al. 1998, Palomo et al. 2007). In addition, the biological activities of the biogenic habitat-forming organism, such as feeding and production of waste, can also influence the abundance and distribution of associated organisms (Ricciardi et al. 1997). Previous experiments designed to separate the physical and biological influences of ecosystem engineers have found mixed results. Some found that the physical structure was more important than the biological activity of the ecosystem engineer in structuring assemblages (Crooks & Khim 1999, Palomo et al. 2007), whilst oth-

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ers found the opposite (Ricciardi et al. 1997). Few previous studies have attempted to experimentally separate the physical and biological effects of an invasive ecosystem engineer (Ricciardi et al. 1997), but understanding the complex mechanisms by which invasive species alter assemblages is crucial in order to appreciate the full extent of their potential impacts and to improve management strategies for their reduction when effects are negative (Watling et al. 2011).

The Pacific oyster *Crassostrea gigas*, an ecosystem engineer originally from Japan and South-east Asia, has become globally invasive due to its extensive use in aquaculture since the 1900s (Bourne 1979). *C. gigas* is of particular concern as an invasive species because of its ability to form dense populations that may dominate entire shores and in some cases may reach densities of over 400 ind. m⁻² (Diederich et al. 2005, Ruesink et al. 2005, Wrange et al. 2010). *C. gigas* has been found to increase biodiversity, modify assemblage structure and change the abundance and distribution of native species in a number of habitats worldwide, including mudflats and mussel beds (Reise et al. 2006, Ruesink 2007, Büttger et al. 2008, Markert et al. 2010), marshes (Escapa et al. 2004), polychaete reefs (Dubois et al. 2006) and rocky platforms (Krassoi et al. 2008, Trimble et al. 2009). However, many of these studies have been observational rather than experimental (but see Kochmann et al. 2008), so causal links remain largely unconfirmed. As the density of *C. gigas* increases, the effect it has on the physical, chemical and biological properties of the environment may change in nature or magnitude (Sousa et al. 2009), but so far no studies have explicitly addressed the effect of increasing densities of *C. gigas* on biodiversity. This is a significant shortcoming in invasion biology because it precludes the ability to make generalisations about abundance-dependent impacts or to predict how impacts may vary as the invasion proceeds (Thomsen et al. 2011a,b).

The influence of *Crassostrea gigas* on other biota may be due to its physical structure (shell), which can displace or facilitate other organisms. Under certain environmental conditions, *C. gigas* can out-compete and displace other sessile organisms, such as eelgrass (Tallis et al. 2009), cockles (Smaal et al. 2005, van den berg et al. 2005), native oysters (Bourne 1979, Krassoi et al. 2008) and blue mussels (Cognie et al. 2006, Diederich 2006). Their shells also provide novel habitat which can facilitate other native and non-indigenous organisms. Because the shell of *C. gigas* is structurally complex, it has been found to increase the abundance and diversity of organisms in

a variety of habitats (Gutierrez et al. 2003, Peterson et al. 2003, Dubois et al. 2006, Markert et al. 2010, Lejart & Hily 2011). Alternatively, diversity can remain unchanged, but the structure of assemblages may differ from those of indigenous biogenic habitats (Kochmann et al. 2008, Markert et al. 2010). The physical structure of *C. gigas* can also alter small-scale hydrodynamics (Moulin et al. 2007) and subsequently affect the establishment of other taxa, since the hydrodynamic properties of the benthic boundary layer (in terms of flow velocity and sediment transport) are important in determining the settlement of particulate matter and larvae (Butman et al. 1988, Eckman et al. 1994).

The biological activities of *Crassostrea gigas* (i.e. filter feeding and biodeposition) can also affect the establishment of other organisms. For example, the movement involved in filter feeding can alter the settlement of particulate matter and larvae by increasing turbulence in the water column (Troost et al. 2009). Concurrently, by filtering particulate matter in the water column, *C. gigas* can compete for food with other filter feeders, such as polychaetes (Ropert & Gouletquer 2000, Dubois et al. 2006), or in some cases, can directly filter the larvae of other organisms (Pechenik et al. 2004). Furthermore, filtration by *C. gigas* may increase water clarity, enhancing light penetration, thereby increasing the growth of algae (Sousa et al. 2009). The deposition of faeces and pseudo-faeces by *C. gigas* can alter the physical and chemical properties of the environment, in terms of increased sedimentation and nutrient enrichment. In extreme cases, this process can lead to toxic levels of ammonium and hydrogen sulphide for other organisms, such as eelgrass (Kelly & Volpe 2007). In some circumstances, however, bio-deposition can facilitate organisms. For example, ammonia excreted by *C. gigas* can increase the growth of algae (Reusch et al. 1994).

Despite the extensive research on impacts of *Crassostrea gigas* (see above), there has been no work to date addressing the effects of *C. gigas* on the establishment of assemblages in intertidal boulder fields. Boulder fields are unique habitats, often inhabited by a range of rare or endemic species (Kangas & Shepard 1984, Chapman 2005). This may include biogenic habitat-forming organisms, which are a particularly important component of biodiversity (Bruno et al. 2003) and are often considered a priority for conservation. *C. gigas* exists in wild populations in a number of habitats globally and, in some places, coexists with biogenic habitat-forming species, such as the honeycomb worm *Sabellaria alveo-*

lata (Cognie et al. 2006), a polychaete which creates reef habitats protected under Annex I of the EU Habitats Directive. Despite the importance of this biogenic habitat, the impacts of *C. gigas* on the establishment of *S. alveolata* reefs have received little attention (Dubois et al. 2006).

The aim of this study was therefore to test the effects of increasing densities of *Crassostrea gigas* on biodiversity and the establishment of *Sabellaria alveolata* on intertidal boulders and to distinguish between the influence of the physical structure of the oysters and their biological activity. An initial survey done to assess differences in the cover of *S. alveolata* on boulders with and without *C. gigas* revealed that there was less cover of *S. alveolata* on boulders with *C. gigas*. This was followed by an experimental manipulation of living and dead oysters to test the following hypotheses: (1) biodiversity on boulders will increase with increasing cover of oysters; (2) the establishment of *S. alveolata* on boulders will be reduced with increasing cover of oysters; (3) if the effects of *C. gigas* are due to its physical structure alone, the same effects on biodiversity and *S. alveolata* would be expected regardless of whether the oysters were living or dead; (4) if the effects are due to the biological activity of *C. gigas* only, the effects on biodiversity and *S. alveolata* would only occur when the oysters were living and there would be no effects of dead oysters; (5) the effects could also be due to a combination of the physical structure and biological activity of *C. gigas*, in which case both living and dead oysters would have an effect, but the influence of living oysters would be different from that of dead oysters.

MATERIALS AND METHODS

Study site

The present study was done in the mid- to low shore area of an intertidal boulder field at Lough Swilly (Ballylin Point, County Donegal, Ireland: 55° 2' 36.12" N, 7° 33' 36.09" W) with recently established populations of wild *Crassostrea gigas* oysters. The boulder field extends approximately 5 km along the coast and is situated in a sheltered estuary that is rarely visited by people. Most of the boulders on the shore are made of sandstone, although granite and shale boulders are also present. The diameter of boulders on the shore ranged from 10 to 200 cm, although the majority were between 18 and 24 cm and the average (\pm SE) was 22.3 \pm 0.5 cm. The density

of boulders was approximately 5 m⁻², and boulders were resting either on bedrock, sediment, small pebbles or other boulders. Most boulders were colonised by a mixture of algae, barnacles, oysters and gastropods on the topside and barnacles, bryozoans, sponges, polychaetes, gastropods and crustaceans on the underside.

Cover of *Sabellaria alveolata* on boulders with and without *Crassostrea gigas*

On a 50 m section parallel to the shore, 40 boulders with oysters and 40 boulders without oysters were identified, numbered and their positions marked on a map. Boulders chosen were of a similar size and rock type and occurred at the mid- to low tide level. Out of these, 20 boulders with oysters and 20 boulders without oysters were randomly selected. The percentage cover of *S. alveolata* on these boulders was estimated by point-intercept sampling using a 10 cm side grid subdivided into 2 cm side quadrats (i.e. 25 intersections) which was randomly placed twice on each of the topside and underside of the boulder to obtain a measure out of 100 for each boulder.

Experimental addition of *Crassostrea gigas* onto boulders

The experiment was asymmetrical and involved 2 fixed and orthogonal factors: (1) 'State' of oysters (2 levels: living or dead) and (2) 'Cover' of oysters (3 levels: 5, 50 and 100% cover) and 1 set of control boulders without any oysters. Seven replicate boulders were allocated randomly to each treatment, giving a total of 49. All boulders used in the study were similar in shape, made of sandstone and were approximately 25 \times 20 \times 10 cm in size and weighed approximately 12 kg. All oysters (living and dead) used in the experiment were collected from nearby mussel beds in Lough Swilly. Oysters in the range 40 to 100 mm maximal length were collected, cleaned of any flora or fauna on their shells and randomly allocated to treatments so that any differences in size and shape would be randomized among treatments. The left and right valves of the dead oysters were glued together so that their physical structure did not differ from that of the living oysters. Oysters were then attached to the tops of boulders using a 2-part epoxy resin (ARALDITE rapid; Huntsman Advanced Materials) as described by Jackson (2009) and allowed to dry for 12 h before the boulders were

deployed at the site. To account for any possible effects of the glue, a procedural control was included, in which only glue was added to 7 boulders. The amount of glue that was added was similar to that of the boulders with 50% cover of oysters. All of the boulders used in this study were collected from the upper shore, because they were free of an existing marine assemblage, but they were also scraped and then cleaned with a blowtorch to ensure that there was no remaining biofilm. In order to account for possible differences between upper and lower shore boulders, another procedural control was included in which 7 boulders from the lower shore were also scraped and cleaned with a blowtorch. Boulders were deployed in mid-April 2010 and were sampled after 4, 9 and 14 m. The first and last sampling periods were chosen because the reproductive peak for *Sabellaria alveolata* is between June and September and the experiment was run for long enough to allow settlement and establishment of this species (Culloty et al. 2010). The length of time between sampling periods was sufficient to allow assemblages disturbed by the non-destructive sampling to fully recover (Chapman & Underwood 1996).

Sampling of experimental boulders

The surface area of each boulder was approximated to that of a sphere and was calculated using the average diameter. The total individual *Sabellaria alveolata* tubes on the topside and underside of the boulders were recorded and combined to obtain a measurement for the whole boulder which was converted to a measure of density per m². All other organisms on the boulders were also identified and counted, but were not removed from the boulders so as to minimise disturbance. Organisms which could not be counted individually in the field, such as algae, bryozoans and barnacles, were recorded as percentage cover using the point-intercept method described in 'Cover of *Sabellaria alveolata* on boulders with and without *Crassostrea gigas*'.

Statistical analyses

To compare the percentage cover of *Sabellaria alveolata* on boulders with and without oysters in the mensurative survey described above, a 2-tailed *t*-test was used.

We conducted univariate analyses of selected variables using the design described in 'Experimental

addition of *Crassostrea gigas* onto boulders'. These included species richness (SR), Shannon-Wiener diversity (H') and Pielou's evenness (J'). Differences in the density of *Sabellaria alveolata* and the density or percentage cover of some other taxa found to be susceptible to the impacts of oysters in previous studies, or found as dominant space occupiers on the shore, were also compared. Specifically, these were bladder-wrack algae *Fucus vesiculosus*, solitary ascidians *Ascidia conchilega* and common periwinkles *Littorina littorea*. The data were analysed with asymmetrical analyses of variance (ANOVA; following Underwood 1993, Glasby 1997) performed in 3 steps: (1) a 1-way ANOVA was done with all 7 treatments, including the 3 different covers of living or dead oysters and the control boulders, to obtain a value for the sum of squares (SS) for the comparison of all treatments, (2) a 2-way ANOVA was done for the factors 'State' and 'Cover' excluding control boulders, (3) a value for the SS for the control versus all others was obtained by subtracting the SS for the 2-way ANOVA (Step 2) from the SS for the 1-way ANOVA (Step 1). Degrees of freedom and mean square (MS) values were similarly derived. An *F*-value for the comparison of control versus others was obtained by dividing MS 'Treatment' by MS 'State × Cover' interaction.

Variation in assemblage structure among treatments at each sampling time was compared using 2-factor permutational ANOVA (PERMANOVA; Anderson 2001) based on Bray-Curtis dissimilarities (Bray & Curtis 1957) of square root transformed data with 9999 permutations under the reduced model using Type I SS. The asymmetrical analyses were achieved by fitting each main effect ('State' and 'Cover') in turn with a Type I (sequential) SS model, then swapping the order of the terms and combining the results of the 2 analyses (Anderson et al. 2008); this can also be used for cases where the cell structure itself is non-independent (M. J. Anderson pers. comm.). The data were ordinated on a 2-dimensional non-metric multidimensional scaling (nMDS) diagram, with the stress values representing the level of distortion of the actual rank order of distance among samples (Clarke 1993). Where significant differences were found, SIMPER (Clarke 1993) analyses were also done and were used to assess the contribution of different taxa to dissimilarities between treatments.

The potential influence of artefacts due to the experimental procedures on multivariate assemblage structure and the density of *Sabellaria alveolata* was tested using 2 analyses: firstly to test for the effects of glue, 1-way PERMANOVAs and 1-way ANOVAs

were done with the factor 'Type of boulder' with 4 levels (blank control, glue control, 50% living oyster or 50% dead oyster boulders). The glue control was only done for the 50% cover treatment due to practical limitations. Secondly, to test for possible effects of using upper shore boulders in the mid- to low shore, a 1-way PERMANOVA and a 2-tailed *t*-test were done comparing upper shore blank controls with mid- to low shore blank controls.

All multivariate analyses were done using the PRIMER package (PRIMER-e). All univariate analyses were done with ANOVA on untransformed data using the software Win-GMAV (Underwood & Chap-

man 2002). Heterogeneity of variance was tested using Cochran's *C*-test. When this was significant, data were square root transformed in order to reduce the probability of inflated Type I errors (Cochran 1947). When significant differences were detected by ANOVA ($p < 0.05$), Student-Newman Keuls (SNK) tests were done to identify patterns of difference.

RESULTS

Coverage by *Sabellaria alveolata* on boulders with or without *Crassostrea gigas*

The mean (\pm SE) percentage cover of *Sabellaria alveolata* on boulders with oysters was significantly less (*t*-test: $p = 0.04$) than on boulders without oysters (10.8 ± 8.7 and $35.6 \pm 10.9\%$, respectively).

Experimental addition of *Crassostrea gigas*

After 4 mo, 6 replicate boulders were found for each treatment. After 9 mo, only 4 were found. This sampling period occurred in January during particularly harsh weather which included snow and hail, making it difficult to locate the boulders. No oysters died during the experiment, and after 14 mo, 6 intact replicates were found in all except the treatment with 5% cover of living oysters, for which 5 replicates were sampled. In this case, analyses were done with $n = 6$. The mean of the 5 available replicates was used as the 6th replicate for this treatment, and the residual degrees of freedom were reduced by 1 (Sokal & Rohlf 1981, Underwood 1997).

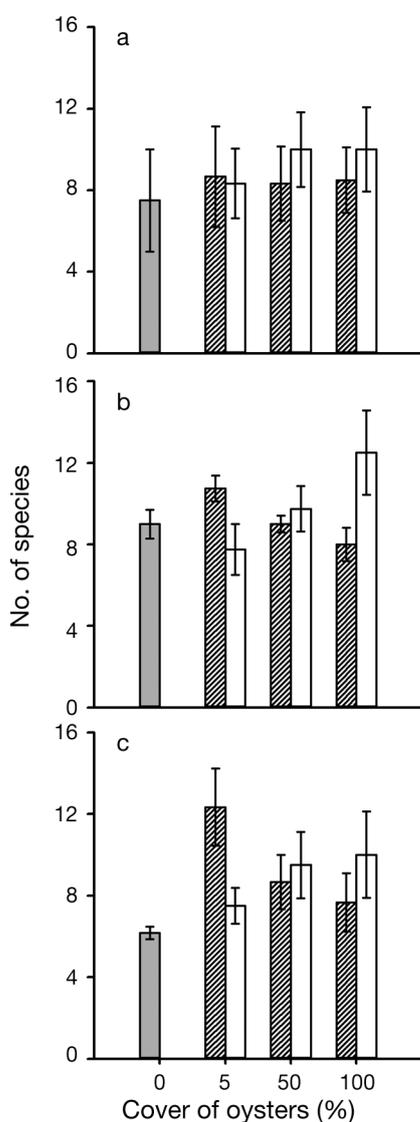


Fig. 1. Mean \pm SE number of species on boulders with no *Crassostrea gigas* oysters (grey bars) or 5, 50 or 100% cover of living (hashed lines) or dead (open bars) oysters after (a) 4, (b) 9 and (c) 14 mo

Effects of *Crassostrea gigas* on diversity and evenness

SR did not differ among treatments after 4 mo (Fig. 1a). After 9 mo, SR was affected by the interaction between state and cover, where boulders with 100% cover of dead oysters had more taxa than those with 5% cover (Fig. 1b, Table 1, SNK procedure). After 14 mo, SR was also affected by the interaction between state and cover, where boulders with 5% cover of living oysters had more taxa than boulders with 100% cover (Fig. 1c, Table 1, SNK procedure). Shannon-Wiener diversity (H') did not differ after 4 and 9 mo (Table 1), but after 14 mo, H' was affected by the interaction between state and cover of oysters, where boulders with 5% cover of living oysters had a

Table 1. Asymmetrical analysis of variance for species richness, Shannon-Wiener diversity and Pielou's evenness on boulders with increasing cover of living and dead *Crassostrea gigas* oysters after 4, 9 and 14 mo. *p < 0.05

Source of variation	4 mo			9 mo			14 mo		
	df	MS	F	df	MS	F	df	MS	F
Species richness									
Treatment	6	5.10	0.21	6	10.95	2.02	6	27.98	2.48
Control vs. Others	1	11.15	3.02	1	1.34	0.05	1	61.02	1.38
State of oysters (S)	1	8.03	2.11	1	3.38	0.61	1	5.44	0.42
Cover of oysters (C)	2	2.03	1.38	2	2.38	0.43	2	6.36	0.49
S × C	2	3.69	0.15	2	28.13	5.10*	2	44.36	3.41*
Residual	65	0.73		39	0.28		65	0.37	
Shannon-Wiener									
Treatment	6	0.12	0.35	6	0.30	2.08	6	0.52	4.89
Control vs. Others	1	0.23	17.88	1	0.52	2.54	1	1.86	4.06
S	1	0.30	0.91	1	0.18	1.54	1	0.07	0.67
C	2	0.09	0.26	2	0.33	2.77	2	0.13	1.21
S × C	2	0.01	0.04	2	0.41	1.75	2	0.46	4.19*
Residual	65	0.01		39	0.01		65	0.00	
Pielou's evenness									
Treatment	6	0.01	1.27	6	0.04	1.70	6	0.03	1.48
Control vs. Others	1	0.00	0.87	1	0.10	20.56*	1	0.14	17.24
S	1	0.00	0.27	1	0.05	2.26	1	0.01	0.48
C	2	0.03	2.68	2	0.05	2.30	2	0.00	0.18
S × C	2	0.01	0.46	2	0.01	0.22	2	0.01	0.53
Residual	65	0.00		39	0.00		65	0.00	

Table 2. Asymmetrical permutational analysis of variance of assemblage structure on untransformed data of boulders with increasing cover of living (L) and dead (D) *Crassostrea gigas* oysters after 4, 9 and 14 mo with 9999 permutations under the reduced model using Type I sum of squares. *p < 0.05, **p < 0.01, ***p < 0.001

Source of variation	4 mo			9 mo			14 mo		
	df	MS	Pseudo F	df	MS	Pseudo F	df	MS	Pseudo F
State of oysters (S)	2	2604.1	1.38	2	3216.6	1.33	2	6779.6	4.60***
Control vs. (L, D)	1	1564.8	0.82	1	3222.9	1.38	1	9051.1	5.65***
L vs. D	1	3643.3	2.05*	1	3210.3	1.40	1	4508.1	2.96**
Cover of oysters (C)	3	2992.1	1.58*	3	3173.7	1.31	3	5777.4	3.92***
S × C	2	1367.6	0.72	2	1135.3	0.47	2	2404.8	1.63
Residual	35	1893.4		22	2415.2		35	1474.4	

greater diversity than boulders with 50 or 100% cover of living oysters (Table 1, SNK procedure). Pielou's evenness (J') did not differ after 4 or 14 mo (Table 1), but after 9 mo, J' of control boulders was less than that of boulders with oysters (Table 1).

Effects of *Crassostrea gigas* on assemblage structure

After 4 mo, assemblage structure differed between boulders with living and boulders with dead oysters and among different cover of oysters (Fig. 2a, Table 2). Boulders with 100% cover of oysters differed in structure from those with 5 or 50% cover of

oysters (post hoc procedure). Boulders with living oysters had a greater density of the gastropods *Gibbula umbilicalis* and *Nucella lapillus*, while boulders with dead oysters had a greater density of the common limpet *Patella vulgata*, the common keel worm *Pomatoceros triqueter* and the scallop *Chlamys varia*. Furthermore, boulders with 100% cover of oysters had a greater density of *G. umbilicalis* and *P. triqueter* than boulders with 5% cover, while boulders with 5% cover had a greater density of *P. vulgata*, *N. lapillus* and *C. varia*. Boulders with 100% cover also had a greater density of *G. umbilicalis* and juvenile *C. gigas* than boulders with 50% cover, which had a greater density of *P. vulgata*, *P. triqueter* and *C. varia* (SIMPER analysis).

After 9 mo, assemblage structure did not differ among treatments (Fig. 2b, Table 2). After 14 mo, however, it differed between control boulders, boulders with living and boulders with dead oysters and among different covers of oysters on boulders (Fig. 2c, Table 2). Control boulders differed in structure from those with 5, 50 or 100% cover of oysters, and boulders with 5% cover differed from those with

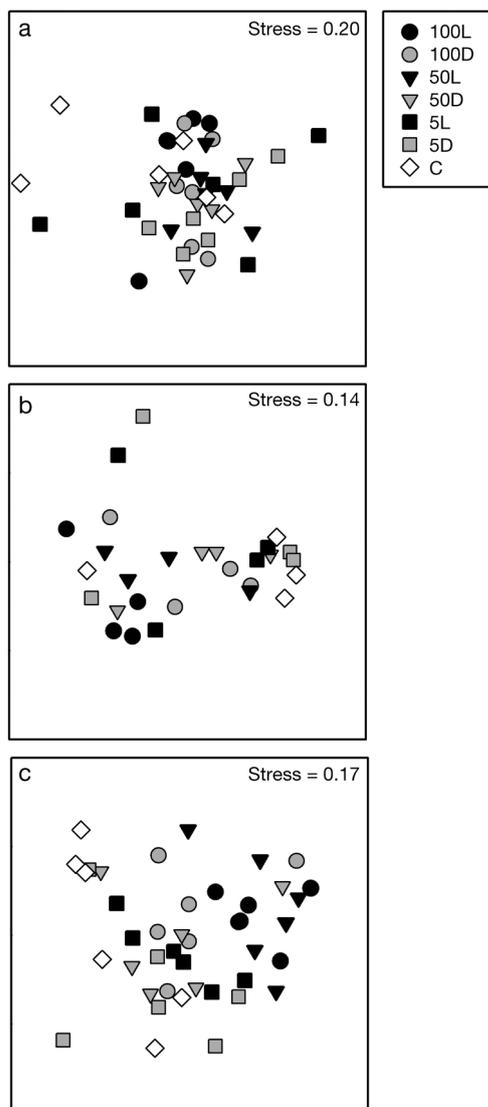


Fig. 2. Non-metric multidimensional scaling plots of square root transformed data of assemblages on experimental boulders after (a) 4, (b) 9 and (c) 14 mo. Black shapes represent boulders with living oysters on them, grey shapes represent boulders with dead oysters on them, and white shapes represent control boulders with no oysters on them. Boulders have 100% cover of oysters (circles), 50% (triangles) or 5% (squares) cover of oysters or no oysters (diamonds). In the legend 'L' denotes living oysters, the letter 'D' denotes dead oysters, and C denotes control boulders

50 or 100% cover of oysters (Fig. 2c, post hoc procedure). Boulders with living oysters had a greater density of *Littorina littorea* and a greater cover of *Fucus vesiculosus* than control boulders or boulders with dead oysters. Boulders with dead oysters had a greater density of *Sabellaria alveolata*, *Patella vulgata* and *Pomatoceros triqueter* than boulders with living oysters and a greater cover of *F. vesiculosus* and density of *L. littorea* and *P. vulgata* than control boulders (SIMPER analysis). In addition, control boulders had a greater density of *S. alveolata* than those with 5, 50 or 100% cover of oysters and a greater density of *P. vulgata* than boulders with 50 or 100% cover. In contrast, there was a greater density of *L. littorea* and a greater cover of *F. vesiculosus* on boulders with 50 or 100% cover of oysters than on control boulders (SIMPER analysis). Interestingly, boulders with 5% cover of living oysters had the greatest density of several organisms including *L. cinerea*, *P. triqueter*, *Gibbula umbilicalis*, *P. vulgata*, the anemone *Actinia equina* and polychaete scale worms of the family Polynoidae.

Effects of *Crassostrea gigas* on the establishment of *Sabellaria alveolata*

After 4 mo, the recruitment of *Sabellaria alveolata* was patchy and there were no differences among treatments (Fig. 3a, Table 3). After 9 and 14 mo, the density of *S. alveolata* was greater on control boulders than on boulders with oysters, regardless of whether the oysters were living or dead (Fig. 3b,c, Table 3). This pattern was more pronounced on boulders with living oysters, but the interaction was not significant, indicating no major influence of the state of the oysters. *S. alveolata* was primarily found on the bottom surfaces of boulders, in 84 of the 120 times it occurred throughout the experiment ($\chi^2 = 19.2$, $df = 1$, $p < 0.0001$).

Effects of *Crassostrea gigas* on the establishment of *Fucus vesiculosus*, *Ascidia conchilega* and *Littorina littorea*

After 4 mo, *Fucus vesiculosus* was not present on any boulder. After 9 mo, there was significantly greater cover of *F. vesiculosus* on boulders with 100% cover of oysters, regardless of whether they were living or not, than on boulders with 5 or 50% cover of oysters (Fig. 4a, Table 3, SNK procedure). After 14 mo, there was significantly greater cover of

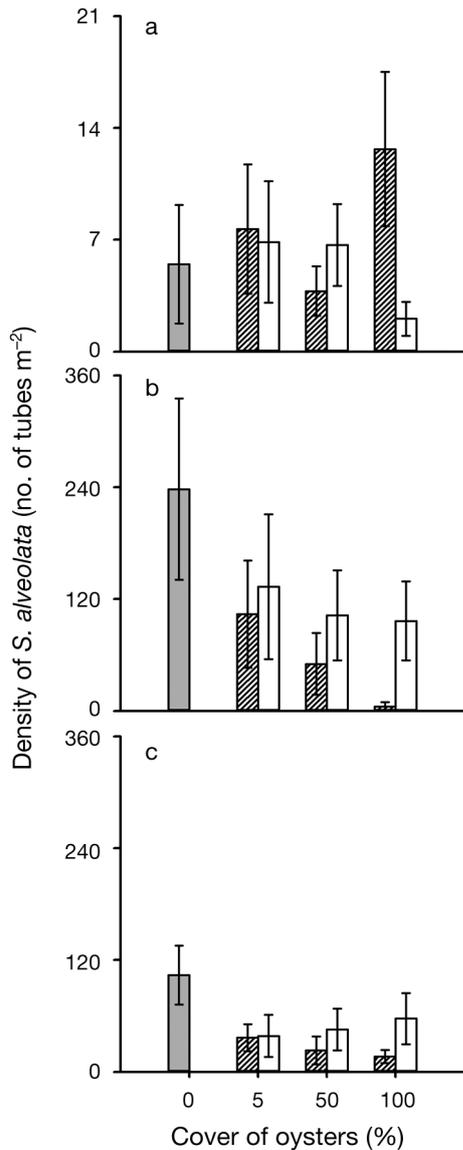


Fig. 3. *Sabellaria alveolata*. Mean \pm SE density (individual tubes m^{-2}) on boulders with no *Crassostrea gigas* oysters (grey bars) or 5, 50 or 100% cover of living (hashed lines) or dead (open bars) oysters after (a) 4, (b) 9 and (c) 14 mo. Note different y-axis scale in (a)

F. vesiculosus on boulders with 50 and 100% cover than on boulders with 5% cover of oysters (Fig. 4b, Table 3, SNK procedure). There was also a significantly greater cover of *F. vesiculosus* on boulders with living oysters than on boulders with dead oysters (Fig. 4b, Table 3, SNK procedure).

After 4 and 9 mo, there was a significantly greater density of *Ascidia conchilega* on boulders with dead oysters than on boulders with living oysters (Fig. 5a,b, Table 3), but after 14 mo the density of *A. conchilega* was almost absent on all boulders and

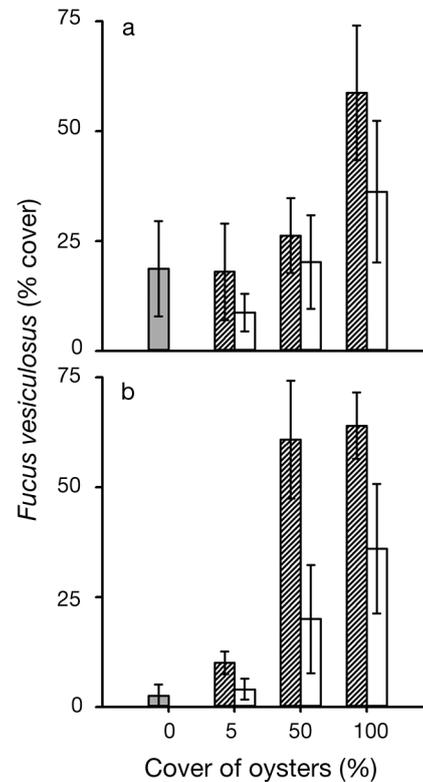


Fig. 4. *Fucus vesiculosus*. Mean \pm SE percent cover on boulders with no *Crassostrea gigas* oysters (grey bars) or 5, 50 or 100% cover of living (hashed lines) or dead (open bars) oysters after (a) 4, (b) 9 and (c) 14 mo

was insufficient for a formal analysis. After 4 mo, there were no differences in the density of *Littorina littorea*. After 9 and 14 mo, although not significant, there was a greater density of *L. littorea* on boulders with oysters than on control boulders (Table 3, Fig. 6b,c).

Effects of the experimental procedure

No artefacts of the experimental procedure in terms of adding glue or using upper shore boulders were found at any time during this experiment either for assemblage structure or for the density of *Sabellaria alveolata*. Assemblage structure was similar on blank control boulders, glue control boulders and boulders with a 50% cover of living or dead oysters after 4 (PERMANOVA: pseudo- $F = 0.703$, $df = 3$, $p = 0.834$) and 9 mo (PERMANOVA: pseudo- $F = 0.822$, $df = 3$, $p = 0.662$). However, after 14 mo, assemblage structure on blank control boulders was the same as that on glue control boulders, but each differed from that on boulders with 50% cover of living or dead oysters (PERMANOVA: pseudo- $F = 2.285$, $df = 3$, $p =$

Table 3. Asymmetrical analysis of variance for density of *Sabellaria alveolata*, cover of *Fucus vesiculosus*, density of *Ascidia conchilega* and density of *Littorina littorea* on boulders with increasing cover of living and dead *Crassostrea gigas* oysters and control boulders (with no oysters) after 4, 9 and 14 mo. After 4 mo, there was insufficient cover of *F. vesiculosus*, and after 14 mo, there was insufficient cover of *A. conchilega* to permit analysis. -: insufficient cover or density for analysis. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$

Source of variation	4 mo			9 mo			14 mo		
	df	MS	F	df	MS	F	df	MS	F
Density of <i>S. alveolata</i>									
Treatment	6	67.80	1.01	6	21069.20	1.53	6	5004.86	1.81
Control vs. Others	1	6.70	0.05	1	83597.58	41.88*	1	23448.07	20.58*
State of oysters (S)	1	73.14	1.14	1	19980.57	2.05	1	4229.81	1.88
Cover of oysters (C)	2	17.40	0.27	2	9422.40	0.97	2	36.35	0.02
S × C	2	146.08	2.28	2	1996.12	0.20	2	1139.29	0.51
Residual	65	2.02		39	603.47		65	77.16	
Cover of <i>F. vesiculosus</i>									
Treatment	-	-	-	6	1110.99	2.19	6	4009.80	7.42****
Control vs. Others	-	-	-	1	476.72	3.12	1	4366.67	4.69
S	-	-	-	1	950.04	1.74	1	5600.03	9.04**
C	-	-	-	2	2466.79	4.51*	2	6115.03	9.87***
S × C	-	-	-	2	152.79	0.28	2	931.03	1.50
Residual	-	-	-	39	27.04		65	17.84	
Density of <i>A. conchilega</i>									
Treatment	6	460.75	2.04	6	102.78	2.04	-	-	-
Control vs. Others	1	48.54	0.21	1	0.00	0.00	-	-	-
S	1	1741.87	7.09**	1	306.04	5.61*	-	-	-
C	2	256.64	1.04	2	22.81	0.42	-	-	-
S × C	2	230.40	0.94	2	132.51	2.43	-	-	-
Residual	65	7.26		39	2.69		-	-	
Density of <i>L. littorea</i>									
Treatment	6	1.04	0.68	6	547.32	0.90	6	267.21	1.02
Control vs. Others	1	0.00	0.00	1	813.52	15.84	1	947.08	14.86
S	1	2.00	1.25	1	104.19	0.16	1	165.53	0.55
C	2	0.81	0.50	2	1131.74	1.76	2	181.59	0.60
S × C	2	1.31	0.82	2	51.36	0.08	2	63.73	0.21
Residual	65	0.05		39	32.02		65	8.72	

0.005, post hoc procedure). After 4 mo, the density of *S. alveolata* did not differ among blank control, glue control or 50% living oyster boulders (ANOVA: $F = 0.45$, $df = 3$, $p = 0.717$). After 9 and 14 mo, the density of *S. alveolata* on blank control and glue control boulders were both greater than on boulders with 50% cover of living or dead oysters (ANOVA: $F = 4.3$, $df = 3$, $p = 0.028$ and $F = 3.66$, $df = 3$, $p = 0.029$, respectively). These results mirrored those from the main experiment and indicate that there were no effects of adding glue, but there were effects of adding oysters to boulders.

The structure of assemblages on blank upper shore boulders was not different from that of assemblages on blank lower shore boulders at 4 (PERMANOVA: pseudo- $F = 0.885$, $df = 1$, $p = 0.528$), 9 (PERMANOVA: pseudo- $F = 0.418$, $df = 1$, $p = 0.889$) or 14 mo (PERMANOVA: pseudo- $F = 0.661$, $df = 1$, $p = 0.703$). Furthermore, the density of *Sabellaria alveolata* on

blank upper shore boulders did not differ from that on blank lower shore boulders at 4 (t -test: $p = 0.720$), 9 (t -test: $p = 0.863$) or 14 mo (t -test: $p = 0.761$). This indicates that there were no effects of using boulders from the upper shore in the experiment.

DISCUSSION

The addition of *Crassostrea gigas* to the tops of boulders altered diversity, evenness, assemblage structure and the establishment of several species, and most effects differed depending on the cover of the oysters. Although the nature and magnitude of some effects differed according to the state of oysters, overall, the influence of their physical structure was stronger than that of their biological activities.

The physical structure of oyster shells provides an increase in habitat complexity which is often

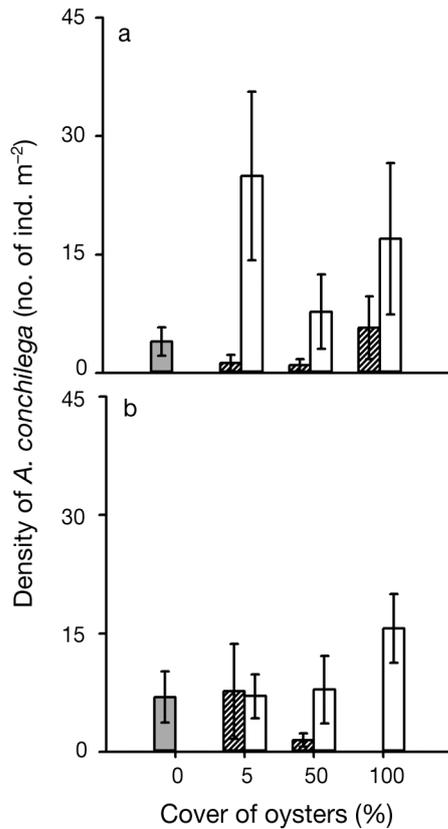


Fig. 5. *Ascidia conchilega*. Mean \pm SE density (ind. m⁻²) on boulders with no *Crassostrea gigas* oysters (grey bars) or 5, 50 or 100% cover of living (hashed lines) or dead (open bars) oysters after (a) 4, (b) 9 and (c) 14 mo

associated with an increase in diversity (McCoy & Bell 1991). Although biodiversity was enhanced at any cover of oysters compared to control boulders, it peaked at low cover (5%), possibly because on boulders with a greater cover (50 or 100%) of oysters, there was less space available for colonisation by other organisms due to space occupied by the oysters and associated organisms, such as *Fucus vesiculosus*. Meanwhile, boulders with a low cover of oysters provided space and a more complex habitat than boulders without oysters. The effects of the biological activity of *Crassostrea gigas* on biodiversity depended on their cover. Boulders with the least cover (5%) of living oysters supported the greatest biodiversity, but at greater cover (50 and 100%), there was a decline relative to this. It is possible that, at greater cover, the biological activities of *C. gigas* inhibit other organisms from becoming established due to competition for food, ingestion of larvae or organic enrichment due to biodeposition.

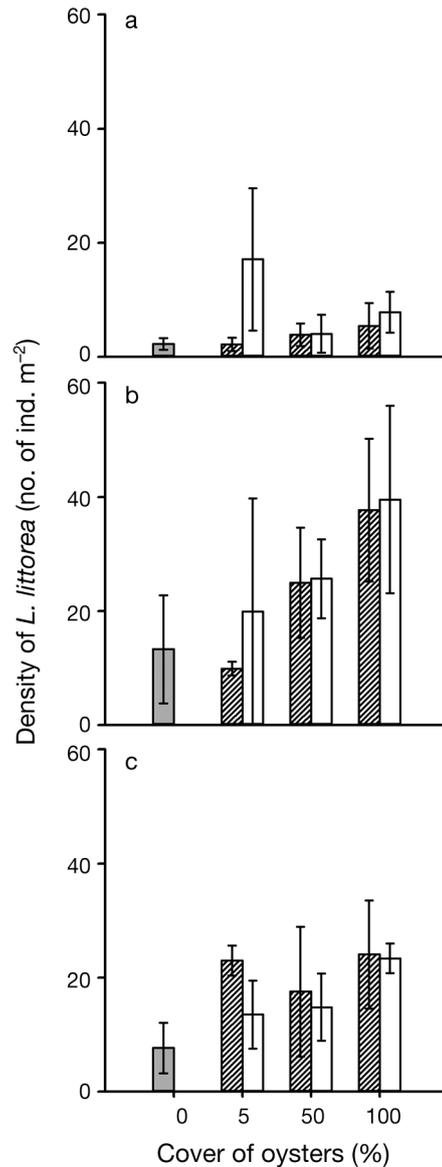


Fig. 6. *Littorina littorea*. Mean \pm SE density (ind. m⁻²) on boulders with no *Crassostrea gigas* oysters (grey bars) or 5, 50 or 100% cover of living (hashed lines) or dead (open bars) oysters after (a) 4, (b) 9 and (c) 14 mo

The biological activity of oysters exacerbated some effects and was solely responsible for others. For instance, the cover of *Fucus vesiculosus* increased with increasing cover of oysters regardless of their state, but was greater on boulders with living than with dead oysters after 14 mo. Nutrient enrichment due to biodeposition from oysters may have enhanced the growth of *F. vesiculosus* (Reusch et al. 1994). The density of *Ascidia conchilega* was less on boulders with living than on those with dead oysters, indicating that this species was affected by the bio-

logical activities of oysters. *A. conchilega* is also a filter feeder, so competition for food with *Crassostrea gigas* is a possible cause of its reduction. Alternatively, *C. gigas* can reduce the settlement of other organisms by decreasing the abundance of larvae in the water column through larviphagy (Troost et al. 2008), although whether this applies to *A. conchilega* is unknown. Strong effects may also result from an increase in the concentration of fine particles in the water column from the biodeposition of oysters. This can obstruct the feeding apparatuses of other filter feeders, reducing their ability to filter feed (Dubois et al. 2009).

The establishment of *Sabellaria alveolata* was greatly reduced at any cover of oysters regardless of their state, supporting the hypothesis that the difference in the cover of *S. alveolata* observed in the mensurative survey was due to the physical structure of oysters. Although oyster shells occupy space, direct competition for space is unlikely in this case since *S. alveolata* mostly occurred on the underside of boulders and *Crassostrea gigas* were only attached to the topside. Alterations to hydrodynamics are another possible cause. Modification of flow regimes caused by the physical structure of oysters (Lenihan 1999, Soniat et al. 2004) can affect the arrival and settlement of larvae, thus affecting assemblage structure (Butman et al. 1988, Eckman et al. 1994, Commito et al. 2005). It is also possible that settlement of *S. alveolata* was unaffected by *C. gigas*, but that post-settlement processes causing increased mortality and/or reduced growth (e.g. due to modifications in the flow of food particles) were responsible for the decrease in its establishment. For example, Moulin et al. (2007) found that dense accumulations of invasive slipper limpets decreased local flow velocities, decreasing the resuspension of particulate matter and thus decreasing the availability of food for other filter feeders.

The effects of invasive species can be caused directly by the invader or indirectly, mediated through their interactions with other organisms, and it is possible that indirect effects were responsible for the reduction of *Sabellaria alveolata*. Indeed, although the indirect effects of invaders are likely to contribute substantially to their overall effects on ecosystems, they are understudied (White et al. 2006). In the current study, it is likely that the reduction in the establishment of *S. alveolata* was caused by indirect effects of *Crassostrea gigas* due to its facilitation of other dominant species. For example, *Fucus vesiculosus*, which increased in cover with increasing cover of *C. gigas*, can reduce the recruitment of other algae

(Kiirikki 1996) and invertebrates (Lewis & Bowman 1975, Grant 1977) by its 'whiplash effect', i.e. removing new recruits through wave-induced thallus movements. It is also possible that algal fronds of *F. vesiculosus* may have smothered the tube ends of *S. alveolata*, thereby inhibiting their ability to feed and grow. Additionally, the increase in density of *Littorina littorea* associated with *C. gigas* may have contributed to the reduction in the establishment of *S. alveolata*. Periwinkles such as these can cause mortality in the newly settled larvae of invertebrates through physical dislodgement or 'bulldozing' effects as a result of their grazing activities (Miller & Carefoot 1989, Hidalgo et al. 2008).

Regardless of the mechanisms, this work highlights that even when present at low cover and by its physical structure alone, *Crassostrea gigas* can markedly reduce the establishment of the honeycomb worm *Sabellaria alveolata*. This polychaete builds some of the most extensive intertidal biogenic reefs in Europe (Desroy et al. 2011), which increase habitat heterogeneity and have a great diversity of associated species (Holt et al. 1998, Frost et al. 2004). The encrusting colonies of *S. alveolata* adhering to boulders are not protected under the habitats directive (Desroy et al. 2011); nonetheless, this work indicates that future development of these structures into reefs can be compromised by invasive oysters. Although the potential impacts of invasive marine organisms which form durable structures, such as shells, have been identified as a priority for management and conservation initiatives (see review by Sousa et al. 2009), little has been done to assess their impact on protected habitats.

Understanding the mechanisms by which invasive species alter receiving ecosystems is paramount to developing effective management strategies. The fact that *Crassostrea gigas* can have strong effects by virtue of its physical structure alone highlights the importance of assessing the total cover (dead and living) of invasive species which form habitats that can persist in the environment long after death. This suggests that dead as well as living oysters should be taken into account when planning mitigation of invaded habitats. Additionally, oyster shells are sometimes used in the creation or restoration of habitats which have been degraded by dredging (Dumbauld et al. 1993) or as protection against shoreline erosion (Piazza et al. 2005). Although shells can enhance the abundance of some commercially important species (Dumbauld et al. 2000), the current study indicates that they may also reduce the establishment of others. Careful consideration of how the

species present in the degraded habitat may be affected is necessary before such management initiatives commence.

Experimental manipulations, such as in our study, are a more powerful method than purely mensurative studies of investigating the impacts of invasive species because they allow inferences concerning the cause and effect of ecological processes to be assigned (Underwood 1997). Due to practical limitations, however, the current study was only done at 1 shore and therefore the results may be context-dependent since experiments in boulder fields done at multiple places do not always yield the same results (Green et al. 2012). However, previous studies on other ecosystem engineers have yielded similar results. Other bivalves have been shown to affect the abundance and distribution of other organisms due to their physical structure alone (Crooks 2002, Branch & Steffani 2004, Ward & Ricciardi 2007). For example, an experiment by Peterson & Andre (1980) found that the growth rates of some bivalves can be reduced by the presence of the dead shells of other dominant bivalve species, but that the magnitude of effects depends on the overall density of bivalves.

The impacts of invasive species on biotic and abiotic properties of ecosystems are often non-linear with respect to invader abundance and can therefore be difficult to predict. In the current study, for example, biodiversity was enhanced at the lowest cover of oysters, but either reached a threshold or began to decline at greater cover depending on the state of the oysters. Investigation of the effects of invasive species across a range of invader abundances can elucidate how their effects may change as the invasion proceeds. Despite this, there are few studies (Aldridge et al. 2008, Pawson et al. 2010) which have explicitly examined the effects of invasive species across a gradient of invasion (Thomsen et al. 2011a,b), as most studies tend to examine 'worst case scenarios', that is, contrasting heavily invaded with uninvaded sites. This leaves the question of how ecosystems respond to low levels of invasion unanswered and, in fact, very little is known about the impact of invaders at low abundances (Elgersma & Ehrenfeld 2011). Knowing the nature and magnitude of impacts as populations of invasive species change can help to make management decisions that avoid detrimental economic and ecological consequences. This is particularly important for species which have great impacts even at small densities or cover (Yokomizo et al. 2009), which our study suggests may be the case for *Crassostrea gigas*.

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