

# Effects of the alien Pacific oyster (*Crassostrea gigas*) on subtidal macrozoobenthos communities

Johan Hollander · Johan Blomfeldt ·  
Per Carlsson · Åsa Strand

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**Abstract** Since 2006, the Pacific oyster *Crassostrea gigas* has been a permanent resident on the west coast of Sweden. Because *C. gigas* is nonindigenous in Scandinavia, it may modify ecosystems and affect the resident biota. Individuals of *C. gigas* often settle in large aggregations, and the physical structure of the resulting reef provides attachment points and refuges for many secondary species. However, *C. gigas* also has the potential to change the macrofaunal community structure of the associated sediment, for example by stabilization or enrichment of the sediment. Here, we assess the macrozoobenthos community of sediments within *C. gigas* reefs and contrast the results with the comparable community within beds of the native blue mussel (*Mytilus edulis*) and with that of uniform bare sediment. We show that the communities within oyster reefs and mussel beds contained more species and had a higher abundance of organisms compared with the bare sediment. In addition, we show significant differences between the communities within oyster reefs and mussel beds and consistently a larger total abundance in the former.

## Introduction

The Pacific oyster *Crassostrea gigas*, originally from Japan, is the most common oyster in commercial aquaculture in Europe, but has repeatedly escaped outside areas of its commercial use (Mann et al. 1991; Shatkin et al. 1997). Because of its subtropical origin, larvae of *C. gigas* were thought not to survive in northern European waters outside the commercial nurseries (Drinkwaard 1999). However, wild populations are now found from Spain to Sweden (Ruesink et al. 2005). This species can occur in dense aggregations, forming large reefs. Since 2006, *C. gigas* has been a common species along the northern part of the west coast of Sweden. The populations seem to be robust against severe winters, since the species has established reefs with large shells that persist across years (Strand et al. 2012). Since the tidal range in Sweden is extremely small (between 10 and 20 cm) and vertical differences in sea level are more regulated by atmospheric pressure, bivalves in Sweden rarely experience dry periods. In addition, the oyster populations in Sweden differ to some extent in terms of coverage compared with average populations elsewhere. Usually, the Pacific oyster creates dense, closely packed reefs with high coverage (Markert et al. 2010), while in Sweden, a low to medium cover (20–80 %) is typical. Dense bivalve communities can affect ecosystems in various ways, including competition for food and space, and alteration of nutrient fluxes and planktonic communities in the water column (Dame 1996).

Reef-building species such as bivalves are habitat modifiers and their structures increase habitat complexity (Crooks 2002), particularly on otherwise uniform soft-bottom habitats. Ecosystem-engineering species (Jones et al. 1994) can positively influence other organisms in several ways, e.g. by producing a heterogeneous environment that

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J. Hollander (✉) · J. Blomfeldt · P. Carlsson  
Department of Biology, Aquatic Ecology, Lund University,  
Lund, Sweden  
e-mail: Johan.Hollander@biol.lu.se

Å. Strand  
Department of Biology and Environmental Sciences - Tjärnö,  
University of Gothenburg, 452 96 Strömstad, Sweden

provides living space (Crooks 2002) and refuges (Escapa et al. 2004), by influencing nutrient levels (Green et al. 2012) and by enhancing nekton abundance (Kingsley-Smith et al. 2012). Although reef-building species increase habitat complexity, they also function to promote sediment stability, which is an important factor that has been confirmed to have an impact on biodiversity (Padilla 2010). This may have significant consequences for primary and secondary productivity and community structure both of the reefs themselves (see reviews by Broekhuizen et al. 2002; McKindsey et al. 2006; Anderson et al. 2006) and also of macrofaunal communities in the associated sediment. A number of studies have assessed the effects of alien oyster communities on macrozoobenthos species living in the sediment, both in association with cultivated (Escapa et al. 2004; Lu and Grant 2008; McKindsey et al. 2011) and wild oyster populations (Kochmann et al. 2008; Markert et al. 2010; Green et al. 2013; Green and Crowe 2014). Recently, it has been discovered that invading *C. gigas* can influence the native community by enhancing local biodiversity (Markert et al. 2010; Kochmann et al. 2008). However, Green et al. (2013) and Green and Crowe (2014) have shown that the level of biodiversity was highly related with the amount of oyster cover, since too high cover of oysters influenced the biodiversity negatively. Accordingly, we know little about the ecological impact that *C. gigas* may have on native communities across the range of locations at which the oyster has been introduced.

Since *C. gigas* inhabits shallow shorelines in Sweden, it overlaps with the native blue mussel (*Mytilus edulis*) and both species construct shell reefs in soft-bottom habitats. Whether *C. gigas* influences the local macrozoobenthos in the sediment is not yet known, but we predict that oyster reefs and mussel beds will both cause significant shifts in biodiversity in contrast to bare soft-bottom habitats. Since shell reefs formed by oysters and beds of blue mussels are likely to function in similar ways, e.g. to stabilize sediment and provide organic enrichment, we expect to find a similar community structure of macrozoobenthos species in the sediment associated with both types of bivalve reefs. We examined these predictions by contrasting abundance and biodiversity of sediment-dwelling macrozoobenthos in alien oyster reefs with those of uniform soft-bottom habitats and native blue mussel beds, and discuss the consistency of these effects across the range of introduction sites.

## Materials and methods

Samples were collected in September 2011 at three different sites close to Strömstad, Sweden (Trälsundet: N 58°54.788', E 11°11.812'; Svallhagen: N 58°52.277', E 11°8.918' and Krokesundet; N 58°51.478', E 11°10.329').

The distances among the three sites were at the scale of kilometres, Trälsundet–Krokesundet: 6.5 km, Trälsundet–Svallhagen: 7.5 km and Svallhagen–Krokesundet: 2.5 km. The sites were chosen randomly, but with the criteria that they included one patch of *C. gigas*, one patch of *M. edulis* and one patch of bare sediment, so that each bottom type was replicated three times. The average distance between the different bottom types within sites from the centre were at Svallhagen 375 m, Krokesundet 275 m and at Trälsundet 250 m. The average size of the bivalve reefs was at Svallhagen 150–200 m, Krokesundet 100–150 m and Trälsundet 100–150 m. All samples were collected at approximately 0.5 m depth. Coverage of oysters or mussels in the bivalve reef areas at the different sites varied between 60 and 80 %. Within each bottom type, we sampled four sediment cores 10–100 m apart. Sediment cores with a diameter of 11.5 cm were collected for macrozoobenthos analysis using a PVC plastic cylinder. With the bivalve reefs, shells were first removed in order to expose the underlying sediment, before sampling with the corer. By 'macrozoobenthos', we designate species that are primarily infaunal, but also include epifauna on top of the sediment. The sediment considered here is the part of the sediment that is directly located under the bivalve structure, or simply the comparable bare sediment. Certain benthic nekton and larger mobile crustaceans may not be represented due to the sampling method, but these species were not the focus of the study. During sampling, the top 10 cm of each sample was kept and placed in marked plastic bags for transportation to the lab facility, where samples were sieved using a 1-mm sieve and preserved in 96 % ethanol. All macrofauna was identified to the lowest possible taxon, with juveniles of *M. edulis* included in the dataset.

Estimating the macrozoobenthos 'species richness' and 'total abundance'

Species richness was calculated as the total number of species in each sample, while total abundance was expressed as the total number of individuals in each sample. Species abundance was extracted as number of individuals per species in each sample. All abundances were calculated as number of individuals  $m^{-2}$ . The effect of bottom type (oyster reef, mussel bed, bare sediment) on 'species richness' and 'total abundance' was tested using a randomized block design (Quinn and Keough 2002) among the three sites. In the model, the factor 'Bottom type' was considered as a fixed factor, while 'Site' was treated as a random block. Total abundance was fourth-root transformed to meet the homogeneity assumptions of parametric tests. All data followed the assumption of normality.

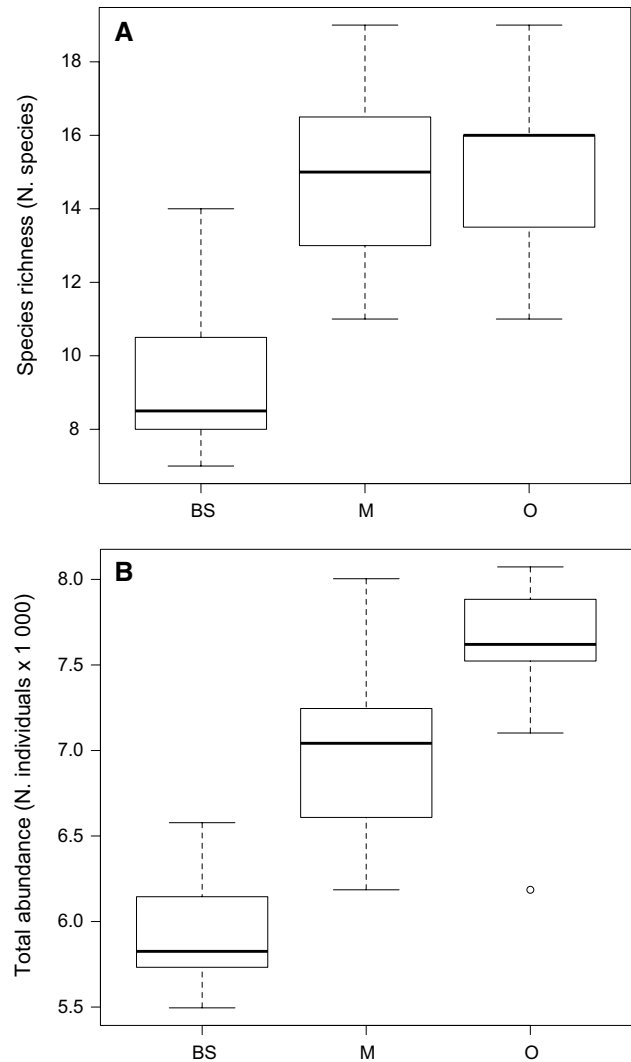
The same data were analysed separately at each site to test differences among the three habitat patches. For these

analyses, cores were not pooled within habitats, but were kept as distinct samples of each habitat. This approach was used because variability across sites could obscure local patch-specific differences. For pairwise post hoc comparisons, Tukey's procedure was used. All univariate statistics were conducted using the statistical package R (R Core Team 2013, version 3.0.2).

#### Assessment of the macrozoobenthos 'species composition' and 'species abundance'

In order to test the potential effects of bottom type on macrozoobenthos 'species composition' and 'species abundance', we applied a PERMANOVA analysis (Anderson 2001). PERMANOVA is a method for assessing the simultaneous response of one or more variables to one or more factors in an ANOVA experimental design on the basis of any distance measure (Bray Curtis similarity), using permutation methods. For this analysis, we used the same model as above, with site as a random block factor and bottom type as a fixed factor, while core was pooled with bottom type.

When each site was analysed separately, the four cores were used as replicates in the model. Species composition was analysed as absence/presence data and species abundance data fourth-root transformed before analysis. PERMANOVA pairwise comparisons between the bottom-type categories were used as a post hoc test ( $t$  tests). Furthermore, we applied a canonical analysis on the principal coordinates (CAP, Anderson and Willis 2003) to ordinate bottom types and sites, where the rate of differentiation determines the distance among groups in multivariate space. In this study, apart from discriminating among bottom-type groups, the CAP analysis finds the strongest correlation among the bottom-type groups with the set of species variables. Accordingly, the procedure can verify which species are associated with bare sediment, mussel beds or oyster reefs. To confirm this association, we utilized Pearson's correlation to test statistically which species caused the observed differences among the bottom types and sites. The methodology of using Pearson's correlation results in a calculated correlation value for each species in relation to each canonical axis. The species-specific correlation values are then compared with the critical value of the Pearson product-moment correlation coefficient ( $R_{crit}$ ) obtained from the number of degrees of freedom. We aimed to examine whether occurrence and abundance of certain species correlates with a specific bottom type. If the species-specific correlation value is larger than the critical value, or less than the negative critical value, the species will be designated to a specific bottom type along the canonical axes. The multivariate statistics were performed using Primer 6.1.13 and Permanova+ 1.0.3 (Primer-E).



**Fig. 1** Effects of presence of *C. gigas* (O), *M. edulis* (M) and bare sediment (BS) on macrozoobenthos **a** species richness and **b** total abundance at three sites on the Swedish west coast

## Results

The three most commonly occurring macrozoobenthos species were *Hydrobia ulvae*, *Tubificoides denedii* and *Hediste diversicolor*, and these species occurred in 36 (100 %), 35 (97 %) and 34 (94 %) of the samples, respectively. The three most abundant species were *H. ulvae* (>14,000 individuals), *Littorina littorea* (>11,500 individuals) and *Tubificoides benedii* (>9,000 individuals). In total, nine species: *Harmothoe imbricata*, *Scoloplos amiger*, *Spirorbis spirorbis*, *Lepidochitona cinerea*, *M. edulis*, *Pavicardium ovale*, *Jaera* sp., *Gammarus lucusta* and *Corophium bonelli* were found exclusively in bivalve beds and five species were exclusively found in oyster beds: *Nereimyra punctata*, *Nephtys caeca*, *Arenicola marina*, *Mya truncata* and *Corbula gibba*, while no species were solely found in the bare sediment or

**Table 1** Pairwise comparison (TukeyHSD) of effects among bottom type (O = *C. gigas*, M = *M. edulis* and BS = bare sediment) on macrozoobenthos species richness and total abundance at three sites on the Swedish west coast

	Species richness		Total abundance	
	Mean difference	<i>P</i>	Mean difference	<i>P</i>
<b>Trälsundet</b>				
BS, O	4.25	<b>0.01</b>	1.96	<b>&lt;0.001</b>
BS, M	3.5	<b>0.03</b>	1.39	<b>&lt;0.001</b>
O, M	0.75	0.79	0.57	<b>0.001</b>
<b>Svallhagen</b>				
BS, O	7.75	<b>0.001</b>	1.48	<b>0.04</b>
BS, M	8	<b>0.001</b>	1.09	0.13
O, M	−0.25	0.98	0.4	0.72
<b>Krokesundet</b>				
BS, O	5	<b>0.004</b>	1.45	<b>&lt;0.001</b>
BS, M	5.25	<b>0.003</b>	0.67	<b>0.05</b>
O, M	−0.25	0.97	0.78	<b>0.02</b>

Significant *P* values are in bold

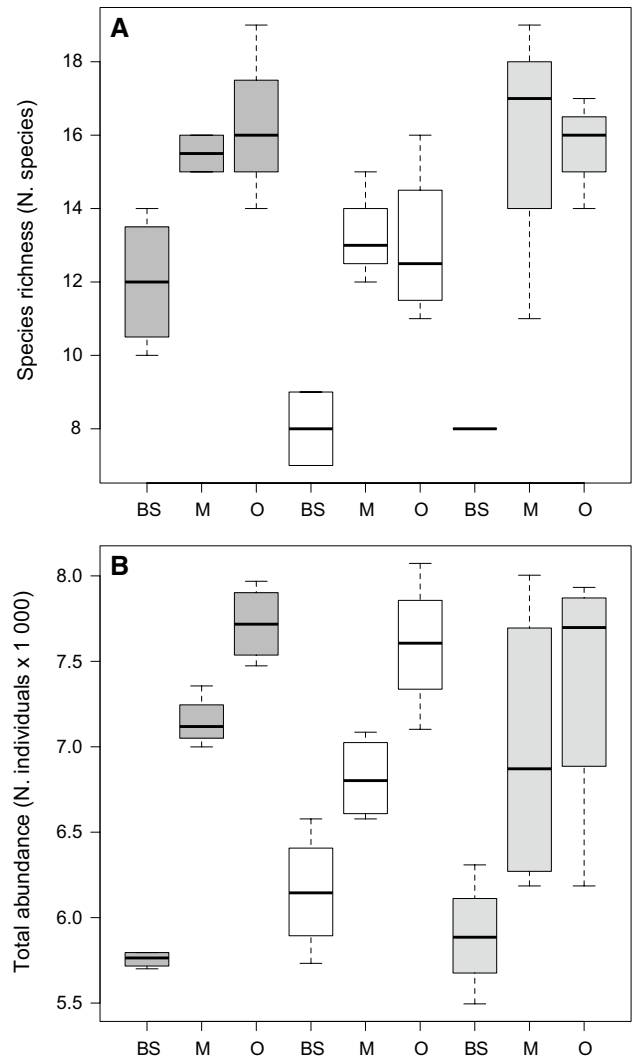
blue mussel beds, i.e. all species found in the bare sediment and blue mussel beds were also found in the oyster beds.

The effects of bottom type on ‘species richness’ and ‘total abundance’ of macrozoobenthos species

The macrozoobenthos species richness was significantly affected by bottom type ( $F_{2,4} = 21.4$ ;  $P < 0.001$ ) (Fig. 1a). The Tukey’s HSD test revealed significantly higher values in both the oyster reef and mussel beds, compared with the bare sediment ( $P < 0.01$ ). On the other hand the comparison between oyster reefs and mussel beds showed large similarities ( $P = 0.99$ ). Furthermore, total abundance showed similar results ( $F_{2,4} = 48.69$ ;  $P < 0.001$ ), since bivalve reefs had a higher abundance compared with the bare sediment ( $P = 0.001$ ). However, total abundance also differed between the oyster reefs and blue mussel beds ( $P = 0.05$ ) (Fig. 1b). When the data were analysed independently, within each site, we found that species richness consistently followed the same pattern. The bivalve reef always demonstrated larger species richness compared with the bare sediment, while the two types of bivalve reefs were similar (Table 1; Fig. 2a). For total abundance, all three bottom types differed among each other at two sites, with oyster reefs having the highest abundance. At the remaining site, only oyster reefs possessed significantly larger total abundance in contrast with the bare sediment (Table 1).

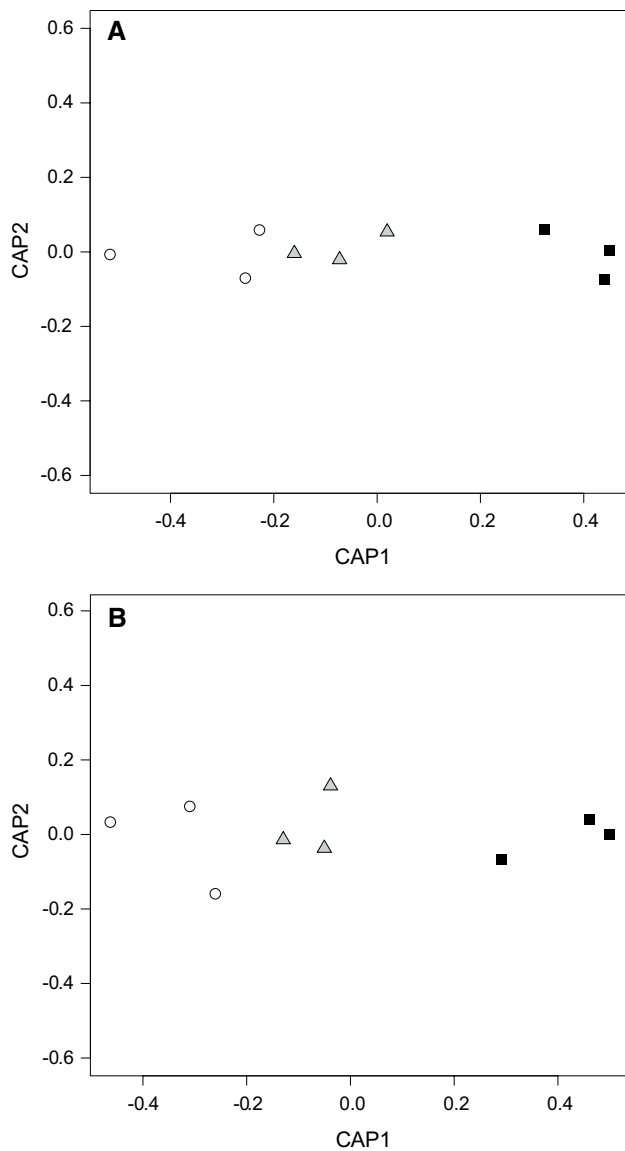
The macrozoobenthos ‘species composition’ and ‘species abundance’—multivariate analysis

Species abundance was significantly affected by bottom type ( $F_{2,4} = 2.09$ ;  $P < 0.03$ ), while species composition was



**Fig. 2** Effects of presence of *C. gigas* (O), *M. edulis* (M) and bare sediment (BS) on macrozoobenthos **a** species richness and **b** total abundance within sites on the Swedish west coast. Dark grey boxes represent Trälsundet, white boxes Krokesundet, while light grey boxes symbolize Svallhagen

not ( $F_{2,4} = 1.30$ ;  $P < 0.24$ , Fig. 3b). Both blue mussel beds and oyster reefs showed differences in species abundance in contrast with the bare sediment (Fig. 3a), although only oyster reefs were significantly different ( $P = 0.05$ ). In order to examine whether this pattern was constant among the three sites, we split the locations and analysed the species composition and species abundance of the macrozoobenthos community separately within each site. Inconsistent with previous results, both species abundance and species composition were significantly affected by bottom type when the sites were analysed separately (Permanova,  $P < 0.05$ ). The pairwise comparison across all sites confirmed significant differences for both species composition and species abundance among all bottom types (Permanova,  $P < 0.05$ , Table 2).



**Fig. 3** CAP analysis of the effects of presence of *C. gigas* (O, open circles), *M. edulis* (M, grey triangles) and bare sediment (BS, black squares) on macrozoobenthos **a** species composition and **b** species abundance on the Swedish west coast

**Table 3** Correlation values obtained during the canonical analysis on the principal coordinates (CAP) of macrozoobenthos species composition and abundance at three sites on the Swedish west coast using bottom type [presence of *C. gigas* (O), *M. edulis* (M) and bare sediment (BS)] as a factor

	CAP1	CAP2
<i>Species composition</i>		
Trälsundet	0.979	0.222
Svallhagen	0.947	0.685
Krokesundet	0.939	0.795
<i>Species abundance</i>		
Trälsundet	0.989	0.889
Svallhagen	0.961	0.849
Krokesundet	0.964	0.887

The analysis was done for each site separately

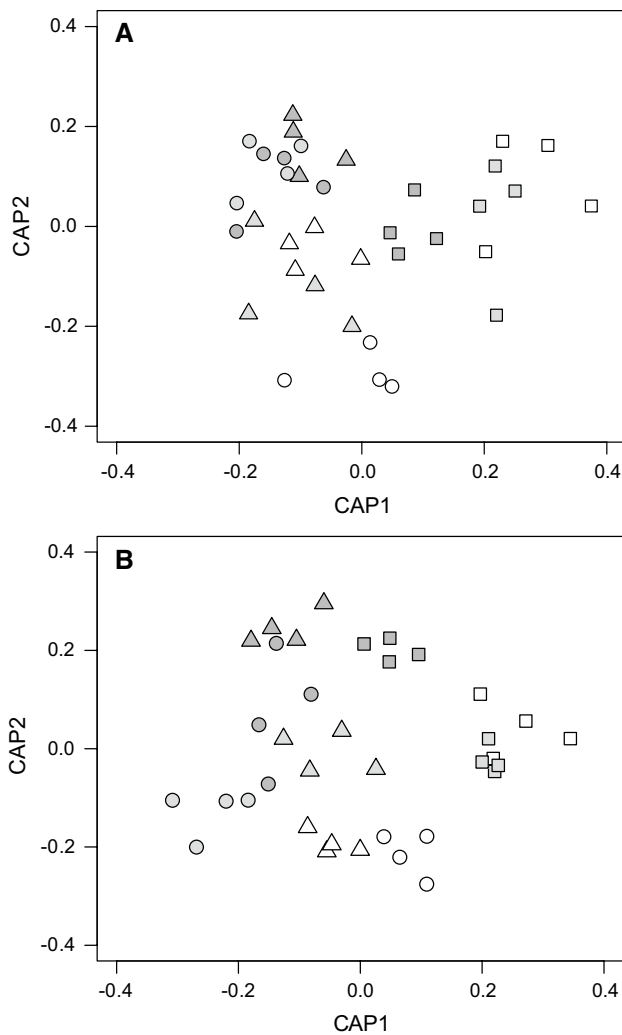
At all three sites, and for both species composition and species abundance, the canonical analysis on the first principal coordinates (CAP1) differentiated bivalve reefs, associated with negative values, from the bare sediment group which clustered at positive values (see Table 3 for all correlations values, Fig. 4a, b). In addition, for both variables at all sites except Trälsundet, the oyster reefs and mussel beds were separated along the second principal coordinates (CAP2), with mussels associated with positive values and oysters with negative values (Fig. 4a, b). At Trälsundet, however, a differentiation between oysters and blue mussels was detectable only in the species abundance data (Fig. 4b).

Despite the obvious differences in species composition and species abundance in the PERMANOVA analysis, the CAP analysis only revealed marginal differences in community structure among macrozoobenthos species between the two bivalve reefs. Species favoured at more than one site often displayed different habitat preferences at different sites (Table 4). This may indicate that site-specific conditions play a greater role in determining the overall community structure of macrozoobenthos species than the type

**Table 2** Pairwise comparison of effects among bottom type (*C. gigas*, *M. edulis* and bare sediment) on macrozoobenthos species composition and species abundance at three sites on the Swedish west coast using PERMANOVA

Test		Trälsundet		Svallhagen		Krokesundet	
T1	T2	<i>t</i>	<i>P</i> (perm)	<i>t</i>	<i>P</i> (perm)	<i>t</i>	<i>P</i> (perm)
<i>Species composition</i>							
BS	O	3.4	0.031	3.4	0.035	2.5	0.027
BS	M	2.7	0.033	2.6	0.026	2.5	0.023
O	M	2.0	0.026	2.4	0.034	2.2	0.028
<i>Species abundance</i>							
BS	O	3.6	0.025	3.6	0.024	2.7	0.031
BS	M	3.0	0.032	2.6	0.038	2.9	0.026
O	M	2.1	0.033	2.6	0.036	2.4	0.021





**Fig. 4** CAP analysis of the effects of presence of *C. gigas* (circles), *M. edulis* (triangles) and bare sediment (squares) on macrozoobenthos **a** species composition and **b** species abundance at three sites; Trälsundet (dark grey), Krokesundet (white) Svallhagen (light grey) on the Swedish west coast. Each analysis was made independently per location although presented here in the same figure

of bivalve reef. Within sites, however, species demonstrated clear preferences for certain habitats (Table 4). We found that five species were favoured by *C. gigas* beds, while 14 additional species were favored by both oyster reefs and mussel beds. Two species preferred the bare sediment, while no species exclusively favoured the mussel beds (Table 4).

## Discussion

We have shown that species richness and total abundance of macrozoobenthos is higher in sediment within bivalve reefs than in the bare sediment nearby and, regarding total

abundance, that oyster reefs demonstrated even more macrozoobenthos individuals than blue mussel beds. We also found variation in macrozoobenthos species composition between oyster reefs and mussel beds, which demonstrates community differences. However, these community differences were not consistent, since they were to a large extent influenced by different geographical locations, indicating that local conditions at each site (e.g. substrate or other factors) may play a large part in determining species composition.

## Macrozoobenthos community structure in bivalve reef environments

The species richness did not differ between oyster reefs and blue mussel beds, although we found discrepancies in the macrozoobenthos community structure between the two. It has previously been stated that bivalve beds cause organic enrichment in soft sediment communities through biodeposition (Dahlback and Gunnarsson 1981; Grenz 1989; Gilbert et al. 1997; McKindsey et al. 2011). Such enrichment may have positive effects on both abundance and species richness, as long as the loading rates are not too great, which would cause hypoxia or even anoxic conditions (see “Discussion” below; Castel et al. 1989). In addition to this enhancement of deposition, the shell matrix constructed by the bivalves physically stabilizes the sediment and, overall, is clearly beneficial for macrozoobenthos species (McKindsey et al. 2011).

Invasions by exotic species that are habitat modifiers, such as reef-building species, may cause the largest impact on the native ecosystem (Crooks 2002). Exotic species may alter several aspects of the environment, such as availability or quality of food, heat or light and by changing the living space (Crooks 2002). In this study, this was true for most variables we assessed, when we compared bivalve reefs with the bare sediment. The oyster reefs and blue mussel beds were on the other hand very similar in species richness. This is to some extent inconsistent with a study by Markert et al. (2010) who, in agreement with our results, found variation between the two bivalve species and the bare sediment, although they additionally found increased macrofaunal species richness in oyster reefs compared with mussel beds. The two studies coincide, however, in assessment of total abundance, because in our survey we found significant separation between the two bivalve species, with the highest abundance of macrozoobenthos species in oyster reefs (see also Kochmann et al. 2008).

Results were generally consistent across sites, although exceptions occurred, e.g. *Marenzelleria viridis* was strongly associated with the bare sediment at one site and bivalve reefs at another, while *H. ulvae* occurred mainly among oysters or among mussels at different sites, indicating that

**Table 4** Macrozoobenthos species favoured by the bivalve reefs (*C. gigas* and *M. edulis*, CAP1,  $n = 12$ ,  $R_{crit} \leq -0.576$ ) and by the bare sediment (CAP2 separated the bivalve species (*C. gigas*,  $n = 12$ ,  $R_{crit} \leq -0.576$ ; *M. edulis*  $n = 12$ ,  $R_{crit} \geq 0.576$ ) at three different sites at the Swedish west coast using Pearson's correlation value in the CAP analysis

	Trälsundet		Svallhagen		Krokesundet	
	SC	SA	SC	SA	SC	SA
<i>Amphithoe rubricata</i>	O + M	O	O + M	O	M	M
<i>Bittium reticulatum</i>		O		O	O	O + M
<i>Capitella capitata</i>	BS				M + BS	M + BS
<i>Cerastoderma edule</i>	O + M	O + M		O		
<i>Corophium volutator</i>	O + M	O + M	O + M	O	O	O
<i>Gammarus lucusta</i>					O	O
<i>Harmothoe imbricata</i>	O + M					
<i>Hediste diversicolor</i>		M		M		BS
<i>Hydrobia ulvae</i>				M		O
<i>Lepidochitona cinerea</i>	O + M	O	O	O		
<i>Littorina littorea</i>	O + M	O				O + M
<i>Littorina saxatilis</i>	O + M	O				
<i>Macoma baltica</i>			O + M	O		
<i>Marenzelleria viridis</i>	BS	M + BS	M	M	M	M
<i>Mya arenaria</i>			O	O		
<i>Mytilus edulis</i>	O + M	O + M	O	O	O + M	M
<i>Nephtys caeca</i>			O	O		
<i>Oligochaeta indet</i>						BS
<i>Pavicardium ovale</i>	O + M	O + M				
<i>Phyllodoce mucosa</i>			O			
<i>Polydora ciliata</i>	BS	BS	M	M		
<i>Pygospio elegans</i>	BS	M + BS	M	M		
<i>Rissoa</i> sp.					O	O
<i>Scolecopsis squamata</i>		BS				
<i>Scoloplos amiger</i>			O	O	M	
<i>Spirorbis spirorbis</i>				M	O	O
<i>Tubificoides denedii</i>						M + BS

SC species composition, SA species abundance

local conditions (and perhaps larval settlement) may sometimes have a greater influence on species distribution than ecosystem engineers.

Molluscs and arthropods typically represented the major taxonomic groups found in the bivalve reefs, while annelid species were less frequent. To some extent, this result was expected and is most probably related to the effects of the physical structure established by the shell matrix of mussels and oysters. The complex structure creates multiple attachment points for secondary sessile species, a larger substrate area for grazing species and provides a refuge for mobile crustaceans, especially juveniles (e.g. Glancy et al. 2003; Quan et al. 2013). However, Markert et al. (2010) found that oligochaetes dominated the bivalve reefs, and such a result may be a strong indicator of oxygen depletion and an increase in toxic  $H_2S$  in the sediment. The most common oligochaete found by these authors was *T. benedii*, a species known for tolerating anoxic conditions and high levels of pollution. Since Markert et al. (2010) studied bivalve populations with a much greater shell cover compared with

our sites, their populations must have caused higher rates of biodeposition. A moderate production of biodeposits favours the macrozoobenthos community since the high food supply is beneficial to infaunal and epifaunal species that feed on organic-rich sediments. But if the biodeposit production from bivalve reefs is too high, this will initiate an increase of  $H_2S$  concentration and oxygen deficiency, and biodiversity will decrease. A strong association of this kind among decomposition rate, biodeposition and the effect on biodiversity has been confirmed by for example Green and Crowe (2014).

#### Macrozoobenthos community structure in bare sediment

Padilla (2010) reasoned that if the native and the invasive bivalve engineer species provide similar functions, the impact on the native community should be quantitative rather than qualitative. To a large extent, contrasting the two bivalve species, this is confirmed by our study, although with minor variation. The greatest differences are noted in total abundance

rather than species richness. If, however, the ecosystem engineer, *C. gigas*, provides substantially different ecosystem services compared with the native environment (i.e. the bare sediment), we would expect to see large variations in biodiversity. Again, this expectation is essentially fulfilled, as we showed variation in community composition of higher taxa between bivalve reefs and the bare sediment. While molluscs and arthropods are in general attracted to shell structures in Swedish coastal waters (Norling and Kautsky 2008), we found that annelids favoured bare sediment (*Scolelepis squamata* and *Oligochaeta indet*). Considering that most of these annelid species burrow in the sediment, they may prefer various types of sand and mud and may be obstructed by bivalve reefs. However, some previous reports have suggested the opposite. Quan et al. (2013) found 40–100 times more annelids in oyster reefs compared with salt marsh areas, and Markert et al. (2010) reported higher occurrence of polychaetes in the bare sediment, while oligochaetes dominated the bivalve reef. Several authors have reasoned that oyster reefs may decrease predation pressure as well as increasing food availability by enhancing biodeposition (Zimmerman 1989; Grabowski 2005; Quan et al. 2012, 2013). More work is required in order to understand these variations.

In conclusion, the presence of oysters was found to increase species richness and abundance of macrozoobenthos in the sediment in comparison with bare sediment away from reefs, and oyster reefs contained higher abundances of organisms compared with blue mussel beds. Species composition was also found to differ between oyster reefs and mussel beds, although the patterns were more affected by site than by bivalve species. As the invasion of *C. gigas* in Sweden continues, sediments such as sand, mud and shell gravel are the main substrates that will be colonized by oysters. In addition, habitats with a mixture of oysters and blue mussels (and perhaps *C. gigas* and native *Ostrea edulis*) are likely to form. This habitat modification is likely to increase the general species richness and abundance of macrozoobenthos in the region.

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