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A Pacific oyster invasion transforms shellfish reef structure by changing the development of associated seaweeds

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Author contributions: Andriana, Eriksson, and van der Ouderaa together designed the study, performed the field sampling and contributed to the writing.

Manuscript highlights:

- A Pacific oyster invasion transforms the structure of intertidal blue mussel reefs
- Native blue mussel reefs promote the development of habitat forming seaweed meadows
- Pacific oysters promote green algae mats and decrease the habitat forming seaweed

Abstract

Biological invasions are reshaping coastal ecosystems across the world. However, understanding the significance of such invasions is often hampered by the lack of process-based research, resulting in a limited mechanistic comprehension of novel ecological interactions and their consequences. The Pacific oyster (*Magallana gigas*) has invaded European coasts, resulting in an astonishing transformation of the intertidal shellfish reef communities in the Wadden Sea; from reefs constructed by blue mussels only (*Mytilus edulis*) to mixed reefs dominated by oysters. Shellfish reefs structure the marine vegetation on soft bottoms by accumulating seaweeds. Nevertheless, assessments of the consequences of the oyster take-over have almost exclusively focused on effects on associated fauna. By constructing small-scale reefs dominated by blue mussels or oysters and following the development of seaweeds over summer, we demonstrated that oysters promoted bloom-forming green algae communities with low primary biomass and low habitat complexity. In contrast, blue mussels promoted the development of meadow-like communities dominated by habitat forming brown seaweeds of the genus *Fucus*, with high primary biomass and high habitat complexity. An additional field survey showed that increasing numbers of Pacific oysters on a recently invaded natural blue mussel reef significantly decreased the development of the *Fucus* meadow in spring. Our results indicate that the invasion of oysters may have dramatic effects on the structure and function of intertidal reef-communities by changing energy flow and habitat-function.

Keywords: biological invasion; *Crassostrea gigas*; ecosystem engineers; foundation species; intertidal ecology; shellfish reef

1 Introduction

Intertidal shellfish reefs are biological hotspots that modify their own habitat by constructing biogenic structures (e.g. Baird et al., 2007). The physical structures of the reefs mitigate hydrodynamic stress and promote habitat complexity, and thereby increase biodiversity, trophic transfer and food web complexity (Christianen et al., 2017b; Engel et al., 2017; Eriksson et al., 2017; van der Zee et al., 2015; van der Zee et al., 2013). In the North Sea, intertidal shellfish reef systems have undergone dramatic changes in the past decades due to an invasion of the Pacific oyster (*Magallana gigas* (Thunberg, 1793); previously *Crassostrea gigas*) that overgrows the dominating native reef forming species; the blue mussel (*Mytilus edulis* L.) (Kochmann et al., 2008; Reise et al., 2017a; Reise et al., 2017b). Today, the consequences of the oyster invasion for the function of intertidal reefs is uncertain, making current risk assessments ambiguous (Herbert et al., 2016; Mortensen et al., 2017).

Pacific oysters and blue mussels alter habitat structure in different ways, and therefore influence sediment quality and the composition of associated fauna differently (Kochmann et al., 2008; Waser et al., 2016). However, there is no confident indication that the Pacific oyster invasion has had negative consequences for the native fauna on the regional scale. In contrast, many invaded blue mussel reefs today have a multi-layered structure, consisting of a mixture of both Pacific oysters and blue mussels, that accommodate a higher biodiversity of associated fauna than comparable pure blue mussel reefs (Markert et al., 2010; Reise et al., 2017b). The spaces formed between the larger Pacific oysters even provide shelter for blue mussels, protecting them from predation by crabs and overgrowth by barnacles (Buschbaum et al., 2016; Kochmann et al., 2008; Reise et al., 2017b). At the same time, competition for resources between shellfish generate a trade-off, where protection and shelter often come at a

cost of slower growth and smaller sizes (Donadi et al., 2013a; Eschweiler and Christensen, 2011).

Intertidal shellfish reefs also function as biological power stations by increasing the net production of the biofilm, the potential production of plankton and the accumulation of seaweed (Asmus and Asmus, 1991; Baird et al., 2007; Donadi et al., 2013b; Engel et al., 2017). However, it is not clear what consequences the current changes in reef structure and function have for primary production. The biofilm is the most important energy source for the intertidal food-web in the Wadden Sea (Christianen et al., 2017a), contributing strongly to trophic transfer. However, the blue mussel reef system is characterised by seaweed, which is a mix of brown, green and red macroalgae that dominate the primary producer biomass on most reefs (Baird et al., 2007). Outside the reefs, macroalgae are found in relatively low abundances due to the lack of hard substratum to attach to. The most conspicuous reef associated seaweed community consists of a habitat forming brown algae, *Fucus vesiculosus* f. *mytili* (Nienburg) Mathieson & Dawes, 2017 (from now on *Fucus*), that forms thick meadows of ca 0.5 m long thalli that cover blue mussel reefs on intertidal flats. The thalli are attached by entanglement in the byssus threads that the mussels produce to attach to each other (Albrecht and Reise, 1994; Albrecht, 1998). The *Fucus* cover develop on the mussel reefs in early spring, mature over the summer and usually disappears again during the winter. Oysters do not produce byssus threads, raising the concern that when oysters overgrow the native blue mussels, the *Fucus* communities will be replaced by fast growing, much less complex green algae, that quickly form mats on hard substrates and exclude other algae by pre-empting space for settlement (Eriksson et al., 2007; Nehls and Büttger, 2007). In this study we addressed the potential effects of the oyster invasion on seaweed meadows, by testing the development of macroalgae on different types of small-scale bivalve aggregations created on the intertidal.

2 Material and Methods

2.1 Bio-manipulation experiment

This study was conducted on an intertidal mudflat south of the island Schiermonnikoog (Dutch Wadden Sea, N 53.466°, E 6.187°). The mudflat is ca. 2 km wide at low tide and structured by reef-forming bivalve species: the invasive Pacific oyster (*Magallana gigas* (Thunberg, 1793); previously *Crassostrea gigas*) and the blue mussel (*Mytilus edulis* L.), which form elevated reefs, and the common cockle (*Cerastoderma edule* L.), which forms submerged banks. These species alter the system by constructing physical structures for associated organisms (Donadi et al., 2015; Eriksson et al., 2017).

We designed a bio-manipulation (BM) experiment to investigate the facilitative effect of different shellfish reef forming species on the development of seaweed. The experiment was set up on the exposed and the sheltered side of a large mixed shellfish reef located ca. 500 meters parallel to the shore and consisting of blue mussels, Pacific oysters and common cockles. The exposed site was 100 m seaward of the shellfish reef close to a gully and characterized by sandy sediment with low organic content and high erosion (organic matter content 1 cm: 0.90 ± 0.15 % weight loss on ignition; organic matter content 5 cm: 0.82 ± 0.14 % weight loss on ignition; plaster erosion: 23.0 ± 1.2 % loss per tide; mean \pm SD). The sheltered site was 300 m leeward of the shellfish reef and characterised by muddy sediment with high organic content and low erosion (organic matter content 1 cm: 1.69 ± 0.55 % weight loss on ignition; organic matter content 5 cm: 1.76 ± 0.28 % weight loss on ignition; plaster erosion: 15.0 ± 2.9 % plaster loss per tide; mean \pm SD) (see sampling methods below).

The bio-manipulation treatments consisted of adding cockles, blue mussels and Pacific oysters to experimental plots with an area of 0.25 m², in four combinations: (i) no addition of bivalves (no addition control - C); (ii) addition of 250 alive cockles (artificial cockle bank - CA); (iii) adding 200 alive blue mussels (artificial blue mussel reef - M); (iv) adding 25 alive

Pacific oysters and 50 alive blue mussels (artificial oyster dominated reef - O). The oyster dominated reef treatment corresponded to ca 60 % cover of oysters and 20 % cover of blue mussels in the plots (Pacific oysters were ca. five times bigger than the blue mussels). All bivalves were collected in-situ on location and distributed evenly over the surface of the plots (Fig. 1). Only individuals free from overgrowth of barnacles or seaweed were used. The blue mussel and oyster reef treatments mimicked the natural variation across the shellfish reef, ranging from blue mussel only to oyster dominated patches, while the cockle treatment mimicked cockle bank densities on the sheltered side of the reef. The first 24 hours of the experiment, all plots were bordered by a 1 dm high metal fence (chicken gauze; mesh size 1 cm) to contain the bivalves until they stabilised. The rest of the experiment a rope was struck between corner poles, to avoid birds predated on the added bivalves. Three replicates of each treatment were randomly assigned to a block of 12 plots in total at each site (exposed and sheltered), resulting in 24 plots in total. These plots were set up in three rows perpendicular to tidal currents. The distance between plots was 3 m on each side (Fig.1).

The experiment was set up in the end of June (22 June 2017) and terminated in October (18 October 2017). Sampling occurred 2, 4, 8, and 14 weeks after the start of the experiment. During this time we documented the development of seaweed in the plots as the percentage of macroalgae coverage, determined to species. We also counted the number of bivalves in each plot (to the species level) and took sediment samples for measurement of sediment organic matter content. The organic matter samples were collected with a plastic syringe (diameter: 2.6 cm) at two different depths, 1 and 5 cm. The samples were placed into pre-labelled plastic bags, stored on ice and put in a -20°C freezer until further processing. Organic matter content was analysed by drying the sediment for 48 hours at 65°C and then determined by the weight loss on ignition after burning at 550°C for four hours. Hydrodynamic erosion was measured for each site using plaster poles (see plaster erosion method in Donadi et al., 2013b). Cockle density in

the cockle treatments was estimated by taking a small core subsample (1 dm²) from the no-addition and cockle addition plots after 4 weeks. After counting the cockles, the sediment and cockles were placed back into the plots.

2.2 Field study

To verify the experimental results, we studied the accumulation of *Fucus* after the winter on two natural mixed shellfish reefs close to the experimental site, one dominated by blue mussels ('the blue mussel reef') and one dominated by Pacific oysters ('the Pacific oyster reef'). The blue mussel reef was only recently invaded by the Pacific oyster. The reef is still dominated by blue mussels, but the past five years oysters have increased to up to 50% cover in some patches. The Pacific oyster dominated reef harbours a mix of Pacific oysters, cockles and blue mussels. *Fucus* dominates the seaweed cover on the reefs, but it normally completely disappears in winter, probably due to storms and scour (pers. obs.). After the winter, *Fucus* quickly regenerates to form a thick meadow that covers the reef again. We visited the reefs in early spring (6 March 2019), just after the *Fucus* cover had emerged and started to grow, to document the development of seaweed depending on the composition of the natural reef substrate – approximating the conditions of the experiment. We placed 16 0.25m² squares in the newly developed *Fucus* meadows across each reef at lower elevations (since *Fucus* do not develop on the oyster dominated ridges). The plots were placed to represent the full gradient of *Fucus* cover on each reef, avoiding areas devoid of *Fucus* and bare spaces; meaning that we can estimate the impacts of mussels and oysters on seaweed development on each reef, but not compare the covers between reefs. First we estimated the cover of *Fucus* and carefully removed the fronds; and then we counted the number of blue mussels and Pacific oysters in each plot.

2.3 Data analysis

The effect of the bio-manipulation on the accumulation of seaweed was analysed with general linear mixed models (GLMM) using the *nlme* package in R (version 3.1-140), crossing

the independent factors bio-manipulation (no addition control, cockle addition, blue mussel addition and oyster addition) and the repeated measure experimental time (2, 4, 8 and 14 weeks). To account for the repeated measure, we included a temporal autocorrelation structure for each plot (random factor) across experimental time. We were particularly interested in if the statistical interaction between the experimental treatments and time was different between the two sites. We therefore analysed each site separately. Transformation of the data in general deteriorated a good fit to the normal distribution and homogenous variances, and was therefore not considered necessary. To distinguish differences between treatment combinations, Tukey's HSD post-hoc tests was performed. We evaluated the stability over time of the reef treatments by fitting similar GLMM's to the number of blue mussels in the blue mussel and oyster addition treatments (crossing experimental manipulation and time), and the number of oysters in the oyster addition treatment (testing the trend over time only). Counts were square root transformed. Stability of the cockle treatment was analyzed by comparing cockle numbers between the small core-subsamples in the no-addition and cockle addition plots, using a GLM with site as a fixed factor.

The impact of the oyster invasion on the development of *Fucus* cover on natural reefs was analyzed by simple linear regressions after visual inspection of distributions. We tested the relation between the number of blue mussels and Pacific oysters on the development of *Fucus* cover on the mussel and oyster dominated reefs separately, because of systematic differences in the cover of *Fucus* between the reefs. In the analyses we used only the alive blue mussels, since these are the ones that produce byssus threads; but both dead and alive oysters were used because also dead oyster shells take up space from the blue mussels.

3 Results

3.1 Bio-manipulation experiment

The bio-manipulations created small-scale bivalve habitats that were stable for about 3 months of experimental time: including blue mussel reefs (mussel addition), Pacific oyster dominated reefs mixed with blue mussels (oyster addition) and cockle banks (cockle addition) (Supplement 1, Fig S1). At the exposed site, both blue mussels and oysters decreased gradually in their respectively reef treatments (Fig. S1a,b). After a storm in August (experimental week 12) all blue mussels and oysters disappeared from the exposed site. At the sheltered site, the mussel additions created stable pure blue mussel reefs over the summer. However, after the storm in August, the mussel reef treatment disintegrated and all blue mussels were washed away, except in the oyster reef treatment. In the oyster reef treatment the blue mussels were protected from the storm by a mixed matrix of dead and alive oysters and more than doubled in abundance between July and September (Fig. S1c,d).

Over the course of the experiment, distinctly different seaweed communities developed in the different bio-manipulation treatments; the artificial mussel reefs facilitated thick brown algae meadows of *Fucus*; the artificial oyster reefs facilitated bloom forming green algal mats dominated by the genus *Ulva*; and the artificial cockle beds did not facilitate seaweed cover at all (Fig. 2). At the exposed site, the cover of brown algae was very low in all treatments, except for a short peak of 20 % cover on the oyster dominated reefs after 2 weeks (Table 1, no significant treatment effects; Fig. 2a-d). However, at the sheltered site, the development of *Fucus* followed the trends in blue mussel abundances. Here, the mussel reef treatments quickly developed a thick meadow of entangled *Fucus* with 3-4 dm long thalli that stayed above 60 % cover; until the reefs were washed away during the storm in August (Table 1, significant interaction between time and the bio-manipulation treatment; Tukey's HSD post-hoc test, $p < 0.001$: mussel addition > oyster addition = cockle addition = no

addition treatment; Fig. 2e-h). In the oyster reef treatment, *Fucus* started to accumulate in late summer, together with the documented increase of mussels inside the oyster matrix, reaching 30 % cover in September.. The oyster reef treatments were otherwise characterised by mats of green algae, with a peak of ca. 40 % cover from the middle of June to July at both the exposed and sheltered sites (Table 1, significant interaction effect between time and biomanipulation; Tukey's HSD post-hoc test, $p < 0.001$: oyster addition > mussel addition = cockle addition = no addition treatment; Fig. 2). Red algae of the genus *Gracilaria* showed a small peak in the mussel reef treatments after 2 weeks at the sheltered site, but in general occurred very sparsely in all treatments during this study (Table 1, no significant treatment effects; Fig. 2).

3.2 Field study

Blue mussels strongly promoted *Fucus* cover and the invasion of the Pacific oyster on the mussel dominated reef significantly decreased the development of *Fucus* (Fig. 3). The plots on the mussel dominated reef had on average 2.5 times as many blue mussels and half of the number of Pacific oysters as the oyster dominated reef (mussel reef: # blue mussels = 254 ± 91 , # Pacific oysters = 80 ± 50 ; oyster reef: # blue mussels = 105 ± 54 , # Pacific oysters = 152 ± 29 ; mean # $m^{-2} \pm SD$). *Fucus* increased strongly with the number of alive mussels both on the mussel reef (linear model: $n=17$, $r=0.895$, $p < 0.001$) and the oyster reef (linear model: $n=16$, $r=0.891$, $p < 0.001$; Fig. 3a). There was a strong negative correlation between oysters and mussel abundances on the reefs (Pearson product-moment correlation: $n=33$, $r=-0.873$, $p < 0.001$). Accordingly, *Fucus* cover decreased with increasing numbers of Pacific oysters (alive and dead shells) both on the mussel reef (linear model: $n=17$, $r=-0.888$, $p < 0.001$) and the oyster reef (linear model: $n=16$, $r=-0.696$, $p < 0.01$; Fig. 3b). For every extra oyster shell found in the plots on the mussel reef, the cover of *Fucus* decreased with 2.0 % (Fig. 3b).

4 Discussion

Different algal communities developed on the different small-scale shellfish reefs that we constructed on the intertidal. On the reefs consisting of native blue mussels, a *Fucus*-dominated meadow community quickly developed that remained throughout the summer. On the Pacific oyster dominated reefs, mats of bloom-forming green algae established instead, and the cover of *Fucus* stayed low throughout the summer. In addition, the invasion of Pacific oysters decreased the development of the *Fucus* meadow after the winter on a previously pure blue mussel dominated reef. This demonstrates that the invasion of Pacific oysters may have great effects on the structure and function of intertidal reef communities. While the green algae dominated reef communities have low primary biomass and low habitat complexity, brown algae such as *Fucus* are important foundation species that promote an array of associated organisms by increasing habitat complexity (Albrecht and Reise, 1994; Dayton, 1975; Jenkins et al., 1999). The contribution of furoid communities to marine ecosystem functioning is well documented and includes; modification of consumer and resource control, nutrient effects on net primary production and biodiversity, predation effects and fish abundance, and increases in sediment accumulation (Albrecht, 1998; Eriksson et al., 2009; Eriksson et al., 2006a; Eriksson et al., 2006b, 2007). On the island of Sylt, Germany, the cover of *Fucus* decreased dramatically on blue mussel reefs in the early 2000s, leading to large dominance shifts in community structures (Buttger et al., 2008). The reefs were recently invaded by Pacific oysters, but the cause of the decline in *Fucus* was not established. Our results provide a mechanistic link that suggest that there may be a direct connection between the invasion of the Pacific oyster and declines in *Fucus* meadows.

The remarkably fast development of primary biomass in our experiment highlights the ecological importance of byssus threads in intertidal ecosystems. The *Fucus* community developed a complete cover of fully grown 3-4 dm long thalli on the artificial mussel reefs in

just 2 weeks by means of entanglement in the byssus threads of the blue mussels.

Entanglement of clonal fragments is a common reproductive strategy among seaweeds (Eriksson and Johansson, 2005; Hurd et al., 2014). However, the importance of fragmentation for building the habitat in our system, where entanglement is the base of a structurally complex kelp community that dominates primary biomass (Albrecht and Reise, 1994; Baird et al., 2004), may be unprecedented in marine ecosystems. This strongly suggests that the ecological consequences brought by the large-scale oyster invasion of intertidal shores are not restricted to direct effects on competing bivalves and associated invertebrates, but may have cascading implications on an ecosystem level, due to fundamental differences in basic ecological functions of blue mussels and oysters.

In general, both the function and stability of the experimental reefs dominated by the invasive oyster were more resilient to hydrodynamic stress than the reefs constructed only with native blue mussels. The ability of the blue mussel reef treatments to attach and accumulate *Fucus* thalli degenerated drastically over time at the exposed site. Exposure has a large impact on byssus production and behavior (Van Winkle, 1970); at high flow rates byssus production decreases (Carrington et al., 2008; Moeser et al., 2006) and blue mussels actively choose to attach to different substrates depending on perturbation rates (wa Kangeri et al., 2014). The blue mussels might even have avoided attaching to *Fucus* thalli at high exposure due to the risk of being pulled away by the additional drag. In contrast, the experimental oyster reefs performed similarly at the different levels of exposure: throughout the summer, the numbers of oysters and green algal development were comparable at the exposed and the sheltered site.

Our results also support that novel and complex interactions between the invading oysters and the native blue mussels currently determine the resilience of these intertidal reef communities (Buschbaum et al., 2016; Eschweiler and Christensen, 2011; Reise et al.,

2017b). As filter feeding ecosystem engineers that share a food source and optimal feeding areas, blue mussels and oysters compete for food (Reise et al., 2017b). However, the large biogenic structure produced by the oysters also provides significant shelter for the smaller blue mussels. Accordingly, blue mussels are often found thriving deep in the oyster matrix where they are protected both from predation by crabs (Eschweiler and Christensen, 2011; Waser et al., 2015) and overgrowth by barnacles (Buschbaum et al., 2016). Here we show that the oyster matrix also protects mussels from physical disturbance from hydrodynamic stress. In August, a storm wiped out all experimental blue mussel reefs, while the blue mussels thrived and even doubled in numbers when protected by the oyster matrix in the experimental oyster reefs.

The invasion of the Pacific oyster has created a novel entity of mixed oyster-mussel reefs that today dominate the intertidal reefs in the Wadden Sea; so-called “oyssel” reefs (Reise et al., 2017b). It has been argued that the oyster-mussel reefs have replaced the ecological function of pure blue mussel beds (Markert et al., 2010) and that these “oyssel” reefs will be more persistent to physical disruption, because oysters are larger and anchor themselves deeper in the sediment than blue mussels (Reise et al., 2017a; Reise et al., 2017b). Here we provide the first experimental evidence that mixed oyster reefs are more resilient to perturbation than pure blue mussel reefs. However, we also demonstrate that the invasion of oysters promote a transformation of furoid meadows to green algae grasslands, with magnitudes lower primary biomass and habitat complexity. This change is driven by a fundamental mechanistic difference between blue mussels and oysters, where the decrease in blue mussels leads to less presence of byssus threads that attach the furoids to the reefs. Marine meadows of furoids, kelps or seagrass are all highly productive communities with significant ecosystem functions and services for associated organisms across the food web;

highlighting the need for ecosystem-based research that includes a mechanistic understanding of ecological processes to document the effects of invasive species.

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Table 1. Results of GLMM testing the effect of shellfish reef treatments (adding mussels, adding oysters, adding cockles and no addition control), and time (five levels); on different algal communities (brown, green and red algae) at an exposed and a sheltered site. Time was included as a repeated measurement.

	brown algae (<i>Fucus</i> sp.)			green algae (<i>Ulva</i> sp.)		red algae (<i>Gracilaria</i> sp.)	
	df	F	p	F	p	F	p
<i>Exposed site:</i>							
Bio manipulation treatment (Bio)	3,8	2.33	0.151	16.69	<0.001	3.56	0.067
Time (T)	1,44	2.6	0.111	0.76	0.388	1.25	0.269
T x Bio	3,44	1.33	0.277	0.51	0.679	0.93	0.434
<i>Sheltered site:</i>							
Bio manipulation treatment (Bio)	3,8	16.29	<0.001	11.52	0.003	1.14	0.391
Time (T)	1,44	2.55	0.1173	1.71	0.198	4.23	0.045
T x Bio	3,44	10.77	<0.001	0.22	0.879	1.76	0.169



Fig. 1. Bio-manipulation treatments: experimental reefs created by not adding any bivalves (no addition treatment), adding 250 cockles (cockle bank treatment), adding 200 blue mussels (mussel reef treatment) and adding 25 Pacific oysters and 50 blue mussels (oyster reef treatment).

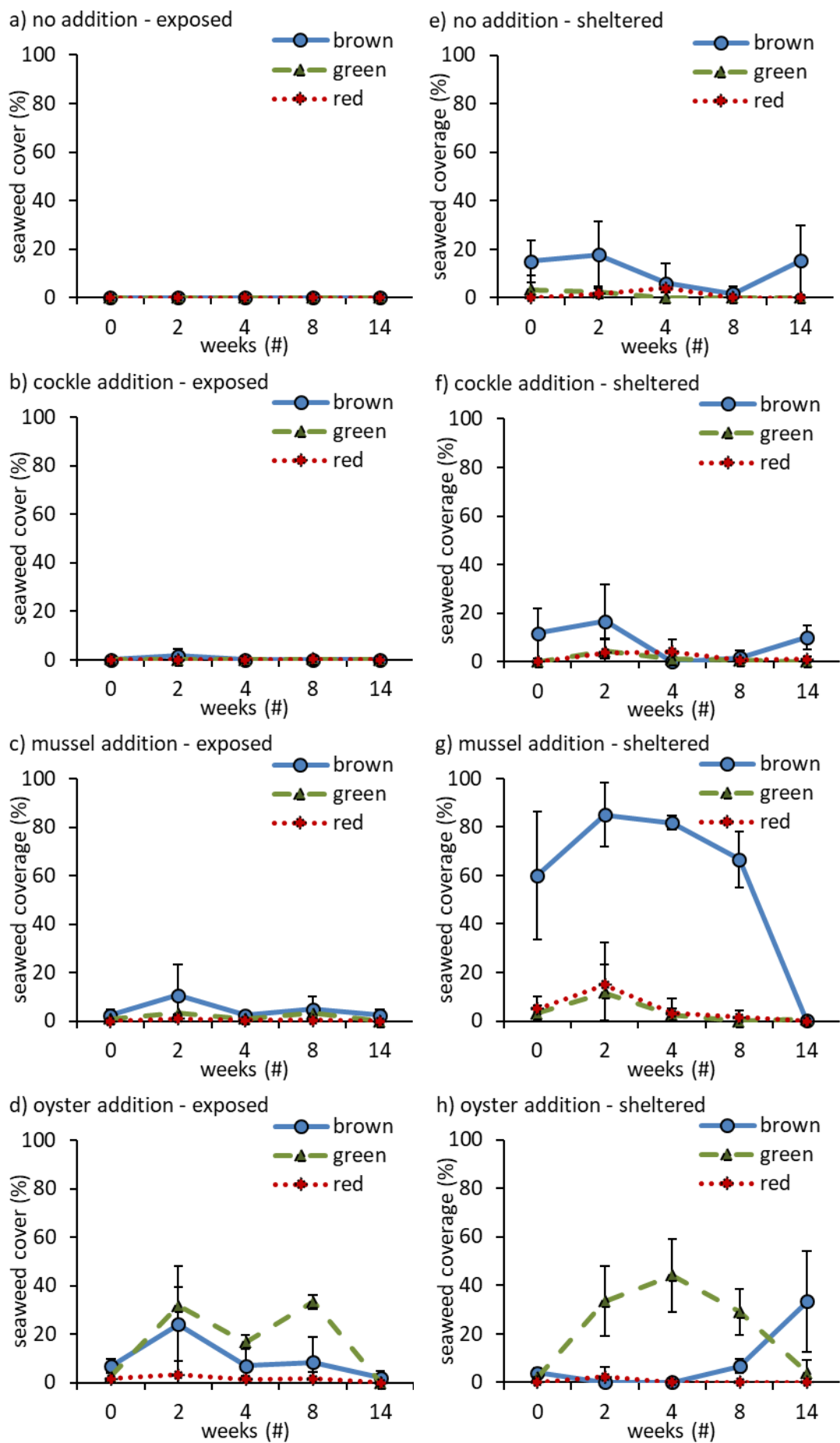


Fig. 2. The development of brown (blue solid lines, circles), red (red dotted lines, diamonds) and green (green striped lines, triangles) macroalgae on different experimental reefs at an exposed (a-d) and a sheltered (e-h) site. Time shows week from the start of the experiment in the beginning of July. The experimental reefs were created by not adding any bivalves (no addition treatment: a & e), adding 250 cockles (cockle bank treatment: b & f), adding 200 blue mussels (mussel reef treatment: c & g) and adding 25 Pacific oysters and 50 blue mussels (oyster reef treatment: d & h). Error bars show standard deviations of the mean values.

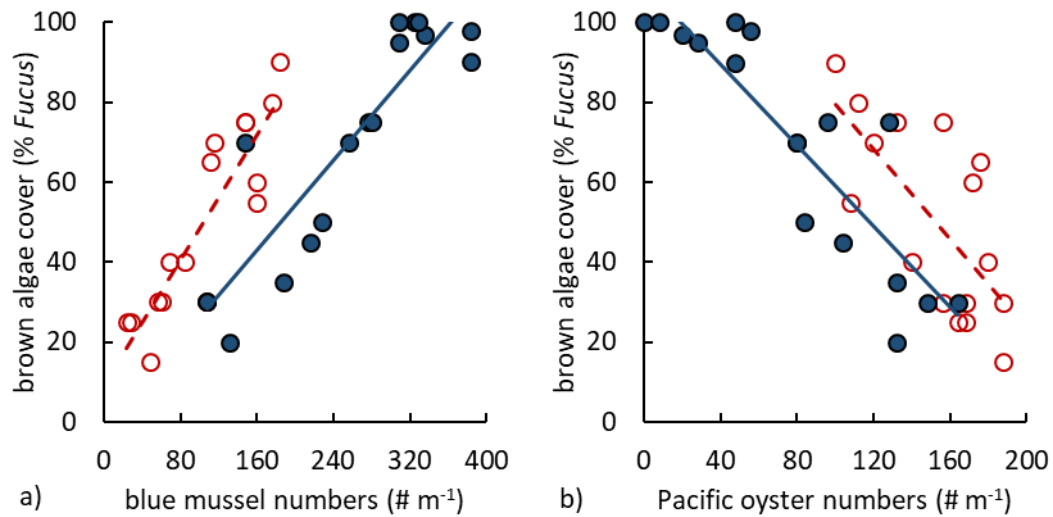


Figure 3. The relation between percentage cover of the brown algae *Fucus vesiculosus* and the number of a) blue mussels and b) Pacific oysters on a blue mussel dominated shellfish reef (solid blue line, filled blue circles) and on a Pacific oysters dominated shellfish reef (dotted red line, open red circles). The lines (both dotted and solid) show statistically significant linear relations ($p < 0.01$).