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Deeply hidden inside introduced biogenic structures – Pacific oyster reefs reduce detrimental barnacle overgrowth on native blue mussels

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ABSTRACT

In sedimentary coastal ecosystems shells of epibenthic organisms such as blue mussels (*Mytilus edulis*) provide the only major attachment surface for barnacle epibionts, which may cause detrimental effects on their mussel basibionts by e.g. reducing growth rate. In the European Wadden Sea, beds of native blue mussels have been invaded by Pacific oysters *Crassostrea gigas*, which transformed these beds into mixed reefs of oysters with mussels. In this study, we determined the spatial distribution of *M. edulis* and their barnacle epibionts (*Semibalanus balanoides*) within the reef matrix. Mean mussel density near the bottom was about twice as high compared to the mussel density near the top of an oyster reef, whereas barnacles on mussels showed a reversed pattern. Barnacle dry weight per mussel was on average 14 times higher near the top than at the bottom. This pattern was confirmed by experimentally placing clean *M. edulis* at the top and on the bottom of oyster reefs at two sites in the Wadden Sea (island of Texel, The Netherlands; island of Sylt, Germany). After an experimental period of five weeks (April and May 2015, the main settlement period of *S. balanoides*), the number of barnacles per mussel was at both sites significantly higher on mussels near the top compared to near the bottom. We conclude that the oyster reef matrix offers a refuge for *M. edulis*: inside reefs they are not only better protected against predators but also against detrimental barnacle overgrowth. This study shows that alien species can cause beneficial effects for native organisms and should not be generally considered as a risk for the recipient marine ecosystems.

1. Introduction

Introduced non-native species can considerably affect native ecosystems and their communities by e.g. altering biodiversity, species interactions, energy flow and evolutionary adaptations (e.g. Vitousek et al., 1997; Grosholz, 2002; Katsanevakis et al., 2014). In the beginning of invasion biology research, direct detrimental impacts of alien organisms on resident species were the most commonly considered consequences of human induced translocation of species across natural barriers (Elton, 1958; Carlton, 1989; Mack et al., 2000; Crooks, 2002). However, influences of non-native species are often more complex and can also include a variety of facilitative effects (Thieltges et al., 2006). It is likely that these are as common as inhibiting effects and therefore, should also be taken appropriately into account when assessing the overall consequences of an alien organism after establishing in a native habitat (Rodriguez, 2006). Especially, non-native habitat-forming species such as epibenthic bivalves and macroalgae can provide additional structures used by native organisms (Crooks, 2002; Gribben et al., 2013). These ecosystem-engineering effects (sensu Jones et al., 1994) are of particular importance in coastal ecosystems where epibenthic biotic structures are generally rare such as in the European Wadden Sea (south-eastern North Sea), which is mainly dominated by unconsolidated sediments. For this region, Buschbaum et al. (2006) and Polte and Buschbaum (2008) showed, for instance, that beds of the introduced Japanese seaweed *Sargassum muticum* (Yendo) Fensholt harbour a much more diverse species assemblage than native macroalgae and provide a suitable habitat for endangered resident fish species. Generally, *S. muticum* is considered a very aggressive invader and a lot of detrimental impacts on native species are reported from many coastal systems, which could not be confirmed for the Wadden Sea (Staehr et al., 2000; Britton-Simmons, 2004; Harries et al., 2007; Lang and Buschbaum, 2010; Engelen et al., 2015; Davidson et al., 2015).

A further ecologically important, habitat forming, non-native species in the south-eastern North Sea is the Pacific oyster *Crassostrea gigas* (Thunberg) with its origin at the Japanese coast (Nehring, 2011). It has been introduced for aquaculture purposes in many countries and today, the oyster is almost worldwide distributed including the Wadden Sea (Ruesink et al., 2005; Diederich, 2005, 2006; Cardoso et al., 2007; Padilla, 2010; Troost, 2010; Van der Zee et al., 2012). Here, first free-living Pacific oysters were detected on beds of blue mussels (*Mytilus edulis* L.) in the 1980s (Reise, 1998; Troost, 2010). Since the late 1990s, Pacific

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oysters naturally occur in the entire region outside the aquacultures (Wehrmann et al., 2000; Troost, 2010) and transformed most intertidal mussel beds into mixed aggregations of mussels and oysters (Diederich, 2006; Troost, 2010). This shift was accompanied by an increase in habitat heterogeneity due to newly constructed biogenic reef structures, formed by the large-sized oysters. However, the associated species communities of former pure mussel beds and oyster reefs are largely the same, including a high number of sessile organisms, which live directly attached to the shells of the bivalves (Kochmann et al., 2008; Markert et al., 2009).

One of the most conspicuous epibionts on mussels and oysters are balanids such as the acorn barnacle *Semibalanus balanoides* (L.). They may completely cover shells of *M. edulis* and hereby cause a reduction in mussel growth and presumably also other life history traits such as reproduction (Buschbaum and Saier, 2001). Kochmann et al. (2008) and Markert et al. (2009) showed that number and biomass of barnacle epigrowth per area are not very different between mussel beds and oyster reefs. Additionally, Retuschat (2009) found no conspicuous differences in barnacle percent coverage on individual mussel and oyster shells. However, these studies did neither investigate the small-scale distribution of barnacles within oyster reefs, although it has been reported that barnacle cyprid larvae may execute a distinct substrate choice (e.g. Crisp et al., 1985; Le Tourneux and Bourget, 1988; Thompsen et al., 1998; Buschbaum, 2001), nor the spatial occurrence of mussels and oysters within an oyster reef.

The latter was done by Eschweiler and Christensen (2011), who revealed that blue mussels actively migrate from the top to the bottom of an oyster reef in an attempt to escape from crab predation. The resulting mussel distribution is a recurrent pattern (Fig. 1), and we now ask how barnacles respond to this stratification of mussels within oyster reefs. If barnacles follow the same pattern, than the advantage for mussels to keep away from crabs could be foiled. If barnacles show a reversed pattern than the advantage of a predation refuge would be reinforced by diminished overgrowth for the mussels.

To quantify the density of mussels and their barnacle epibionts, we conducted field investigations in different height layers of an oyster reef. We hypothesized that due to the known defence strategy against predation, most *M. edulis* occur near the bottom where, as a positive side effect, mussels become less overgrown and are, therefore, better protected from detrimental impacts caused by barnacles. This was tested by performing field experiments on barnacle recruitment on mussels at two spatially distinct oyster reefs in the Wadden Sea.

Fig. 1. Mixed reef of introduced Pacific oysters *Crassostrea gigas* and blue mussels *Mytilus edulis* (white arrow) in the northern Wadden Sea near the island of Sylt.

2. Materials and methods

2.1. Study area and experimental sites

Field surveys on mussel abundance and its barnacle epibionts were carried out in a mixed bed of native *M. edulis* and introduced *C. gigas* located on tidal flats in the north-east of the island of Sylt in the northern Wadden Sea (Germany, North Sea, 55°02′N, 008°26′E; Fig. 2). Since the introduction of *C. gigas* into the area for aquaculture purposes in the mid of the 1980s, all former naturally pure blue mussel beds have been overgrown by Pacific oysters and both mussels and oysters are now occurring in mixed reefs (Nehls and Büttger, 2007; Eschweiler and Christensen, 2011). Tides are semi-diurnal with an average tidal range of about 2 m. Mean water temperature is 15 °C in summer and 4 °C in winter and salinity usually remains close to 30 psu. For a comprehensive description of the area and its biota see Reise (1985) and Gätje and Reise (1998).

Field experiments on barnacle recruitment on clean *M. edulis* placed at the top and on the bottom of a Pacific oyster reef were performed at two sites, at the above mentioned area near the island of Sylt and at an oyster reef north-east of the island of Texel in the western Wadden Sea (The Netherlands, 53°09′N, 004°58′E; Fig. 2). At the latter site, tides have a range of about 1.5 m and salinity mainly varies from 25 to 31 psu (Van Aken, 2003, 2008a; Cardoso et al., 2007). Average water temperature is 17 °C in summer and 5 °C in winter (Van Aken, 2008b).

We chose these two sites and oyster reefs for our field experiments because they represent the end points of a habitat continuum in the Wadden Sea and are, therefore, suitable to test for general and large-scale patterns in barnacle recruitment on *M. edulis* living in Pacific oyster reefs.

2.2. Position and density of *M. edulis* inside an oyster reef

To obtain density distributions of *M. edulis* occurring in different strata of an oyster reef, samples were collected in the uppermost 10 cm (top layer) and in the layer 10 cm above the ground (bottom layer) from an oyster reef near the island of Sylt (Fig. 2) by using a stratified random sampling design. The total height of the oyster reef measured from the sediment surface to the uppermost bivalves was about 20 cm. The samples were collected in August 2015 by using a metal frame of 25 × 25 cm (625 cm^2). A total of six replicate samples per layer were investigated. All mussels with a shell length of >40 mm, which occurred inside the frame in the respective layer, were counted. Smaller *M. edulis* were not considered because they are barely overgrown by balanids (Buschbaum and Saier, 2001) presumably to the ability of small-sized mussels to clean their shells with their foot (Theisen, 1972).

2.3. Barnacle coverage and dry weight on *M. edulis*

Extent of barnacle overgrowth on *M. edulis* at the top and bottom of an oyster reef was quantified by analysing barnacle coverage on the mussels, which have been collected by the six replicate samples per layer for the density distribution analysis (see Section 2.2).

Barnacle coverage of each mussel with a shell length of >40 mm was estimated to the nearest 25%. Afterwards, barnacles attached to the mussel were scratched off using a knife and then dried at 75 °C for three days. All investigated mussels of a sample were counted and dry weight of barnacles was determined to the nearest 0.01 g, which allowed calculation of mean barnacle dry weight per mussel for each sample. In total, we examined 145 mussels from the top and 328 *M. edulis* from the bottom layer, respectively. Besides the dominating barnacle *S. balanoides* also the non-native *Austrominius modestus* occurred in low numbers on the mussels.