Colonisation success of introduced oysters is driven by wave-related exposure

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INVASION NOTE

Colonisation success of introduced oysters is driven by wave-related exposure

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Abstract The Pacific oyster, *Magallana gigas*, is an extremely successful invader with established populations in marine and estuarine habitats almost all over the world. Ecological implications of the introduction of this species to indigenous communities are well documented. However, the processes by which this species successfully establishes in a recipient community is still insufficiently understood. The early detection of the oyster at the island of Helgoland (North Sea) provided the ideal opportunity to investigate whether physical mechanisms, such as wave-exposure, influence their successful colonisation. We hypothesized that oyster colonisation benefits from wave-protected conditions. For this purpose, we evaluated colonisation success of *M. gigas* among wave-protected sites and wave-exposed sites along the island's pier system. The densities of *M. gigas* were significantly higher at wave-protected sites than at wave-exposed sites, and the frequency distributions of oyster lengths indicated better growth and higher survival rates in the harbours. This higher colonisation success at wave-protected sites may be explained by the relative retention time of water masses in the harbours, probably resulting in both reduced larval drift and lower energy demands for secretion formation (i.e. firmer binding to the substrate). The fact that the density of *M. gigas* can vary greatly on small spatial scales depending on exposure corroborates a multiple exposure sampling approach to monitor oyster populations in order to avoid potential overestimations of population sizes in given areas.

Keywords *Magallana gigas* · Wave exposure · North sea · Abundance · Length frequency distribution · Neobiota

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Introduction

Globalisation and climate change have accelerated the spread of non-indigenous species (NIS) in the world‘s oceans in the last decades (e.g. Bellard et al. 2013; Hulme 2017). Invasive species can lead to significant changes in communities or even entire ecosystems, e.g. through loss of biodiversity and changes in ecosystem functions and services (e.g. Sala et al. 2000; Butchart et al. 2010). The colonisation success of NIS depends on several factors, which fall broadly into two categories: (1) the species' autecological characteristics and competitive strength in coping with environmental conditions (Byers 2002; Stachowicz et al. 2002), and (2) interspecific interactions in the newly introduced area (Kennedy et al. 2002; Meiners et al. 2004).

The Pacific oyster *Magallana gigas* (formerly *Crassostrea gigas*; Salvi and Mariottini 2016; Bayne et al. 2017) is one of the most successful marine invaders with established populations beyond its natural range (see Ruesink et al. 2005 and references therein). Pacific oysters are well established in different habitat types from sandy and muddy tidal flats, where they preferably attach to the blue mussel or to each other (Diederich 2005), to rocky shores (Ruesink 2007) and artificial hard substrates such as rocky dikes and harbour facilities (Smaal et al. 2009).

The species had been introduced to various localities along the North Sea coast during past decades for aquaculture activities (e.g. Oosterschelde estuary, 1964; North Frisian Wadden Sea near the island of Sylt, 1986; see Reise 1998; Wehrmann et al. 2000). Its successful reproduction and the recruitment of oysters outside of the aquaculture facilities on intertidal mussel beds and artificial hard substrates led to their spread in the Wadden Sea until juvenile Pacific oysters were found for the first time in the centre of the German Bight, i.e. at the island of Helgoland in 2003 (Franke and Gutow 2004).

The changes caused by the introduction of the Pacific oyster on native assemblages are well documented (e.g. Ruesink et al. 2005; Green and Growe 2014). However, less effort has been devoted to understand the underlying processes by which the oysters successfully establish within recipient assemblages. The timely discovery of the invader at Helgoland created the ideal opportunity to study how densities of Pacific oysters in a new area vary on small spatial scales (hundreds of metres to few kilometres) and whether physical mechanisms, such as wave-exposure, affect successful establishment.

As recruitment of Pacific oysters seems to be enhanced in wave-protected conditions (Robinson et al. 2005; Ruesink 2007), we tested if wave-protected artificial harbours provide particularly beneficial conditions for the species. For this purpose, we compared the abundances and length-frequency distributions of *M. gigas* between wave-protected sites and wave-exposed sites along the pier system around the island of Helgoland.

Material and methods

Study sites

Seven wave-protected sites (i.e. in the two harbours of the island) and seven wave-exposed sites (i.e. outside the harbours) were randomly chosen. The 14 sites were distributed along the almost 6000 m long pier system of the island of Helgoland in the German Bight, North Sea (54° 11′ N, 7° 53′ E; Fig. 1). The maximum water velocity (as an indication of exposure) at the wave-exposed sites of Helgoland was more than two times higher than at the wave-protected sites (Molis et al. 2015). Species assemblages did not differ among study sites, being predominantly a mosaic of barnacles, green algae (*Ulva* spp.) and red seaweeds (*Porphyra* spp., *Mastocarpus stellatus*, *Chondrus crispus*) in the mid-to-low intertidal. Ten replicate quadrats (0.25 m^2) were placed at the vertical pier walls at each site by SCUBA divers. In each replicate quadrat, all oysters were counted and measured (maximum shell length, to the nearest 1.0 mm) in 2005 and 2006. This procedure was repeated in 2012. Each of the three sampling campaigns took place in late spring or summer months. In total, 140 quadrats were sampled for the two different degrees of exposure per year (10 replicates × 7 sites × 2 exposures = 140). Further details of the sampling campaigns are shown in the Supplement (see Tab. S1).

Data analysis

The effect of wave exposure on the abundance of *Magallana gigas* over time was tested with a repeated-measures ANOVA using the seven replicate sites for each wave exposure. The ten sampling quadrats

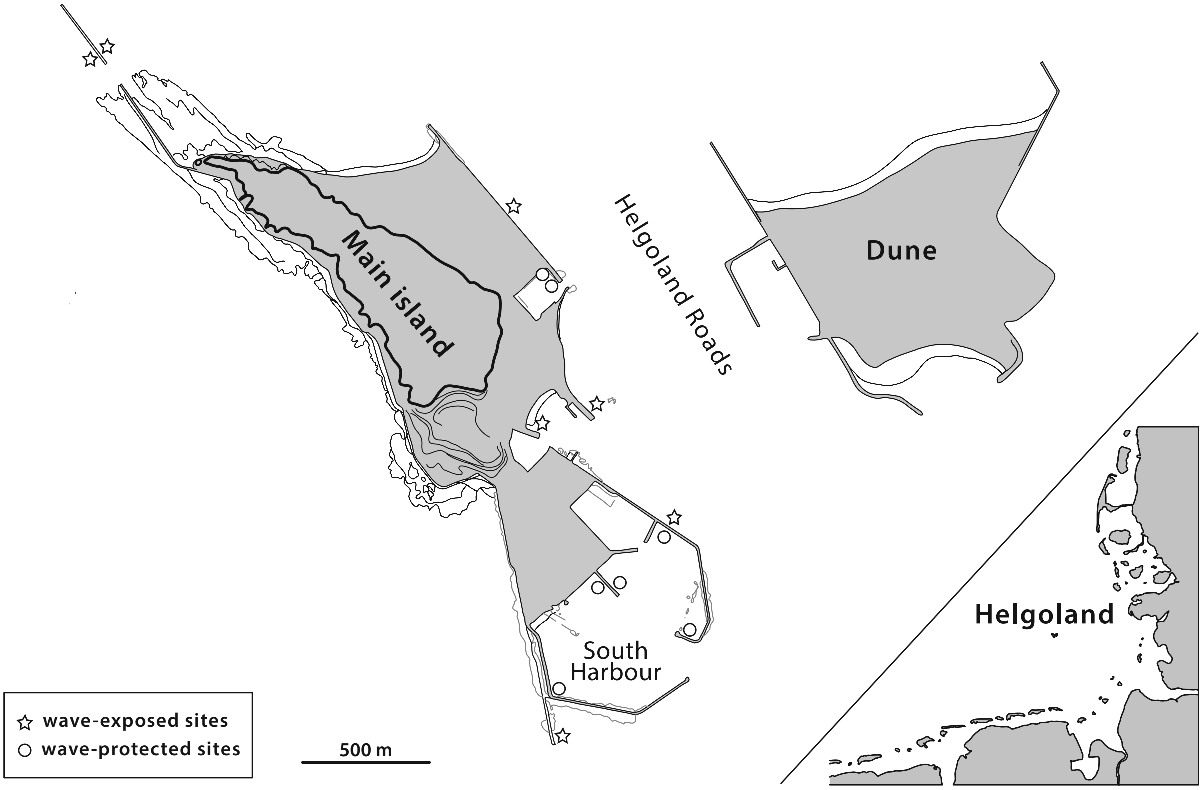

Fig. 1 Map of Helgoland and its location in the German Bight, North Sea (bottom right corner). Symbols indicate the positions of the wave-exposed (asterisks) and wave-protected sites (circles). (Modified from Beermann 2014)

were averaged for each site. Time (factor levels: '2005', '2006', '2012') was treated as repeated measures within-subject factor, and the wave exposure (2 factor levels: 'protected', 'exposed') was a between-subject factor. Prior to ANOVA, the data were tested for homogeneity of variances using Cochran's C test. In case of heteroscedasticity, the data were log (x + 1)-transformed.

The analysis of the different size classes of *M. gigas* was conducted by comparing the medians of frequencies via Kruskal–Wallis according to Sokal and Rohlf (1995).

All tests were performed with the software package Statistica Version 10.0 MR1 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

The abundances of *Magallana gigas* were significantly higher at wave-protected sites than at wave-exposed sites ($F_{1,12} = 69.17, p < 0.001$) (Fig. 2). This pattern was consistent throughout time—oyster individuals were significantly more abundant at wave-protected than at wave-exposed sites in 2005 ($p < 0.05$) and 2006 ($p < 0.05$) as well as in 2012 ($p < 0.001$). At the same time, oyster abundances at both wave-protected and wave-exposed sites increased distinctly between 2005/2006 and 2012 (more than 15 and 10 times respectively).

The length-frequency distributions of oysters at wave-protected sites revealed a similar pattern each year, with most individuals in the 10–20 mm size class (2005: $H_{K–W} = 76.53, p < 0.001$; 2006: $H_{K–W} = 75.91$, $p < 0.001$; 2012: $H_{K–W} = 58.81$, $p < 0.001$) (Fig. 3). Larger individuals (50 mm and larger) increased slightly over the years, and individuals larger than 80 mm were not found until 2012. In 2005, no individuals were detected at wave-exposed sites (Fig. 3). In the following year, most individuals were again found in the 10–20 mm size class as at the wave-protected sites ($H_{K–W} = 43.87, p < 0.001$). In 2012, the

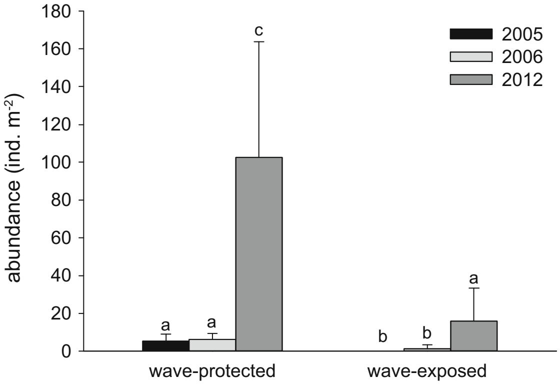

Fig. 2 Effect of wave exposure on abundance of *Magallana gigas* through time. Error bars are standard deviation among replicated sites. Student–Newman–Keuls (SNK) post hoc test was run for wave exposure and year combinations. Different letters indicate statistically significant differences ($p < 0.001$) between means of replicated sites per exposure per year (n = 7). Please note that no individuals were detected at wave-exposed sites in 2005

first two size classes (i.e. 0–10 and 10–20 mm) differed significantly from the other size classes ($H_{K-W} = 91.00$, $p < 0.001$), where only very few individuals per class were found.

Discussion

Abundances

Higher abundances of *Magallana gigas* were observed at wave-protected sites. This contradicts common distribution patterns of sessile filter-feeders, mainly mytilids, barnacles and tubeworms, which are known to predominate especially wave-exposed areas caused by an increased replenishment of food, higher oxygenation inputs and/or decreased predator pressure due to wave shock (e.g. Scrosati and Heaven 2008; Arribas et al. 2014).

Oysters seem to be an exception to the general pattern of filter feeders. An increased occurrence of *M. gigas* and other oyster species under sheltered conditions has been reported, for example, from coastal marine (Ruesink 2007) and estuarine areas (Robinson et al. 2005) as well as from harbour sites (Blockley and Chapman 2008). The success of oyster colonisation at wave-protected sites may be explained by (1) the relative retention of water masses in the harbours and the associated reduced drift of the larvae and (2) the reduced whiplash effect on newly settled larvae, i.e. their removal by wave-induced movement of algal thalli (e.g. Leonard 1999; Beermann et al. 2013). This may also explain that it obviously took longer for oysters to settle at exposed sites, as no oysters were found here in 2005, while a few individuals (up to 11 individuals/0.25 m^2) were found at all wave-protected sites.

Length frequency distributions

The observed patterns in length frequency distributions indicated better growth and higher survival rates at wave-protected sites, i.e. larger individuals of *M. gigas* occurred almost exclusively in the harbours. This is in contrast to some previous findings, which demonstrated high growth potential of oysters (e.g. Brown 1988; Campbell and Hall 2019) and other bivalves (Bayne and Newell and references therein 1983) primarily through increased food supply more likely to be found in habitats exposed to waves and currents. Large oysters, however, have also been detected in sheltered waters with relatively low food supply associated with a decoupling of shell and somatic growth, i.e. good shell growth, but underdeveloped somatic growth (e.g. Brown and Hartwick 1988; Chávez-Villalba et al. 2010). Furthermore, a high wave load at the exposed sites may have resulted in reallocation of energy from shell/soft tissue growth into secretion formation—for a firmer binding to the substrate—as shown for other bivalves, e.g. *Mytilus galloprovincialis* and the black-lip pearl oyster, *Pinctada margaritifera* (e.g. Babarro and Carrington 2011; Kishore et al. 2014).

A seemingly increased mortality rate of *M. gigas* at wave-exposed sites appears to be primarily caused by processes directly related to wave exposure, such as detachment/dislodgment from the substrate (e.g. Alvarado and Castilla 1996). Different predation mortality between the two different exposure levels is rather unlikely, as in the North Sea a generally low pressure by the main benthic predators, the starfish *Asterias rubens* and the shore crab *Carcinus maenas*, which prefer blue mussels to oysters, is reported (Diederich 2005).

In conclusion, oyster populations of *Magallana gigas* are characterized by large variation on small spatial scales in non-native habitats. Wave exposure

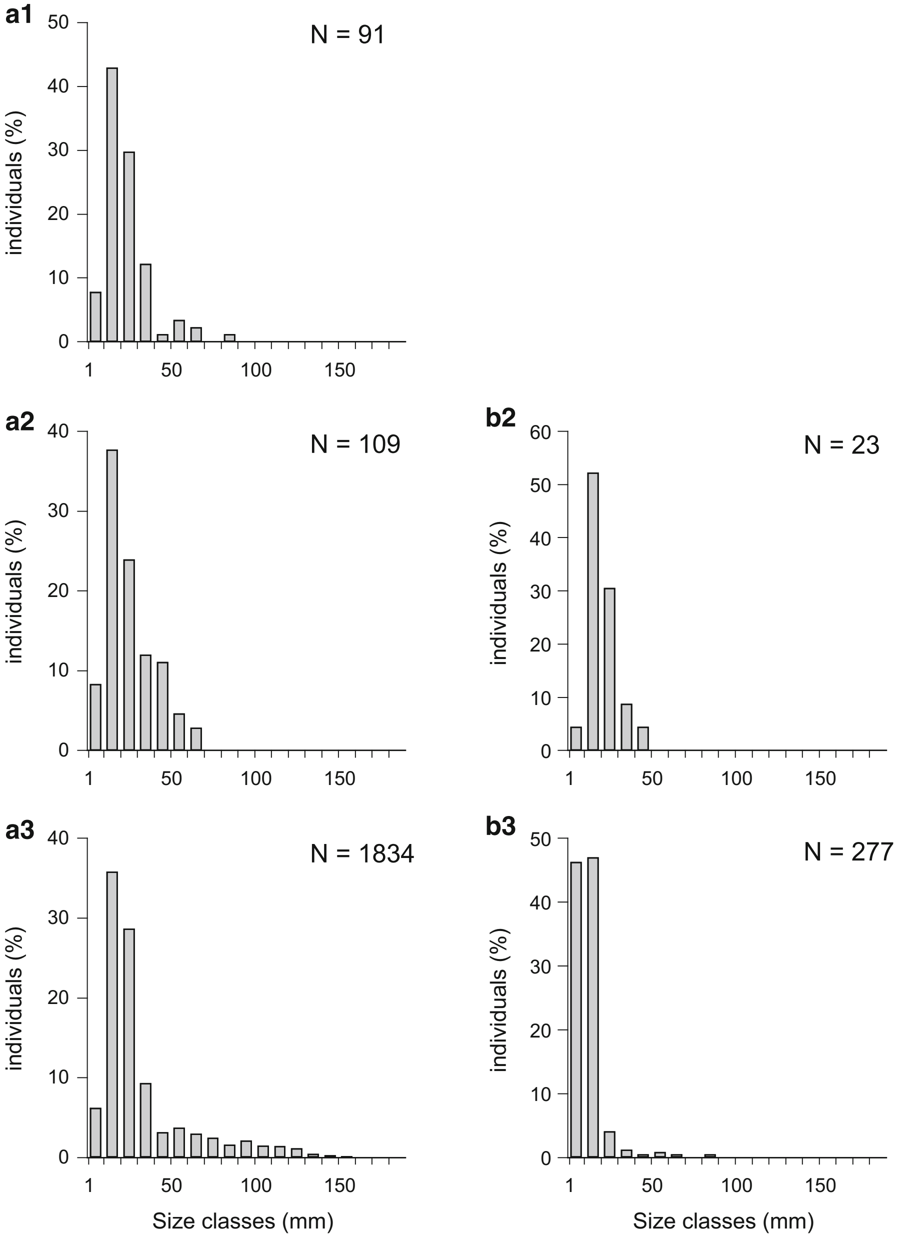

Fig. 3 Length frequencies (size class interval = 10 mm) of *Magallana gigas* at wave-protected (**a**) and wave-exposed sites (**b**) in 2005 (**1**), 2006 (**2**) and 2012 (**3**). Please note that no individuals were detected at wave-exposed sites in 2005 (**b1**)

seems to have a profound impact on colonisation, and thus, establishment success. Artificial harbours that are largely protected from wave load, can serve as a preferred oyster habitat. Consequently, monitoring programmes that aim at capturing NIS must be carefully evaluated, as surveys are often restricted to harbours and marinas (e.g. Rohde et al. 2017; Kraus et al. 2019). We argue that potential overestimations of local oyster populations can be avoided by a multiple-exposure sampling approach.

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