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Introduced marine ecosystem engineers change native biotic habitats but not necessarily associated species interactions

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ABSTRACT

Introduced bioengineering organisms may fundamentally change native coastal ecosystems by modifying existing benthic habitat structures and thereby habitat-specific species interactions. The introduction of the Pacific oyster *Magallana gigas* into the sedimentary coastal area of the south-eastern North Sea and its preferred settlement on native blue mussel shells caused a large-scale shift from monospecific *Mytilus edulis* beds to current mixed reefs of mussels and oysters. To investigate whether the newly developed biotic habitat affects the occurrence of associated native key organisms and their ecological functions, we studied the long-term density trajectory of the gastropod *Littorina littorea* and its grazing activity on barnacles attached to Pacific oyster reefs in the northern Wadden Sea. We found no significant correlation between oyster and snail densities on blue mussel beds in the last two decades, which spans a time-period from the beginning of Pacific oyster establishment to today's oyster dominance. A manipulative field experiment revealed that snail density significantly affects the recruitment success of barnacles *Semibalanus balanoides* on oyster shells with the highest number of barnacle recruits at snail exclusion. Thus, density and grazing activity of the snail *L. littorea* may control barnacle population dynamics on epibenthic bivalve beds in the Wadden Sea. This interspecific interaction was already known for blue mussel beds before the oyster invasion and, therefore, we conclude that despite the strong modifications that non-native ecosystem engineers cause in native biotic habitats, the ecological functions of associated key species can remain unchanged.

1. Introduction

Worldwide, marine ecosystems are characterized by an increasing number of non-native species due to an intensification of global trade and transport as well as marine aquaculture (Gollasch, 2006; Ruiz et al., 1997). After establishment in the new environment, introduced species can cause major effects on native species communities and population dynamics (Grosholz et al., 2000; Mack et al., 2000; Reise et al., 2017a; Anton et al., 2019), and may also alter the physical nature of the ecosystem itself. In case of physical structural changes caused by non-native species, they act as ecosystem engineers, which may modify habitats and interactions by affecting resources and stressors such as living space and food with cascading effects on resident organisms (Jones et al., 1994, 1997; Crooks, 2002, 2009; Guy-Haim et al., 2018).

Soft-bottom coastal systems, for instance, are regularly affected by non-native ecosystem engineering organisms because they provide novel habitats in an environment dominated by unstable sediments and poor of epibenthic structures (Bouma et al., 2009). In sedimentary marine environments, non-native bivalves have been intensively investigated (Sousa et al., 2009), as they are well known to cause diverse ecological effects because they can occur at high densities and compromise a major proportion of the benthic faunal biomass (Sousa et al., 2009; Buschbaum et al., 2012; Reise et al., 2017a). For example, different species of mytilid mussels may physically change the environment as they tend to form dense beds at the sediment surface by attaching byssal threads to conspecifics (Aguilera et al., 2017). This results in the production of large amounts of shell material and the development of highly structured bioaggregates (Guitiérrez et al., 2003; Buschbaum et al., 2009). For instance, this was shown for the date mussel *Arcuatula senhousia* (Benson, 1842; formerly named *Musculista senhousia*) in many coastal ecosystems, worldwide (Reusch and Williams, 1998; Crooks and Khim, 1999).

Another prominent non-indigenous species on a global scale is the Pacific oyster *Magallana* (formerly *Crassostrea*) *gigas* (Thunberg 1793), which has been intentionally introduced for aquaculture purposes in many regions (Ruesink et al., 2006). Nowadays, it shows an almost

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worldwide distribution at temperate and subtropical coasts (Ruesink et al., 2005).

Since the 1960s, *M. gigas* has been introduced to several north-western European coasts and has expanded rapidly into the natural environment where it forms extensive and dense reef structures (Troost, 2010). A strong expansion of *M. gigas* happened in the European Wadden Sea, which represents the sedimentary coast of the south-eastern North Sea. At the beginning of feral oyster establishment in the 1980s and 1990s, native epibenthic mussel beds of *Mytilus edulis* (L.) provided the only extensive natural hard and settlement substrate for planktonic oyster larvae. Nowadays, almost all intertidal blue mussel beds are heavily populated with *M. gigas* and, therefore, a native habitat has been transformed to novel multi-layered mixed reefs of introduced oysters and resident mussels (Reise et al., 2017a).

As in other native ecosystems affected by established competitive non-indigenous species, the effects of *M. gigas* have also been intensively investigated in the Wadden Sea. Initially, these studies focused on the occurrence and dynamics of native mussels because it was feared that the invader may outcompete *M. edulis* (Diederich, 2005). Afterwards, consequences on the density and diversity of species, which were formerly associated with indigenous monospecific *M. edulis* beds, were also considered (Kochmann et al., 2008; Markert et al., 2010). The general outcome was, that the transformation from mussel beds to mixed reefs can cause density shifts of single resident species but neither native mussels nor associated species were suppressed.

However, besides investigations on species and community level, only very few studies deal with potential changes in species interactions within bivalve aggregations after the transition from pure blue mussel beds to mixed reefs of oysters and mussels in the Wadden Sea (Waser et al., 2015).

An important process within former blue mussel beds was related to the grazing activity of snails *Littorina littorea* (L.), which achieved high densities of several hundreds of snails per m^{-2} (Albrecht, 1998). The snails consumed epibionts attached to the mussel shells and thereby regulated the occurrence of sessile algal and invertebrate species such as barnacles, which usually use *M. edulis* shells as a suitable settlement substrate (Buschbaum, 2000). In the context described above, the following questions arose: Has the transformation from blue mussel beds to mixed reefs caused changes in snail abundances? To what extent is the snail grazing activity on sessile associated organisms still a community shaping species interaction within the newly developed mixed reefs of mussels and oysters?

To analyze the long-term density development of *L. littorea* on bivalve aggregations in the northern Wadden Sea, we used abundance data provided by an ongoing monitoring program and compared snail densities over a time period of 18 years. To examine grazing effects of snails in present oyster reefs we performed a manipulative field experiment and measured the recruitment success of the acorn barnacle *Semibalanus balanoides* L. on Pacific oyster shells at different snail densities. We hypothesized, that due to the similar physical structure and only available major natural hard substrate in the Wadden Sea, oyster reefs also provide a suitable habitat for *L. littorea*. Therefore, we additionally hypothesized that the change from mussel beds to mixed reefs did not negatively affect snail population dynamics. If so, *L. littorea* would still play an important role for the population dynamics of many associated species within bivalve aggregations in the sedimentary south-eastern North Sea and our study would show that introduced bio-engineers can modify native habitats but not consequently the existing species interactions.

2. Material and methods

2.1. Study area

Investigations and experiments were performed in a tidal basin located between the German island of Sylt and the Danish island of Rømø in the northern Wadden Sea (called List Tidal Basin, Fig. 1). Intertidal flats of the area are dominated by sand and make up to about 40% of the total basin. Tides are semidiurnal with a mean tidal range of about 2.0 m. The mean water temperature is 4 °C in winter and 15 °C in summer with an average salinity of 30. For a more detailed description of biota, geology, hydrography and sediments of the survey area, see Austen (1994), Reise et al. (1994) and Gätje and Reise (1998).

In the past, about 1% of the intertidal zone of the basin was covered by epibenthic mussel beds but they have been densely populated by introduced Pacific oysters *Magallana gigas* since the beginning of the 2000s (Reise et al., 2017a). Nowadays, all former mussel beds have changed to mixed reefs of mussels and oysters, which also caused the development of a newly multi-layered biotic structure with most blue mussels occurring underneath a canopy of oysters near the bottom of the reef (Buschbaum et al., 2016; Reise et al., 2017a). A detailed description of the Pacific oyster invasion trajectory in the northern Wadden Sea, the reef development and reef ecology is given by Reise et al. (2017a, b).

Like monospecific mussel beds in the past, current mixed reefs represent the only major natural hard-bottom habitats in the Wadden Sea. They show a specific community and mussel and oyster shells are regularly colonized with sessile species such as the non-native Australian barnacle *Austrominus modestus* (Darwin, 1854) and the Acorn barnacle *Semibalanus balanoides* (L.). Additionally, due to good food and living conditions some mobile species such as the gastropod *Littorina littorea* reach high densities within these biogenic structures throughout the entire Wadden Sea (Thieltges et al., 2013). They have the ability to control patterns of distribution and abundance of associated sessile species due to their grazing and bulldozing activity on the bivalve shells (Buschbaum, 2000).

2.2. Density development of Pacific oysters, native Littorina littorea and blue mussels

To analyze the long-term density patterns of introduced *M. gigas*, native *L. littorea* and blue mussels in the northern Wadden Sea, we selected two representative sites near the island of Sylt where former *M. edulis* beds have been changed to mixed reefs of mussels and Pacific oysters (Fig. 1). At both sites (A and B), investigations on oyster, snail and blue mussel densities started in 1999, i.e. before the massive spreading of *M. gigas.* Since then, oyster, snail and blue mussel abundances were determined on an annual basis in summer from August to September (except for the time period 1999–2002 at site A for oysters and 1999 at site B for snails, when no data were recorded).

Density quantification was done by using a tube corer with a diameter of 12 cm (113 cm^2 sampling area), which was randomly pushed 30 cm deep in the bivalve aggregations. The obtained samples were washed over a 1 mm sieve and all remained *L. littorea*, *M. gigas* and *M. edulis* were counted. Number of replicates per mussel bed/oyster reef and sampling date varied from 10 to 25 (Table 1). These regular and still ongoing investigations were conducted in the frame of a long-term blue mussel bed monitoring program in the Wadden Sea initiated by the federal state Schleswig Holstein, which provided blue mussel, snail and oyster densities data for this study.

2.3. Grazing experiment

To examine the effect of periwinkle grazing activity on barnacle recruitment success in newly developed mixed reefs of mussels and oysters, we conducted a field experiment with different snail densities. A natural density of 300 snails m^{-2} was taken as a basis to define the number of *L. littorea* per treatment. This value lies within the natural density variability of *L. littorea* in the area (Saier, 2000). All snails had a size from 8 to 12 mm shell height (measured from base to apex). For periwinkle density manipulation, we used circular cages (32 cm in diameter, 20 cm high) made of polyethylene mesh (mesh size 0.5 cm). Plastic rings stabilized the upper and downer end of the cages. All cages

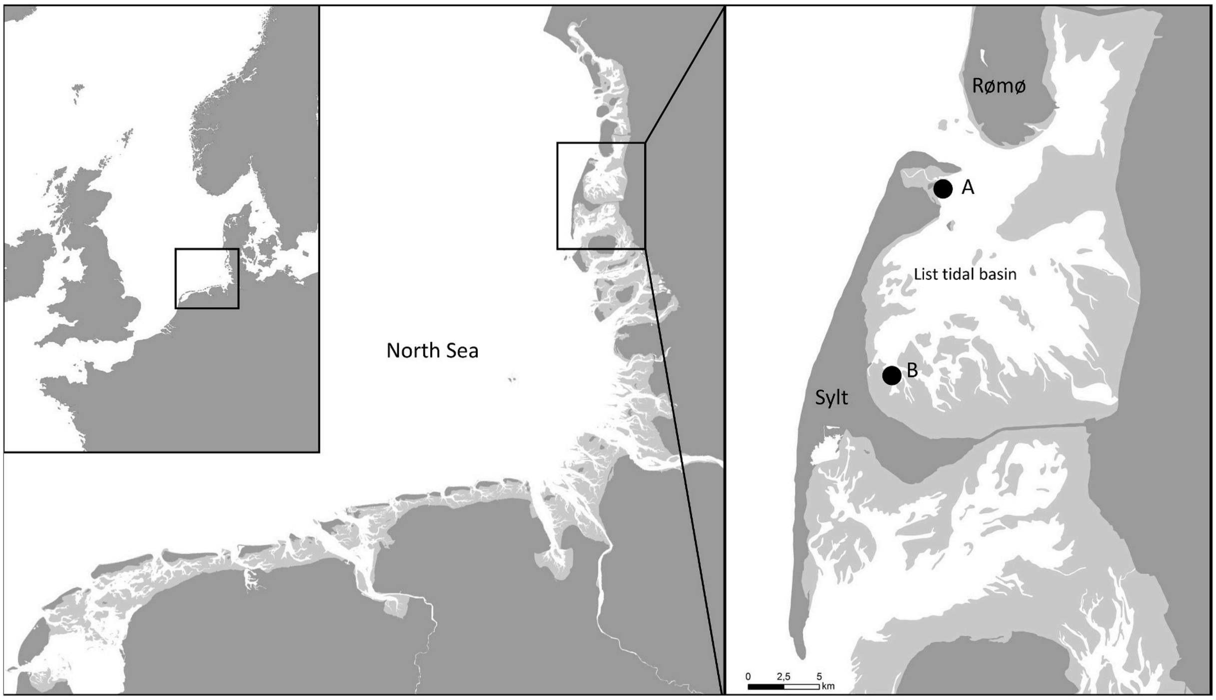

Fig. 1. The Wadden Sea coast in the south eastern North Sea (left). Sampling (A and B) and experimental (A) sites are located at the leeside of the island Sylt.

were fixed in the sediment with six iron rods per cage (50 cm length; 6 mm in diameter). The cage top was also covered with the polyethylene mesh to prevent snail migration and to keep periwinkle density constant for the experimental period in spring 2015. Each cage contained 25 *M. gigas* with a shell length from 8 to 18 cm. This number of oysters completely covered the encaged bottom area of $804\ \text{cm}^{-2}$. In the field experiment, we only used Pacific oysters as settlement substrate for barnacles because blue mussels mainly occur in deeper layers of these newly developed mixed reefs while most oysters stay on top. Near the bottom, *M. edulis* finds a refuge from barnacle epibionts because barnacle larvae preferentially settle on oysters at the top layer (Buschbaum et al., 2016). Additionally, *L. littorea* is more abundant at the top than at the bottom of an oyster reef (Goedknegt et al., 2020) and, therefore, our experimental set-up represents the current natural conditions in our study area. Oysters were collected from a reef close to the experimental site and all epibionts were carefully removed with an oyster knife and a brush before the beginning of the experiment. Six experimental treatments were established:

1. No snails in the cages
2. Reduced natural density of snails (12 snails per cage)
3. Natural snail density (24 snails per cage)
4. Three-fold natural density of snails (72 snails per cage)
5. Open cages with 5 holes in the walls (cage control)
6. A control without a cage but with a plastic ring to hold the oysters in place

The cages were randomly distributed in the field in a distance of about 30 m to an oyster reef at site A, where the oysters were collected for the experiment. After an experimental period of 25 days (April 10th – May 05th 2015) most *S. balanoides* had settled and barnacle epigrowth on the shells was determined by using a method similar to Bertness (1984) and Buschbaum (2000). We placed a clear sheet of PVC (same diameter of the cages) with 100 randomly distributed holes of 4 mm on top of the cages after removing the roofs and snails within the cages. Afterwards, we counted the holes with balanids visible underneath and obtained the barnacle percent cover per cage, which was a rough estimate of barnacle recruitment success within the cages. All treatments were six-fold replicated ($n = 6$ per condition). However, in the course of the experiment one cage of the no snail treatment and one cage of the natural snail density treatment were lost. Thus, only five replicates of these treatments were used in the analysis at the end of the experiment.

2.4. *Statistical analysis*

All analyses were performed in the R statistical environment, version 1.1.463 (R. Core Team, 2017). Results were calculated as mean values with standard error (SE). Correlations between *M. gigas* or *M. edulis* density and *L. littorea* density data at site A and B, respectively, were analysed for years in which density data for all three species were available. To test for a correlation between oyster and blue mussel densities as well as between *M. gigas* or *M. edulis* against *L. Littorina* densities, we used the R function ‘cor.test’ (method = “spearman”). The correlation between one bivalve species density and *L. littorea* density in dependence on the other bivalve species density was conducted with the partial rank correlation method of Spearman and we used the function ‘pcor.test’ provided by the ‘MASS’ package in R. The snail grazing experiment was analysed by means of analysis of variance (ANOVA). Cochran’s test was used to test for heterogeneity of variances. Due to homoscedasticity of variances no data transformation was applied. Different snail densities as experimental factor and dependent barnacle recruitment were analysed by using the Tukey’s Honest-Significant-Difference (HSD) multiple comparison test. Effects were considered to be statistically significant, if p-value was <0.05.

3. Results

3.1. *Long-term density patterns of Pacific oysters, native blue mussels and native Littorina littorea*

At both sites, Pacific oyster, blue mussel and snail densities showed temporal fluctuations (Fig. 2).

The establishment phase of *M. gigas* in the northern Wadden Sea began in the early 1990s but abundances remained rather low until 2001 (Reise et al., 2017b) and first densities higher than 100 ind. m^{-2} were detected at site A and site B in 2003 (Table 1). At both sites, Pacific

Table 1
Densities (mean value ± standard error) of *Littorina littorea*, *Magallana gigas* and *Mytilus edulis* at site A and site B in the time period from 1999 to 2017. Number of samples (n) per site and year varied from 10 to 25.

		Littorina littorea (ind. m^{-2})		*Magallana gigas* (ind. m^{-2})		*Mytilus edulis* (ind. m^{-2})	
year	number of samples (n)	site A	site B	site A	site B	site A	site B
1999	10	97 ± 294	no data	no data	9 ± 27	1381 ± 803	2920 ± 1403
2000	10	265 ± 374	212 ± 612	no data	18 ± 36	1080 ± 596	2708 ± 1880
2001	10	150 ± 222	106 ± 215	no data	9 ± 27	1071 ± 770	2106 ± 1284
2002	10	372 ± 277	186 ± 106	no data	9 ± 27	1504 ± 369	1850 ± 1296
2003	25	312 ± 294	227 ± 240	294 ± 278	146 ± 201	1552 ± 633	2170 ± 1257
2004	23	419 ± 355	297 ± 352	485 ± 312	248 ± 254	1116 ± 553	1975 ± 1472
2005	25	340 ± 291	188 ± 248	442 ± 282	432 ± 515	1257 ± 849	1490 ± 1248
2006	25	297 ± 393	219 ± 232	903 ± 1028	1338 ± 939	1501 ± 913	1085 ± 707
2007	25	556 ± 542	191 ± 255	1607 ± 966	2011 ± 718	1310 ± 611	694 ± 562
2008	25	428 ± 411	223 ± 289	793 ± 346	1207 ± 480	899 ± 570	793 ± 542
2009	25	701 ± 513	190 ± 187	588 ± 231	960 ± 489	896 ± 423	633 ± 273
2010	20	367 ± 405	442 ± 467	677 ± 846	274 ± 376	690 ± 292	1584 ± 966
2011	25	446 ± 242	234 ± 228	644 ± 345	340 ± 263	1522 ± 730	1781 ± 874
2012	25	223 ± 191	110 ± 141	425 ± 490	375 ± 219	1614 ± 995	2396 ± 1204
2013	25	290 ± 202	127 ± 173	195 ± 164	1175 ± 938	1225 ± 527	2227 ± 1366
2014	25	110 ± 156	156 ± 156	662 ± 563	591 ± 643	1012 ± 710	487 ± 405
2015	25	205 ± 274	262 ± 261	694 ± 513	1030 ± 583	1377 ± 1097	1003 ± 1061
2016	25	57 ± 88	177 ± 191	99 ± 123	283 ± 250	1332 ± 1200	518 ± 263
2017	25	216 ± 294	135 ± 172	181 ± 168	223 ± 164	1427 ± 1219	716 ± 565

oyster abundance increased until 2007 and more than 1500 ind. m^{-2} were reached. Afterwards, *M. gigas* densities decreased but increased again in 2014 until 2016 at site A and in 2011 until 2013 at site B, which was followed by a density decrease at both sites until 2017. Thus, site A and B showed some similarities in temporal density pattern of *M. gigas*.

Mean blue mussel abundance at site A was between 1000 and 1500 ind. m^{-2} from 1999 to 2007 (Table 1). Similar densities were quantified from 2011 to 2017. From 2008 to 2010, mussel densities were a bit lower with 600 and 800 ind. m^{-2}. Thus, the density of *M. edulis* at site A remained rather stable during the investigation period.

At site B, mussel densities showed higher fluctuations with highest densities of about 2900 ind. m^{-2} at the beginning of the investigation period in 1999 and lowest densities with about 500 ind. m^{-2} in 2014 (Table 1). We did not find any significant correlation between oyster and mussel densities, neither at site A (Spearman correlation $R = -0.204$, $p = 0.466$) nor at site B (Spearman correlation $R = -0.457$, $p = 0.056$).

Mean densities of *L. littorea* showed different patterns at both study sites and varied over the investigation period from about 50 to 700 ind. m^{-2} at site A and 100 to 450 ind. m^{-2} at site B, respectively (Table 1). At site A, we did not detect any significant correlation between *M. gigas* and *L. littorea* densities (Spearman correlation $R = -0.060$, $p = 0.832$) and also not between *M. edulis* and *L. littorea* densities (Spearman correlation $R = -0.311$, $p = 0.260$). At site B, we found the same pattern with no significant correlation between *M. gigas* and *L. littorea* densities (Spearman correlation $R = 0.274$, $p = 0.272$) and no significant correlation between *M. edulis* and *L. littorea* densities (Spearman correlation $R = -0.183$, $p = 0.467$).

Additionally, factoring in the density of mussels did not change the correlation between oyster and snail densities (partial Spearman correlation site A: $R = -0.003$, $p = 0.992$; site B: $R = -0.217$, $p = 0.401$), nor did the density of oysters affect the correlation between mussels and snails (partial Spearman correlation site A: $R = -0.305$, $p = 0.288$; site B: $R = -0.067$, $p = 0.798$).

3.2. *Grazing effects on newly-settled barnacles*

Barnacle coverage on oyster shells (i.e. barnacle recruitment success) was significantly different between the manipulated *L. littorea* density treatments (one-way ANOVA, $F = 86.5$, $df = 1$, $p < 0.001$, Fig. 3). Most barnacles recruited at the absence of snails (71.8 ± 5.26% barnacle coverage) and barnacle coverage decreased with increasing snail densities with lowest barnacle occurrence at a three-fold natural snail density (29.83 ± 5.91% barnacle coverage). The mean percentage of recruited barnacles differed significantly between the four treatments with manipulated snail densities (Tukey's test $p < 0.02$ for all pairwise comparisons), except for the comparison of reduced and natural snail density, where no statistical difference between barnacle percent coverage was detected (Tukey's test $p = 0.704$).

Additionally, we detected significant differences in barnacle coverage between the natural snail density treatment, open cages and untreated areas with highest barnacle coverage in the natural snail density treatment (one-way ANOVA, $F = 117.4$, $df = 1$, $p < 0.0001$; Tukey's test $p < 0.002$ for all pairwise comparisons).

At the end of the experiment all snails in the cages were found. Thus, snail densities of the different treatments were constant during the experimental period.

4. Discussion

Our long-term analysis of Pacific oyster, native *M. edulis* and *L. littorea* densities at two bivalve aggregations in the northern Wadden Sea does not show any correlation between these three species. Therefore, population dynamics of Pacific oysters, blue mussels and *L. littorea* seem to be independent from each other at our study sites. The field experiment on the ecological function of *L. littorea* within Pacific oyster reefs reveals that snail grazing and bulldozing activity is an important factor affecting barnacle overgrowth on oyster shells in these newly developed structures.

4.1. *Long-term density pattern of Littorina littorea on epibenthic bivalve aggregations*

Before the introduction of the Pacific oyster into the European Wadden Sea, blue mussel beds already represented a preferred habitat

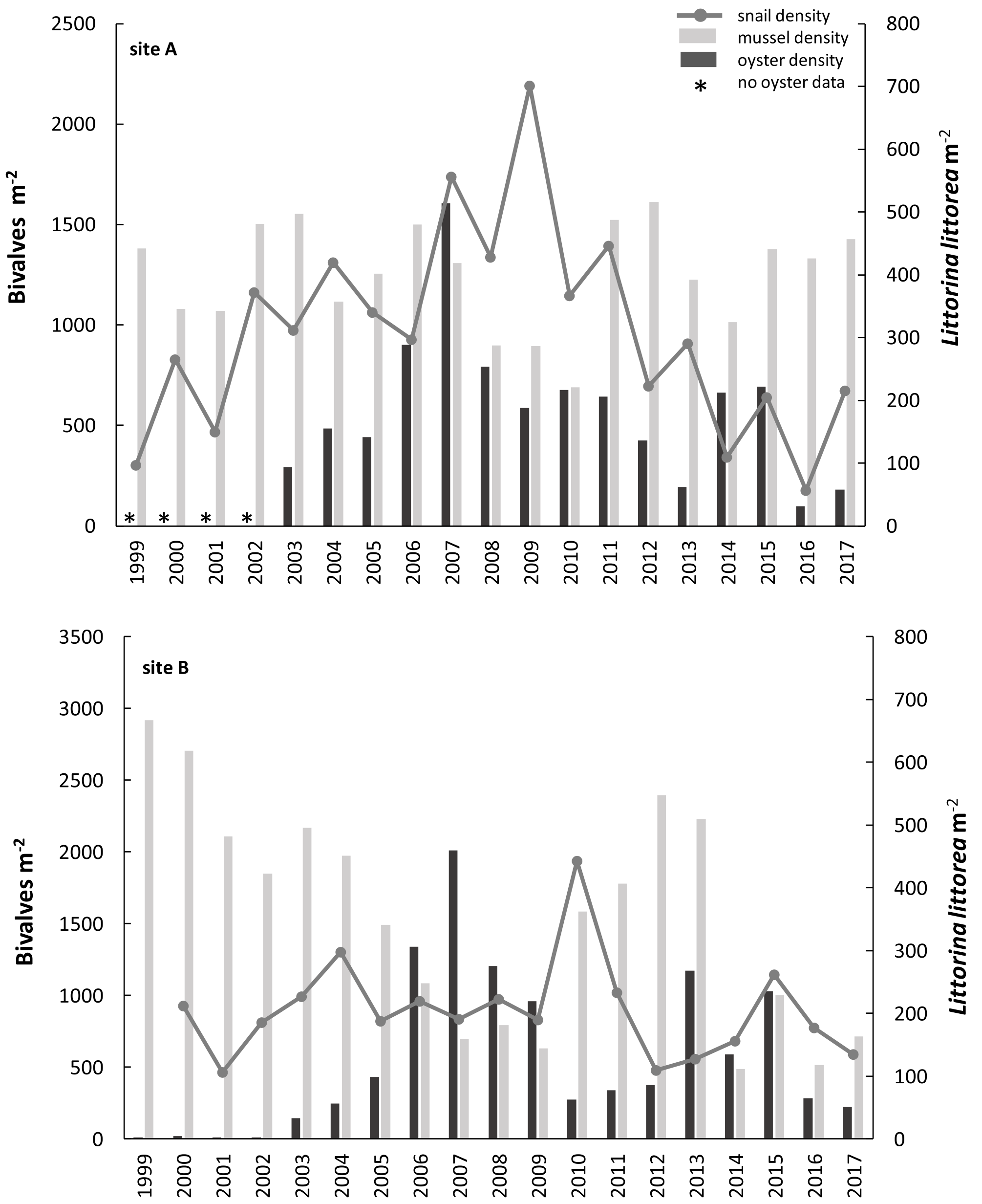

Fig. 2. Mean densities (individuals m^{-2}) of *Littorina littorea* (line), blue mussels *Mytilus edulis* and Pacific oysters *Magallana gigas* (bars) at two locations (site A and B) in the northern Wadden Sea near the island of Sylt from 1999 to 2017.

for native *L. littorea*. Here, snails achieved much higher densities than in the surrounding sedimentary areas (Wilhelmsen and Reise, 1994; Buschbaum, 2000), because epibenthic bivalve aggregations provide suitable food conditions and an appropriate attachment substratum. However, densities of *L. littorea* associated to epibenthic biotic structures may show strong interannual fluctuations, which may be caused by variations in snail recruitment success, varying predation intensity by e.g. crabs (Scherer and Reise, 1981), infestation by parasites (Lauckner, 1984; Eschweiler et al., 2009) and overgrowth on *L. littorea* shells by epibionts (Eschweiler and Buschbaum, 2011). For example, Thieltges and Buschbaum (2007) show that shell-boring polychaete worms facilitate detrimental barnacle fouling on *L. littorea.* Additionally, shell-boring worms reduce the shell strength of *L. littorea* and thereby indirectly increase predation pressure on infested snails in comparison to uninfested snails (Buschbaum et al., 2007). Thus, population dynamics of *L. littorea* are affected by a variety and interacting factors.

The introduction, establishment and spread of *M. gigas* on native blue mussel beds in the intertidal zone of the Wadden Sea caused a transformation of the existing biotic habitat because the mono-dominance of resident mussels has turned into co-dominance of *M. edulis* and Pacific oysters (Reise et al., 2017a). This shift was associated with the development of novel, multi-layered mixed reefs with most *M. edulis* occurring near the bottom of the reef. Blue mussels migrate actively to deeper layers, where they are better protected against predation and detrimental barnacle epibionts relative to more exposed positions (Eschweiler and Christensen, 2011; Waser et al., 2015; Buschbaum et al., 2016). Since the beginning of the 2000s, the reef structure has become more and more complex because Pacific oyster abundances strongly increased and already settled individual oysters attained larger sizes while shell material of dead oysters accumulated within the reef (Reise et al., 2017a). Additionally, attachment of juvenile *M. gigas* was highest to conspecifics at the upper end of the reef, which caused the current specific distribution pattern with a dominance of oysters in the top-layer (Fig. 4). Overall, the three-dimensional oyster matrix exceeds the structural complexity of former pure mussel beds and increases the surface available for epifauna and algae (Lejart and Hily,

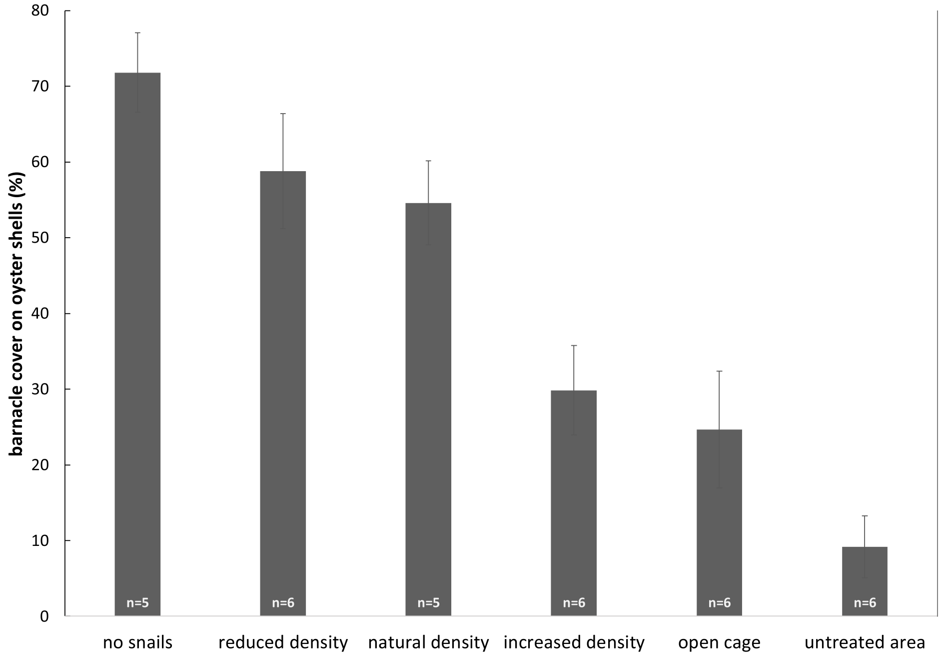

Fig. 3. Mean percentage of barnacle cover (±standard error) on shells of Pacific oysters *Magallana gigas* in treatments with different densities of *Littorina littorea* after an experimental period of three weeks in May 2015.

2011). Therefore, we expected that associated species such as *L. littorea* are also affected and show changes in their densities, because it is described from several coasts worldwide that successfully established *M. gigas* populations may alter the abundance and distribution of native species (Troost, 2010; Green and Crowe, 2014). Indeed, Kochmann et al. (2008) found significantly higher densities of snails in experimentally constructed monospecific oyster reefs than in beds only consisting of mussels in the northern Wadden Sea. A similar pattern was detected by Markert et al. (2010) on a bivalve aggregation located near the island of Juist in the southern Wadden Sea, where *L. littorea* density was also higher on oyster dominated areas in comparison to areas with mussel dominance. Higher *L. littorea* densities with increasing oyster coverage on mussel beds was also found by Green and Crowe (2014) at the coast of Northern Ireland.

In contrast to these short-term studies, we did not detect such a relationship by our long-term analysis on snail and oyster densities at our two study sites in the northern Wadden Sea. Presumably, such a relationship would also not have been detected when considering oyster coverage or biomass, because these parameters correlate with oyster densities in the study area (Reise et al., 2017b). Because of the complex structure which provides more shelter it is quite possible that *L. littorea* prefers oyster dominated bivalve aggregations in comparison to mussel beds without oysters when given the choice between both habitat types. Nevertheless, in the long run snail population dynamics have not been affected and Pacific oyster establishment did not cause an expected increase of *L. littorea* densities. Even if oyster reefs may potentially harbor higher densities of *L. littorea*, density patterns of *L. littorea* are presumably still more controlled by other already mentioned biotic factors such as reproduction success, parasite infection, overgrowth by epibionts and predation pressure (Buschbaum and Reise, 1999; Buschbaum et al., 2007). These factors may conceal the facilitative effects of *M. gigas* for *L. littorea*. For example, Markert et al. (2010) found a strongly increased number of predatory crabs in oyster reefs in comparison to mussel patches.

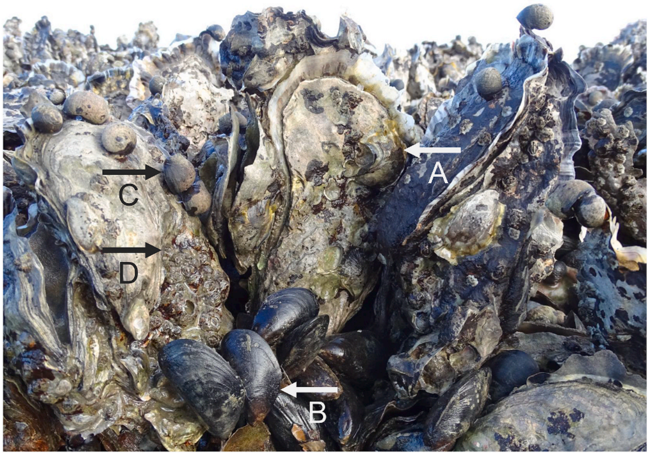

Fig. 4. Multi-layered structure of a Pacific oyster reef in the northern Wadden Sea with introduced Pacific oysters *Magallana gigas* (A) at the top-layer and native blue mussels *Mytilus edulis* (B) mainly occurring near the bottom. Periwinkles *Littorina littorea* (C) achieve high densities in this biogenic habitat and graze on young stages of barnacles (D) being attached to the bivalve shells.

Despite the large-scale establishment of Pacific oysters on native blue mussel beds, total bed area of epibenthic bivalve aggregations showed no strong fluctuations in the entire Wadden Sea ecosystem and is nowadays not higher than before the oyster introduction (Folmer et al., 2014, 2017). Therefore, we conclude that also on a large spatial scale the change from pure blue mussel beds to mixed reefs of native *M. edulis* and introduced *M. gigas* was hitherto without strong effects on the population dynamics of associated *L. littorea*.

4.2. *Grazing effects of Littorina littorea on newly established oyster reefs*

Invertebrate grazers and especially gastropods are known to structure species communities in many rocky and sedimentary coastal ecosystems (Anderson and Underwood, 1997; Poore et al., 2012). This is also the case in the Wadden Sea, where *L. littorea* represents one of the most common benthic grazers, which colonizes most available natural (e.g. sedimentary tidal flats) and artificial habitats (e.g. boulders used for coastal protection measures) in the intertidal zone but achieves highest densities on epibenthic bivalve aggregations.

It has been revealed for former native blue mussel beds, that the snails feed on microalgal films covering the bivalve shells and that *L. littorea* consume attached epibionts (Wilhelmsen and Reise, 1994; Albrecht, 1998; Buschbaum and Reise, 1999). Fenske (1997) suggested that the high availability of food resources and living space on mussel aggregations in the Wadden Sea prevented intraspecific competition in *L. littorea*, which may explain the high abundances observed in this habitat in comparison to e.g. bare sedimentary areas.

Indeed, snail densities of up to 2000 individuals m^{-2} have been observed (Saier, 2000) and caused a strong grazing pressure with regulating effects on the occurrence of ephemeral algae and of barnacles (Albrecht, 1998; Buschbaum, 2000). For this reason, we considered the barnacle species *Semibalanus balanoides* as a suitable model organism to test whether *L. littorea* still plays a structuring role for associated organisms in novel oyster reefs. An experimental reduction of grazing and bulldozing pressure by *L. littorea* resulted in increased barnacle recruitment in our study, while barnacle numbers decreased with increasing snail density. Thus, our results show the same relation between snail densities and barnacle recruitment in oyster reefs as Buschbaum (2000) found in blue mussel beds. Interestingly, we found a significant higher barnacle coverage in the treatment with natural snail densities in the cages in comparison to open cages and untreated areas. This indicates that besides snail grazing and bulldozing pressure further factors may have affected barnacle recruitment success, which may have caused low barnacle coverage in the open cages and untreated areas. By using cages, we did not only manipulate snail densities but also excluded further potential consumers of barnacles such as crabs and fish. These predators had access to the open cages and untreated areas in our experiment and, therefore, may have additionally reduced barnacle coverage in these treatments.

Pacific oysters did not only change the morphological characteristics of mussel beds as a whole but also the oyster shells themselves show a different texture than *M. edulis* shells. Besides the larger size, the shell surface of *M. gigas* is much rougher, which may facilitate the attachment of other organisms including barnacles, because barnacle cyprid larvae are known to be attracted by uneven surfaces at settlement (Crisp and Barnes, 1954; Chabot and Bourget, 1988). This may result in a high epibiotic load of individual *M. gigas*, which might cause detrimental effects like reducing oyster growth rates and condition (e.g. Arakawa, 1990; Royer et al., 2006). Such an effect was shown for blue mussels when overgrown with barnacles in the Wadden Sea (Buschbaum and Saier, 2001) and is, therefore, also very likely for *M. gigas* in the area.

Our long-term analysis reveals that *L. littorea* densities in the newly established oyster reefs are similar to snail densities in former monospecific blue mussel beds. Additionally, the field experiment shows that grazing and bulldozing activity of *L. littorea* still represents an important functional trait of snails on oyster reefs in the Wadden Sea. It reduces and may control the recruitment success of barnacles on Pacific oyster shells but presumably also of other harmful epibionts such as macroalgae (Albrecht, 1998; Guitérrez and Palomo, 2016). This question is worth to be investigated in future studies.

Considering biodiversity in the Wadden Sea, introduced ecosystem engineering Pacific oysters have transformed native mussel beds into completely new structured habitats, but the novel mixed reefs do not constitute a threat to the resident associated species occurrence, because no native species was outcompeted (Kochmann et al., 2008). On the contrary, the reef structures also facilitate the occurrence of some resident organisms (Markert et al., 2010). As a consequence, former key species interactions still take place as our field experiment on *L. littorea* and barnacles shows. The still existing mechanisms are also of advantage for the invader itself, because snails make no difference between a mussel or oyster shell and curtail the epibiotic load on the shell surface on both species by their grazing and bulldozing activity. Thus, since Pacific oysters have been introduced into the Wadden Sea, they have found in *L. littorea* a domestic partner with mutual benefits.

Author statement

Annika Cornelius and Christian Buschbaum conducted all field and writing work for this manuscript together with equal shares of total work.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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