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Invading oysters and native mussels: from hostile takeover to compatible bedfellows

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Abstract. Unintended species introductions may offer valuable insights into the functioning of species assemblages. A spectacular invasion of introduced Pacific oysters *Magallana* (formerly *Crassostrea*) *gigas* in the northern Wadden Sea (eastern North Sea, NE Atlantic) has relegated resident mussels *Mytilus edulis* on their beds to subtenant status. At the beginning of feral oyster establishment, mussel beds offered suitable sites with ample substrate to settle upon. After larval attachment to mussels, the fast-growing *M. gigas* overtopped and smothered their basibionts. With increasing Pacific oyster abundance and size, oyster larvae preferentially settled upon oysters, and the ecological impact of the invaders on the residents changed from competitive displacement to accommodation of mussels underneath a canopy of oysters. Oysters took the best feeding positions while mussels received shelter from predation and detrimental epibionts. The resident's mono-dominance has turned into co-dominance with an alien, persisting in novel, multi-layered mixed reefs of oysters with mussels, which we term "oyssel reefs." The first 26 yr of the Pacific oyster's conquest of mussel beds in the northern Wadden Sea may question the overcome notions of natural balance, superiority of pristine over novel species combinations, and of introduced alien species threatening biodiversity and ecosystem stability in general.

Key words: coexistence; competition; ecosystem engineering; facilitation; invasive species; *Magallana;* (*Crassostrea*) *gigas Mytilus edulis;* Wadden Sea.

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INTRODUCTION

In spite of the ecological insights that have been inferred from species invasions (Sax et al. 2005, 2007), invasions and impacts of nonnative species are usually considered a great threat to biodiversity and ecosystem functioning (Simberloff et al. 2013, Murcia et al. 2014, Wilson 2016). However, it has also suggested that biological globalization, caused by human-mediated breakdown of barriers to natural dispersal, may often be adaptive to other challenges of the Anthropocene such as global warming (Davis et al. 2011, Ellis et al. 2012, Corlett 2015).

While introduced predators and pathogens have often caused dramatic declines or even extinctions in resident prey, competition from introduced plants has rarely caused large-scale displacements or extinctions in resident plant species (Davis 2003, Gurevitch and Padilla 2004, Sax and Gaines 2008, Simberloff 2011). Like in plants, one may assume that introduced suspension-feeding bivalves tend toward modest effects on resident species. Although sharing a common resource, variable conditions in space and time may lead to niche partitioning. However, introduced bivalves can have strong effects on resident bivalves by developing mono-dominance (Nichols et al. 1990, Strayer et al. 1999, Crooks 2001, Branch and Steffani 2004, Sousa et al. 2009). How can alien bivalves outperform native ones, which evolved in interaction with their home environment for a long time? May the introduction of alien bivalves eventually entail the extinction of native ones with a possible time lag (Sax and Gaines 2008)?

We investigated the effects of Pacific oysters *Magallana gigas* (Thunberg 1793; Salvi et al. [2014] divided the former genus *Crassostrea* into Pacific *Magallana* and Atlantic *Crassostrea* species based on large genetic divergence) settling on Atlantic mussels *Mytilus edulis* L. in the sedimentary Wadden Sea (eastern North Sea, NE Atlantic). We attempt to explain the relation between invading oysters and resident mussels throughout the first 26 yr of invasion. In 1986, a sea-based oyster farm located near the island of Sylt began introducing about one million half-grown *M. gigas* from British hatcheries via an Irish oyster nursery. Five years later, we found first feral oysters on mussel beds near the farm (Reise 1998, Reise et al. 2017). Pacific oysters and native mussels are both gregarious epibenthic suspension feeders and have planktonic larvae drifting about one month in coastal currents. In soft-sediment environments, both require living or dead shells as substrate for attachment, where they turn out to be strong ecosystem engineers (Diederich 2005, Fey et al. 2010, Markert et al. 2010, Troost 2010, Commito et al. 2014).

The successful settlement of *M. gigas* on crowded mussel beds seems to be a paradox. According to Gause's principle and implicit in Darwin's writing, similar species with similar food requirements and living at the same places should exclude each other unless habitat heterogeneity allows for niche partitioning (Hutchinson 1978:152 ff; Fig. 1A). This may be the case in introduced Pacific oysters and Atlantic mussels. Similar to fouling barnacles, young oysters attached to adult mussels but unlike barnacles, oysters outgrew their basibionts and smothered overgrown mussels to death, suggesting a high potential for competitive displacement. However, slight dissimilarities in traits (Table 1), variable habitat conditions and food supplies, may lead to sharing the common resources (Fig. 1B). Furthermore, if invaders are capable habitat modifiers (ecosystem engineers sensu Jones et al. 1994), potentially competing residents or other invaders may be supplied with new habitats (Wonham et al. 2005, Sousa et al. 2009, Green et al. 2012), and competitive exclusion can be averted (Fig. 1C).

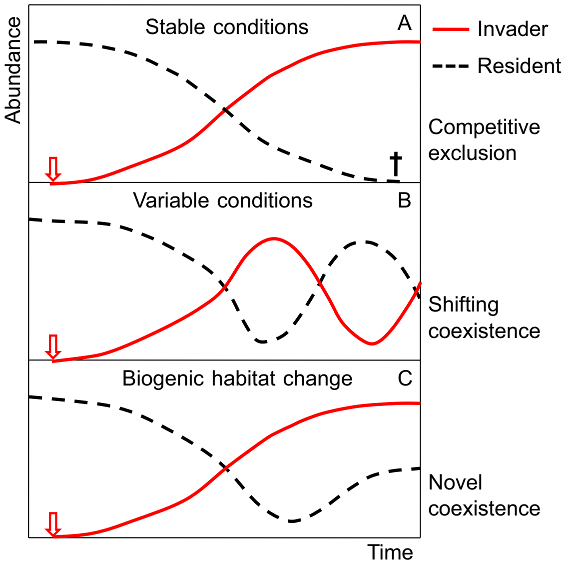

Fig. 1. Competition trajectories of invader and resident populations leading to (A) the exclusion of an inferior resident in rather homogeneous and stable habitats, (B) shifting coexistence in heterogeneous and variable habitats, or (C) novel coexistence through biogenic habitat modification. Arrow indicates arrival of invader.

With this study, we challenge the expectation that Pacific oysters will ultimately exclude

Table 1. Selected differences in traits between Atlantic mussels *Mytilus edulis* and Pacific oysters *Magallana gigas* as observed in the Wadden Sea (Diederich 2005, Troost 2010, Dankers and Fey-Hofstede 2015, Reise et al. 2017).

Traits	*Mytilus edulis*	*Magallana gigas*
Shell shape	Almost constant	Highly adaptable
Shell growth in 1st year (mm)	Up to 30	Up to 90
Shell max. length (mm)	Up to 90	Up to 330
Shell thickness (mm)	Up to 2	Up to 24
Attachment to substrate	Flexible with threads	Rigidly glued
Spawning time	Spring to autumn, mainly in May	July–August
Spawning temperature (°C)	>12	>18
Juvenile settlement	All year, mainly May–July	August–October
Life span (years)	Up to 10	Up to 20 or more

Atlantic mussels from the Wadden Sea. Our hypothesis of perpetual coexistence is tested by analyzing the invasion history over the first 26 yr. Specifically, we ask whether (1) settling preference of oysters has changed over time, (2) mussels find any refuge inside or outside the zone of oyster dominance, (3) dominance of oysters could have positive side effects on mussels, and (4) oyster and mussel traits could lead to persisting co-dominance of oysters and mussels. Methodically, we combine observations on current abundance variation in time and space with past abundances inferred from digging through layers of past shell deposits. For causal inferences, we link our observations with published experiments conducted in the same area.

STUDY AREA AND METHODS

The study area and its biota at the leeside of a barrier island (Sylt in the eastern North Sea) in the cold temperate zone are described in detail in Gätje and Reise (1998). Tides are semi-diurnal with amplitudes of 2 m, exposing wide flats of mud and sand (Fig. 2). About half of the high tide volume in the tidal basin between barrier island and mainland is exchanged each tide with the coastal North Sea. Salinity remains close to 30. Severe winters with drifting ice shoals disturbing epibenthos in the tidal zone occurred on average every nine years, but their frequency is declining (Schmelzer et al. 2016). Mussel beds occur in muddy and sandy areas of the lower tidal zone and shallow subtidal, and have hardly

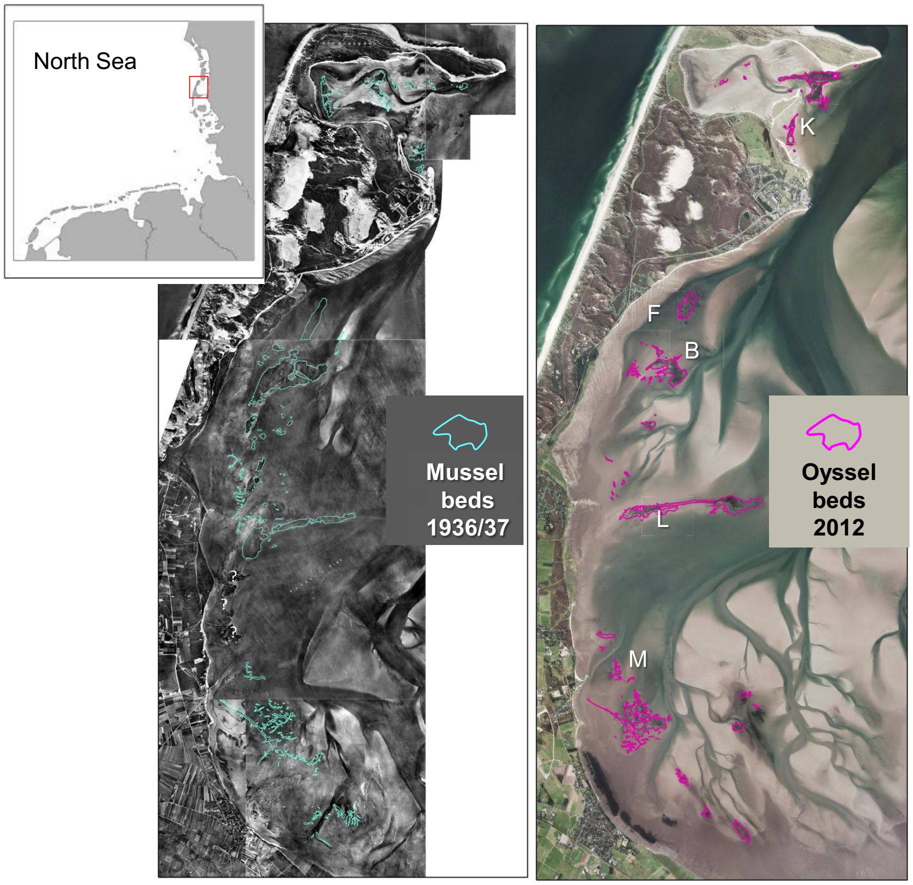

Fig. 2. Aerial photographs of northern Sylt with tidal flats exposed at low tide in 1936/37 with mussel beds (blue contours) and in 2012 with beds composed of mussels and oysters ("oyssel" beds, red contours). K, Königshafen; F, oysterfarm; B, Blidsel; L, Leghörn; M, Munkmarsch.

changed their spatial pattern since the 1930s (Büttger et al. 2014, Fig. 2).

This study commenced with the first feral Pacific oyster found attached to a mussel valve in 1991. This was about 4 km away from the only oyster farm in the region, founded in 1986. Introduced *Magallana gigas* are enclosed in net bags tied to trestles at low tide level (Reise 1998, K and F in Fig. 2, respectively). Outside the farm, mussel beds offer ample substrate for oyster attachment, covering about 0.3 km^2 of the sediment surface in the area. Other hard substrates like stones in a few places, the introduced hard structures of coastal defense, harbor walls, boats, or stray rubbish also provide attachment, but quantitatively this remained of minor importance relative to the extent of mussel beds.

In 1991 to 1996, we recorded substrate types to which feral oysters had attached. All oysters encountered on mussel beds and in their vicinity within the entire area were included (Reise 1998). With increasing abundance of feral oysters, also oysters themselves became important for attachment. Therefore, in July to September 2006, the survey was repeated but confined to six representative sites with beds composed of mussels and oysters. In January 2016, we surveyed a 1-km line at low tide level crossing beds of mussels and oysters and scattered clumps of oysters by recording the basibionts. The declining sample area from 1991–1996 to 2016 was a response to the increasing abundance of oysters.

In an attempt to study the succession of mussel beds to oyster reefs, holes were dug in 2016 with a spade at two beds with oysters and mussels (B and M in Fig. 2), down to a depth of 1 m. We chose these two sites because we visited them regularly since the oyster invasion had commenced, and thus know that mussels and later mussels and oysters covered these sites continuously. At a vertical side of the holes, we sieved consecutive layers of 0.15 m thickness and approximate cross-areas of 400 cm^2 through a 1-mm mesh. We identified unbroken shell material to species level, counted it, and measured maximum diameter. Due to the similarity of results between the two holes, we left it at two sites.

Mussel beds are highly variable in outer appearance and spatial extent. In predominating, flat beds, interspersed elevated ridges and hummocks can regularly be observed, and patches can occur from mean tide level to shallow subtidal (Kuenen 1942, Verwey 1952, van de Koppel et al. 2005). To capture variation in space, we chose to sample hummocks at top, slope, and bottom in July 2006 and again in April 2016. Selected representative hummocks were approximately 1 m in height with about half below and above mean low tide level, and visually dominated by mussels at the top and oysters at slopes and bottom. In 2006, samples of 400 cm^2 at the three levels were not replicated and taken at site B, and six replicates were taken in 2016 at site K (for B and K, see Fig. 2) to characterize the general pattern. We recorded biovolume in 2016 using calibrated beakers.

Oyster abundance and size on mussel beds were surveyed during low tide in 1995, 1999, and 2003 (Diederich et al. 2005). For this study on long-term dynamics of oyster and mussel abundances, a cluster of beds near Munkmarsch harbor (M in Fig. 2) was selected for annual sampling in August to September from 2001 to 2016 (Table 2). This site reflected the dynamics of mussel and oyster abundances in the entire tidal basin (Büttger et al. 2015). For oysters, the total sample area varied from 0.24 m^2 with six replicates in 2014 to 28.9 m^2 with 130 replicates in 2001. For mussels, samples of 0.04 m^2 were taken in 2003, 2006–2009, and from 2011 to 2016, with a total sample area varying from 0.16 m^2 with four replicates in 2007 to 0.52 m^2 with 13 replicates in

Table 2. Total sample size in m^2 with number of replicates (*n*) for oysters and mussels in the years 2001 to 2016 at a cluster of beds near Munkmarsch (M in Fig. 2).

Year	*Magallana gigas*	*Mytilus edulis*	Year	*M. gigas*	*M. edulis*
2001	28.90 (130)	0	2009	0.64 (16)	0.52 (13)
2002	10.00 (40)	0	2010	1.36 (34)	0
2003	3.00 (75)	0.20 (5)	2011	0.32 (8)	0.24 (6)
2004	2.80 (70)	0	2012	0.40 (10)	0.40 (10)
2005	1.60 (40)	0	2013	0.32 (8)	0.32 (8)
2006	0.24 (40)	0.24 (6)	2014	0.24 (6)	0.24 (6)
2007	1.20 (30)	0.16 (4)	2015	0.28 (7)	0.28 (7)
2008	0.56 (14)	0.20 (5)	2016	0.32 (8)	0.32 (8)

Note: At low oyster density, we inspected replicates of 0.25 m^2 visually from above, and at high oyster and mussel density, replicates of 0.04 m^2 were sieved.

2009. Inconsistencies were due to time constraints caused by returning tides. The lower size limit of young oysters taken into account was 20 mm Ø and for mussels 10 mm shell length.

To test whether effects of competition could be observed in this bed, we correlated mean mussel densities per year to oyster densities. Since the ice winter of 2009 led to a marked population crash of oysters, we added a factor grouping years into before and after the population decline into our model. To further investigate the direction of competitive interactions, we performed a phase shift analysis by correlating mussel densities to oyster densities up to three years before and after each observation and kept the model with highest explanatory power. All analyses were performed using the R statistical environment (R Core Team 2017).

RESULTS

Oyster attachment

Initially, most Pacific oysters attached to mussels (Table 3). Ten years later, in 2006, the successful establishment of *Magallana gigas* had changed mussel beds, with large oysters projecting beyond the layer of mussels, attracting now most of the competent oyster larvae which found ample attachment on oyster shells >100 mm on most beds (Fig. 3, Table 3). The important role of mussels as settlement substrate passed over to oysters themselves. This positive feedback process leads to oysters settling upon oysters, and after 20 yr, in 2016, *Mytilus edulis* became almost insignificant as attachment substrate, and mussels were released from the threat of getting smothered by attached oysters (Table 3, Fig. 7).

Table 3. Mollusk and barnacle shells with attached *Magallana gigas* on mixed mussel and oyster beds near the island of Sylt in 1991–1996 (n = 574 oysters; from Reise 1998), 2006 (n = 589), and 2016 (n = 598) in percent of identified basibiont shells.

Shell taxon	1991–1996	2006	2016
Mytilus edulis	88.3	18.2	2.5
Magallana gigas	0.3	65.7	94.5
Cerastoderma edule	3.3	2.2	0.3
Mya arenaria	3.1	0.3	0.8
Ensis (*directus*) *leei*	0.9	0.2	0.3
Ostrea edulis	0.7	0.0	0.0
Littorina littorea	1.8	0.8	1.2
Crepidula fornicata	0.5	0.8	0.0
Barnacles	1.1	11.7	0.3

From mussel beds to "oyssel reefs"

Underneath the living layer of oysters and mussels, excavations in 2016 revealed upright valves of oysters down to 0.35 m below mud surface, followed by 0.1 m with more or less horizontally deposited valves (Fig. 3 right). No valves of *M. gigas* were encountered below 0.45 m. Valves of mussels were abundant down to 0.15 m below mud surface, comparatively scarce from 0.15 to 0.3 m, and then abundant again from 0.3 to 0.7 m. Below, black mud deposits were abruptly replaced by gray sand containing valves of cockles *Cerastoderma edule*.

Mussels generate conspicuous hummocks by accreting mud and shell material. High hummocks were dominated by mussels at the top and by aggregates of oysters at slope and bottom (Fig. 4). A comparison between 2006 and 2016 revealed a similar pattern of mussels and oysters except that in 2016, mussel abundance was low at the subtidal bottom of hummocks. At the top, oysters remained much smaller than at the slopes and bottom.

In the area, mussels and oysters generally increase in mean size along the tidal gradient with largest individuals occurring in the lower intertidal and shallow subtidal zone (Buschbaum and Saier 2001, Diederich 2006), which is also reflected in total biovolume (from 25,000 at the top to 36,250 cm^3/m^2 at the bottom of hummocks). Mussels tended to attach to upright oysters (or clumps of oysters) just above the mud surface, in interspaces of partly fused shells, or within gaping dead oysters, while young oysters tended to attach to the protruding upper parts of large oysters (see insets in Figs. 3, 4). From top to bottom of hummocks, mussels not only declined in abundance but also lost their dominant biogenic role to oysters.

Large oysters took vast expanses of former mussel beds over physically (Fig. 3). By filling gaps, coverage of the sediment and biovolume (biomass) had increased compared to mussel beds. In the understory of towering oyster aggregates, mussels still occur (see left inset in Fig. 4). This currently last phase of the oyster invasion constitutes a co-dominance of oysters and

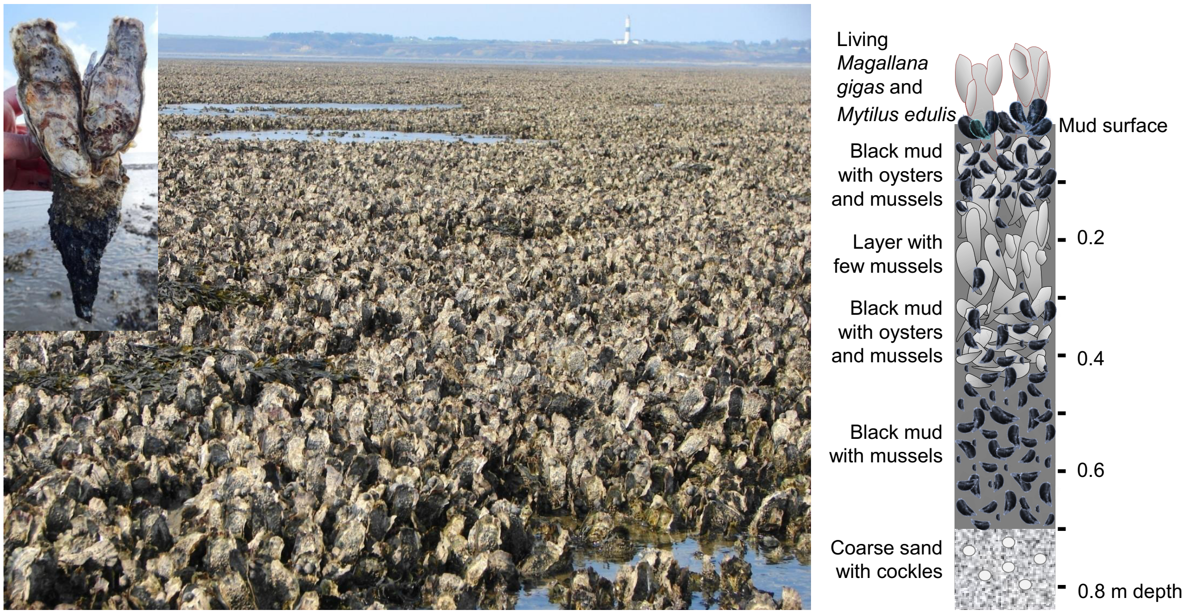

Fig. 3. Feral Pacific oysters occupying a former bed of Atlantic mussels in April 2009 (L in Fig. 2). Mussels remain hidden between large oysters. Inset shows oysters settling upon oysters. Right: scheme of shell layers underneath the living oysters and mussels, excavated in 2016 (B and M in Fig. 2).

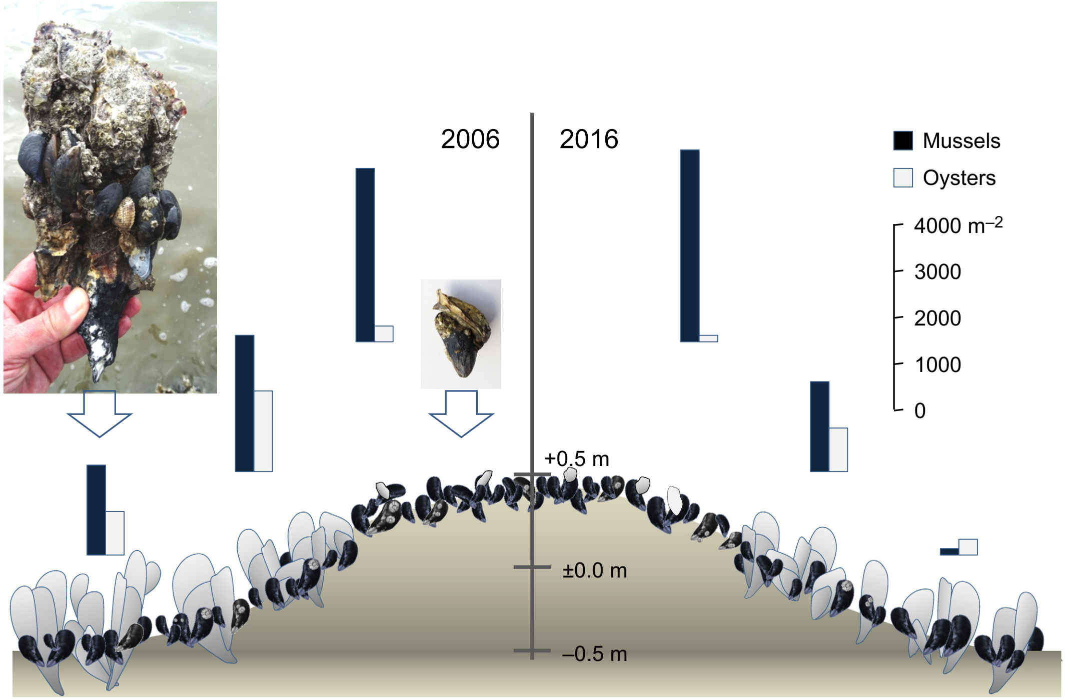

Fig. 4. Recurrent zonation in 2006 and 2016 at hummocks within mixed beds of mussels and oysters with dominance of mussels on the top and co-dominance at slope and bottom; insets show individual mussel with attached young oyster and multi-generational aggregate of oysters with belt of mussels at mud surface. Elevation ranged from approximately +0.5 to −0.5 m relative to mean low tide level.

mussels and may be termed mixed epibenthic bivalve beds or in short "oyssel reefs."

Mussel and oyster abundances

First, feral *M. gigas* were found in 1991 and abundances remained low until 2003 when 300 individuals/m^2 were exceeded and then staid above that level (Fig. 5). An exponential population increase from 2001 to 2007 followed. Two years without recruitment (2007 and 2008) caused a subsequent decline in abundance. Then, a severe ice winter (2009/2010) caused mass mortality (for details see Büttger et al. 2011). Consecutively, two more winters with ice retarded recovery, but from 2012 onwards, the oyster population increased exponentially again, reaching abundances of >2500 individuals/m^2 in 2015 before recruitment failure recurred (for more details, see Reise et al. 2017).

Mean mussel abundances on mussel beds in the List tidal basin at Sylt ranged from 1070 to 2339 individuals/m^2 before Pacific oysters became abundant (Asmus 1987, Reise et al. 1994, Büttger et al. 2008, *unpublished data*). Since 2003, mean mussel abundances have remained rather low, ranging from 205 to 1482 m^{-2}. Mussel abundances at beds near Munkmarsch harbor were particularly low when the oyster population reached its first peak in 2007 and in the period with ice winters (2009–2012; Fig. 5). Thereafter, mussel abundances followed the recovery of the oyster population until 2015.

While the correlation between oyster and mussel densities was overall rather weak ($R^2 = 0.150$, $P = 0.239$), grouping into years before and after the ice-induced population decline already improved the explanatory power of our model ($R^2 = 0.498$, $P = 0.163$). However, the best fit was obtained when the abundance of mussels was correlated to the abundance of oysters in the year before (i.e., time shift +1, $R^2 = 0.838$, $P = 0.009$, Fig. 6); especially, the highly significant interaction term between oyster density and time before/after the population decline ($F_{1,6} = 20.756$, $P = 0.004$) suggests a significant negative response of mussels to oysters in before 2009 and a significant positive response from 2010 onwards (Fig. 6). The severe ice winter 2009/2010 therefore appears to mark or

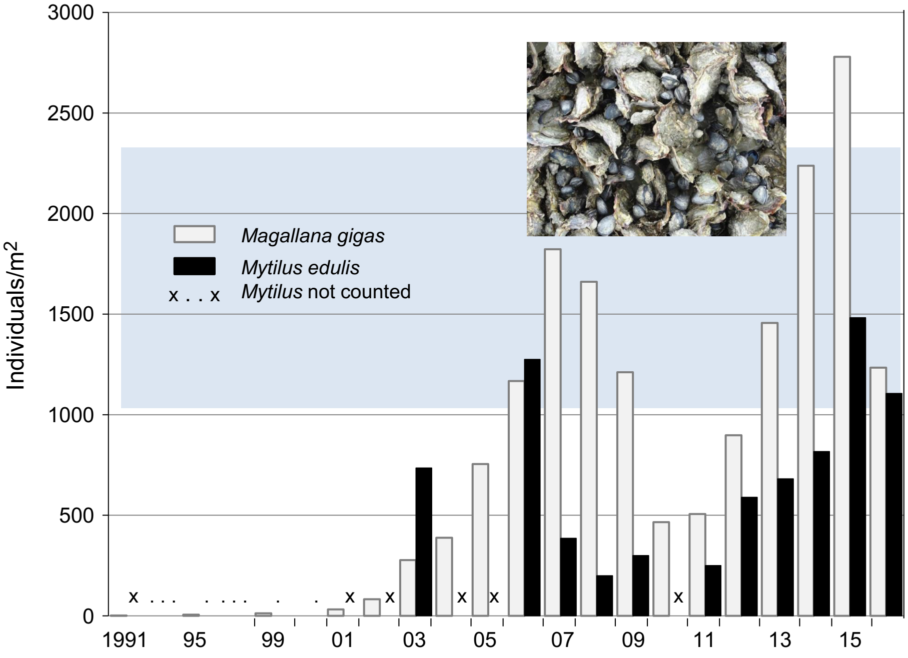

Fig. 5. Abundances of oysters (>20 mm) and mussels (>10 mm) per m^2 on mussel beds near Munkmarsch harbor. Oysters were assessed annually since 2001 and mussels in 2003, 2006 to 2009, and 2011 to 2016. Inset shows crowded oysters and mussels. Shading refers to range of mussel abundances on mussel beds prior to 2003 (Asmus 1987, Reise et al. 1994, Büttger et al. 2008, Büttger et al., *unpublished data*).

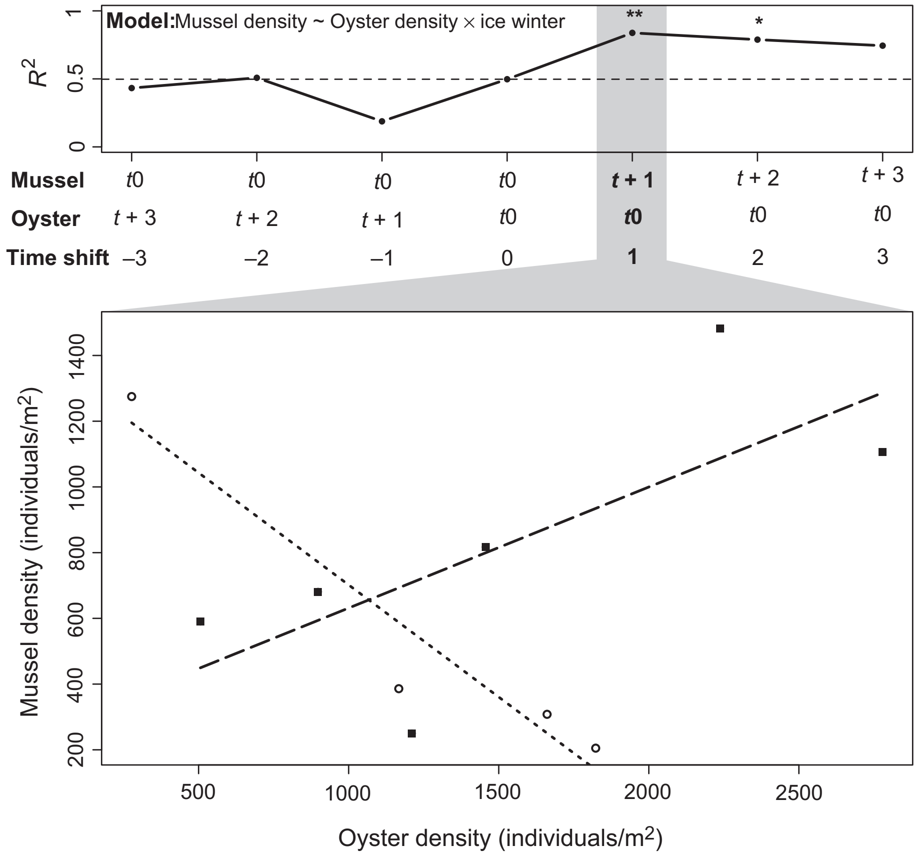

Fig. 6. Time-shifted correlation between oyster and mussel densities. The upper panel shows the explanatory power of models from a time shift analysis shifting yearly oyster and mussel densities relative to each other. Significance over all models are marked by ** when $P < 0.01$ and * when $P < 0.05$. The lower panel shows the correlation of the best fitting model of a time shift of 1, that is, correlating mussel abundance to oyster abundance of the previous year. Open circles and dotted line mark years before, and solid squares and dashed line show years after the ice winter of 2009/2010.

has caused a change in the relation between oysters and mussels.

DISCUSSION

The impact of an invader may change over time, and our data of Pacific oysters on Atlantic mussel beds nicely demonstrate this (Fig. 7). First, these oysters were foes to individual mussels by smothering them, taking their space and food. In a homogeneous and stable environment with complete habitat overlap, mussels would have been subject to competitive exclusion (Fig. 1A). This was prevented not only by habitat heterogeneity such as tops of hummocks and intercepting ice winters (Fig. 1B) but also by oysters settling on oysters and accommodating mussels in the understory of complex three-dimensional reefs once these have been built up (Fig. 1C). Nevertheless, foes did not become friends because mussels now have to share resources with their new bedfellows (Fig. 7). On the other hand, a severe winter with ice shoals dragging forth and back did not erase oyssel reef structures. These may provide better refuges against predation than pure mussel beds after physical disturbances.

Oysters settling on mussel beds

In marine soft-bottom habitats, solid surfaces for attachment are scarce and competent larvae settle either on conspecifics or on other shellfish species, living or dead (Wahl 1989). If the epibiont is

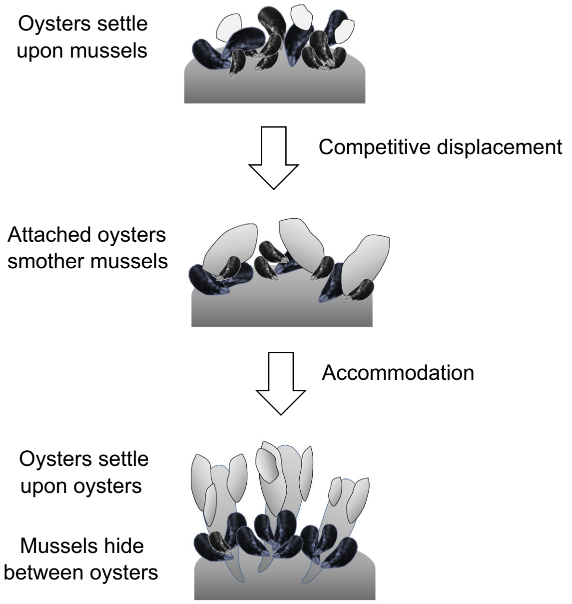

Fig. 7. Impact of invading oysters on resident mussel beds, changing from competitive displacement to accommodation of mussels in oyssel reefs.

achieving a larger size than its basibiont, the latter will die as in the case of *Magellana gigas* and *Mytilus edulis*. In addition to other sources of mortality, such as predation by birds and starfish or by severe winters (Nehls et al. 1997, Saier 2001, Strasser et al. 2001), this negatively affected the mussel population. However, once more and more oysters had attained large (>100 mm) size with upward growth under crowded conditions (Fig. 7), oyster larvae settled preferentially on oysters, and mussels became redundant for the attachment (Table 3, Fig. 3). The direct displacement of mussels by oysters became a transient phenomenon.

Spatially, mussels seem to perform better than oysters where tidal emergence entails thermal stress and limits time for suspension feeding as at the top of hummocks (Fig. 4). Such locations at the tidal growth ceiling of oysters constitute refuges for mussels from competing oysters. This pattern contrasts with subtidal reef tops of *Crassostrea virginica* where enhanced flow increases food supply while positions at the bottom may be subject to adverse sedimentation or hypoxia (Lenihan 1999). In the Wadden Sea, high tidal range with strong bi-directional currents and waves generates a different regime with better growth from top to bottom.

In experiments at our study site, oysters preferentially settled on oysters rather than mussels, while mussels settled on both (Diederich 2005). On the other hand, substrates fouled with barnacles were preferred by settling mussels (Buschbaum and Saier 2001), while settling oysters made no difference (Diederich 2005). This left room for mixing as well as spatial segregation between Pacific oysters and resident mussels. Furthermore, mussel beds differ in suitability for settling oysters. When covered by fucoid algae, mussels are partly endobenthic and not fouled (Albrecht and Reise 1994), and Diederich (2005) found reduced oyster recruitment under algal cover. At tops of hummocks, oysters remained feeble (Fig. 4), and in other regions of the Wadden Sea, entire mussel beds with only a few oysters present remained common (Nehls et al. 2009, Fey et al. 2010, van den Ende et al. 2016, *own observations*). It is not clear whether this will be transient or become a permanent pattern.

We conclude that (1) direct killing of mussels by overgrowing oysters was a transient phase because once crowded oysters were protruding above mussels, oysters settled primarily on oysters, and (2) some mussel beds or parts of them will probably remain dominated by mussels and not oysters. Thus, a continued coexistence of both species in the Wadden Sea is highly probable.

The transformation of mussel beds to oyssel reefs

We observed the transformation from mussel beds to oyssel reefs directly from the beginning in the 1990s (Fig. 5). Shell layers deposited below bed surface also reflect this transformation (Fig. 3). Spatially, the zoned pattern from top to bottom at hummocks may also mirror the temporal development from pure mussel dominance to co-dominance of oysters and mussels (Fig. 4). However, why could *M. gigas* settle successfully on crowded mussel beds? This contradicts ecological competition theory unless food is not limiting. Local food depletion over mussel beds may be rather common for mussels in the Wadden Sea. Mussel beds tend to be elongated and positioned perpendicular to main currents. By this, food depletion on the beds may become mitigated (van de Koppel et al. 2005). Although Pacific oysters copied this spatial structure initially, we also observed scattered clumps of oysters gradually filling troughs between already conquered elevated beds of mussels. Oyssel reefs eventually adopt a more coherent pattern (Fig. 3). Further studies should clarify whether oysters are less prone to food limitation by their upright growth than mussels.

The most likely explanation for the paradox of a suspension feeder successfully invading a densely packed assemblage of suspension feeders may be the well-known invasion asymmetry from biomes with higher to biomes with lower phylogenetic diversity (Vermeij 1991, Fridley and Sax 2014). Although mussels can be assumed to be well adapted to regional and local conditions in the Wadden Sea (i.e., having large labial palps in murky waters, Theisen 1977), oysters may have achieved superiority by evolving in the richer biotic region of the NW Pacific with many competitive interactions (Vermeij 1978). This may have overcome a potential home field advantage of mussels.

When settling upon mussels in mussel beds, young oysters may benefit from top feeding positions but at the same time expose themselves to predators such as the abundant green crab *Carcinus maenas*. However, the risk might be low, since these crabs prefer to prey on thin-shelled mussels and only prey on young oysters when given no choice (Pickering and Quijon 2011, *personal observation*). This may explain why young oysters could occupy top feeding positions while young mussels tend to seek shelter between and below adult mussels or oysters. When positioned at the top, mussels moved downward as soon as crabs had access in experiments in our study area (Eschweiler and Christensen 2011). The higher survival at the base of the large oysters was, however, traded off for retarded growth (see also Waser et al. 2015, 2016). Furthermore, below the canopy of oysters, detrimental overgrowth by barnacles on mussels was low relative to exposed positions (Buschbaum et al. 2016). This may help mussels to overcome curtailed food in the association with oysters above them. Similar effects mediated by habitat complexity may also benefit young oysters in reefs of *C. virginica* (Grabowski 2004).

In conclusion, the transformation from mussel beds to oyssel reefs could commence because Pacific oysters are competitively superior over resident mussels due to their long evolutionary history with manifold biotic interactions. Oysters relegate mussels to less profitable feeding positions, but they survive because of improved shelter. Therefore, the functional base of this coexistence is that oysters get the better feeding positions while mussels get shelter.

Are oyssel reefs more stable than mussel beds?

The three-dimensional oyster matrix became more complex in the course of time. Individual oysters increased in shell length and young oysters attached to the projecting upper ends (Figs. 3, 7), and empty valves accumulated in reefs. This offers shelter for mussels in the understory, and the byssus thread network of mussels probably helped in keeping shell material in the reef, adding weight and complexity. In October and December 2013, two exceptional storm surges left no discernible traces on the novel oyssel reefs at Sylt (*personal observations*). The massive oyster shell layer deposited on beds within two to three decades (Fig. 3 right) also suggests high resistance of oyssel reefs to physical disruption. This exceeds the magnitude of pure mussel shell deposits. Maybe past disturbances had reduced this layer from time to time.

Large oysters were found to be deeply anchored in the mud (inset in Fig. 3) and often were still attached to valves of previous generations already buried completely. This is different to pure mussel beds where the intermeshed mussels resemble a carpet on top of the sediment, being more susceptible to dislodgement by waves or scouring ice floes (Nehls and Thiel 1993, Donker et al. 2015). Although oysters suffered high mortality during severe ice winters (Büttger et al. 2011), the structure of oyssel reefs persisted and offered ample substrate for subsequent settlement of oyster larvae (Reise et al. 2017) as well as shelter for settling mussels (Fig. 5).

The transformation from mono-dominance on mussel beds to co-dominance on oyssel reefs may also improve stability against biotic threats. Two species with their different reproductive seasons and settling behavior (Table 1) are unlikely affected in the same way by weather, predation, diseases, and other adverse effects. For example, siltation of mussel beds by fucoid cover with negative effects on mussels (Albrecht and Reise 1994) is rare on oyssel beds (Kochmann et al. 2008, *personal observations*). We conclude that oyssel reefs will be more persistent to physical disruption and resilient to biotic threats in the Wadden Sea than pure mussel beds had been.

The changing effects of oysters on mussels

We suggest a change in effects of oysters on mussels with inhibition from 2006 to 2009 and facilitation from 2010 to 2015 (Fig. 6). Inhibition may be caused by suffocation and overcrowding, while facilitation is due to the provision of shelter with increasing reef complexity. In the vertical sequence of shell layers (Fig. 3 right), the intermittent gap with few mussels within the layer of oysters may indicate this phase shift in the relationship between oysters and mussels. Although the best fit between oyster and mussel densities is observed when oyster abundance of the previous year is used to predict current mussel densities, which suggests a causal relationship, we cannot exclude external factors shifting to the observed correlation because the external factors operate on different time scales for both species. However, it is safe to assume that the potential influence of oysters exerted on mussels is context-dependent, concurring with a combination of the models sketched in Fig. 1B and C.

Introduced aliens have been categorized into "noninvasive" when presumed or measured effects were not significant and "invasive" when invaders changed resident biota or affected stakeholder interests (IUCN Global Invasive Species Database: http://www.issg.org/database; Blackburn et al. 2014, Ojaveer et al. 2015). However, this categorization may be misleading when impacts of invading populations are context-dependent as with Pacific oysters on mussel beds. Effects of introduced alien species on residents changing along spatial and temporal scales have also been documented by Buschbaum et al. (2006), Strayer et al. (2006), Ricciardi et al. (2013), and Schilthuizen et al. (2016), suggesting that this is a general phenomenon. Particularly, a sign change of perceivable effects over time might therefore question the usefulness of categorizing introduced species into "noninvasive" and "invasive."

Evaluating the impact

Combined abundance (Fig. 5) and biovolume (wet weight biomass; Büttger et al. 2015, and *own observation*) attain higher values in oyssel reefs than are known from mussels in pure mussel beds in the Wadden Sea. This suggests that the combined filter feeding capacity of oyssel reefs will usually exceed that of mussel beds by consuming more coastal bacterio- and phytoplankton (Fig. 1C). The positive correlation between mussel and oyster abundances since the interception of severe winters (Fig. 6) suggests that overall filter feeding capacity will remain at an increased level although average abundance of mussels in oyssel reefs tends to be lower than in mussel beds before the oysters took over.

Oyssel reefs in the Wadden Sea may be resistant against storm or ice disturbance, more resilient when affected by biotic agents, and may be better adapted to cope with climatic warming than pure mussel beds (Diederich et al. 2005, Fey et al. 2010, Thomas et al. 2016). However, it would be too simplistic to argue that oyssel reefs are better than mussel beds. The transformation from mussel beds to oyssel reefs also entails losers. Examples are a lower abundance and impaired growth of mussels and less food for mussel-feeding birds (van der Zee et al. 2012, Markert et al. 2013, Waser et al. 2016). In face of the highly dynamic population of oysters (Reise et al. 2017) and mussels, it would be euphemistic to regard oyssel reefs as a new or alternate equilibrium state.

Also from anthropocentric perspective, the change from mussel beds to oyssel reefs is ambiguous. For gourmets, it is a matter of taste. From conservation point of view, the transformation is regrettable if pure mussel beds will irreversibly vanish with cascading effects on the food web. Prevention has failed and the oyster population is now ineradicable. Therefore, we recommend avoiding pejorative terms such as "biopollution" (sensu Elliott 2003, Olenin et al. 2011) and acknowledge the adaptive properties of the novel assemblage to changes in the Anthropocene (sensu Hobbs et al. 2009, Corlett 2015). Thus, oyssel reefs should be accepted as a historical contingency in the Wadden Sea.

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