



# Impact on bird fauna of a non-native oyster expanding into blue mussel beds in the Dutch Wadden Sea



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## ABSTRACT

Intertidal mussel beds are important for intertidal ecosystems, because they feature a high taxonomic diversity and abundance of benthic organisms and are important foraging grounds for many avian species. After the introduction of the Pacific oyster (*Crassostrea gigas*) into the European Wadden Sea, many mussel beds developed into oyster dominated bivalve beds. Despite the fact that oysters have been colonizing many European intertidal areas for about two decades, their impact on the ecosystem is still poorly understood. Here, we investigated the impact of oysters on the condition of mussels and on the spatial distribution of birds on 18 bivalve beds with different grades of oyster occurrence throughout the Dutch Wadden Sea. Moreover, in comparing bird densities on bivalve beds with densities expected on the total intertidal area, we could detect which species exhibit a preference for the structured habitat. Overall, 50 different bird species were observed on the beds, of which about half regularly frequent intertidal flats. Most of these species showed a preference for bivalve beds. The condition of mussels decreased with the oyster dominance, whereas the majority of bird species was not affected by the oyster occurrence. However, three of the four species that were negatively affected depend on intertidal mussels as food source. Even though the Pacific oyster is a nonnative species, attempts to fight it may do more harm to avian biodiversity than good.

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## 1. Introduction

Shallow intertidal systems are characterized by their high primary productivity and great abundance of benthic primary consumers, including many mollusk, polychaete, and crustacean species. Consequently, these ecosystems are important nursery areas for aquatic secondary consumers such as shrimps, crabs and fishes and are major feeding grounds for many waterbird species that benefit from the high productivity (Pihl and Rosenberg, 1982; Zwarts and Wanink, 1993; van de Kam et al., 2004). The highest productivity is often found in habitats rich in three-dimensional structure, and one of these complex habitats in shallow intertidal systems is created by blue mussels (*Mytilus edulis*), which aggregate with conspecifics and accordingly form mussel beds. Although mussel beds only account for up to 5% of the intertidal area

(Folmer et al., 2014), they represent an important feature of the intertidal ecosystem by providing hard substrate and increasing habitat complexity, reducing hydrodynamics, and modifying the sediment by depositing large amounts of pseudo-feces and other fine particles (Gutierrez et al., 2003). Many studies have shown that these beds have an important effect on the benthic community (Asmus, 1987; Dittmann, 1990; Markert et al., 2009) and that the beds themselves are important foraging grounds for avian consumers (Zwarts and Drent, 1981; Goss-Custard et al., 1982; Nehls et al., 1997; van de Kam et al., 2004).

In the past, intertidal mussel beds were severely overfished on several occasions, such as in the Wash, UK (Atkinson et al., 2003) and in the Dutch Wadden Sea (Ens, 2006). The overfishing is in line with the general observation that the degradation of coastal ecosystems is most often due to human exploitation (Lotze et al., 2006). However, more recently, many intertidal systems in Europe are experiencing drastic changes resulting from the invasion of the Pacific oyster (*Crassostrea gigas*). The introduction of *C. gigas*, native to marine waters of Japan and South-east Asia, led to a transformation of many intertidal mussel beds into mixed bivalve beds or even into oyster reefs (Nehls et al.,

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2009; Fey et al., 2010; Troost, 2010). As a result, bivalve beds in an increasing number of European intertidal areas consist solely of mixed mussel and oyster populations (Nehls et al., 2009). While both species similarly provide hard substrate for sessile species (Kochmann et al., 2008), differences between mussels and oysters arise in the three-dimensional structure, heterogeneity and formed micro-habitats, due to the spatial arrangement of shells and individual shell traits (surface area and shell texture) (Gutierrez et al., 2003).

Furthermore, the bed morphology differs between both species, due to different attachment mechanisms. Mussels are adhered to the substratum by a byssus, an assemblage of numerous extracellular, collagenous fibers ending in an adhesive plaque that attaches to the substrate (Bell and Gosline, 1996). Byssal threads are temporary features, which generally exhibit longevities of around 8 weeks (Bell and Gosline, 1996; Moeser and Carrington, 2006). The continuous process of generating new threads leads to flexible and dynamic meshworks of individual mussels (van de Koppel et al., 2005). Lacking a permanent anchorage in the substrate, mussel beds are further subject to a dynamic large scale distribution, being particularly vulnerable to storms and ice scouring (Nehls and Thiel, 1993; Büttger et al., 2011; Donker et al., 2015). In contrast, oysters attach themselves permanently by generating an organic-inorganic adhesive (Burkett et al., 2010). Even after the death of individuals, oyster shells often remain anchored in the sediment. The complex of dead and alive oysters serves as settling ground for oyster larvae, which preferably settle on conspecifics (Diederich, 2005). In the long run, the process of multiple settlement leads to the creation of rigid and persisting structures (Reise and Beusekom, 2008; Walles et al., 2015). For many macroinvertebrate species, the complex structures formed by these two bivalves are likely to provide different resources in terms of nesting sites, shelter from predators and feeding opportunities, thus leading to differences in the species community (Markert et al., 2009). Moreover, the conversion of mussel beds into oyster dominated beds may ultimately lead to a change of the food web structure (Baird et al., 2012) as well as of the feeding opportunities for secondary consumers (Eschweiler and Christensen, 2011; Waser et al., 2015).

Intertidal mussel beds are valued and protected because of their contribution to biodiversity, especially avian biodiversity, so it is important to know how the spread of Pacific oysters will affect avian biodiversity. It has been suggested, that molluscivorous species, like the Eurasian Oystercatcher (*Haematopus ostralegus*) and the Common Eider (*Somateria mollissima*) may be particularly negatively affected by the invasion of the oysters (Scheiffarth et al., 2007; Markert et al., 2013), since mussels as their preferred prey are in direct competition with the oysters and therefore may exhibit a reduced body condition (Troost, 2009) resulting in a reduced prey profitability for the birds. A consolidation of oysters may additionally hamper access to the mussels. Other waterbird species commonly present on mussel beds, like for example the Eurasian Curlew (*Numenius arquata*), the Common Redshank (*Tringa totanus*), or the Black-headed Gull (*Larus ridibundus*) feed on the associated fauna (Ens and Alting, 1996; Nehls et al., 1997; Goss-Custard et al., 2006; Folmer et al., 2010) and might be little affected by the habitat change (Scheiffarth et al., 2007; Markert et al., 2013). Earlier investigations however, compared the bird abundance of the present oyster-transformed beds with historic abundance data on pure mussel beds. Furthermore, these observations were limited in terms of investigated bird species and study sites, only focusing on one locality with a very low number of focal species (Markert et al., 2013) making it difficult to draw general conclusions.

In this study, we investigated the spatial distribution of waterbirds on bivalve beds with different grades of Pacific oyster occurrence. To do so, we studied 18 bivalve beds in the Dutch Wadden Sea in terms of bed properties and linked these to the appearance and number of different bird species between the years 2010 and 2013. In order to ascertain to what extent the different species show a preference for bivalve beds to habitats of less structural complexity, we furthermore used

counts of birds during high tide on high tide roosts in the vicinity of tidal flats. Assuming that all birds counted during high tide on a roost will be distributed across the emerging tidal flats closest to that specific roost, it is possible to estimate the mean abundance of the different species during low tide.

The sampling design, together with data on numbers of birds during high tide at high tide roosts allowed us to investigate two main research questions: (a) Which bird species prefer bivalve beds as a low-tide feeding habitat? (b) What is the impact of the composition of the bivalve bed (i.e. the predominance of Pacific oysters) on the avian community?

## 2. Materials and methods

### 2.1. Properties of bivalve beds

The 18 investigated bivalve beds were located throughout the Dutch part of the Wadden Sea (Fig. 1). In this area, three different types of intertidal bivalve beds can be distinguished: mussel dominated beds, where oysters are absent or occur only in very low numbers; beds with a balanced proportion of mussels and oysters and beds where oysters dominate in terms of biomass (van Stralen et al., 2012). In order to identify the proportion between both mussels and oysters, the study sites were mapped and different mussel bed properties were measured twice a year, in spring and autumn, between 2010 and 2013. Firstly, the contours of each bed were determined by walking around the bed with a hand-held GPS device following a common definition of a mussel bed (de Vlas et al., 2005). The contours gave on the one hand the spatial extent (area) of the beds and on the other hand, contours were used to delimit and create a set of multiple random sampling points. All created sample points were visited. Those points that were covered by mussels or oysters were sampled for epibenthos with a rectangular frame of  $0.0225 \text{ m}^{-2}$  ( $15 \times 15 \text{ cm}$ ). The samples were sieved (1 mm square meshes) in the field and subsequently sorted for mussels and oysters. These were counted and sized individually using digital calipers, to the nearest 0.01 mm, in the laboratory. In order to estimate the ratio between mussel and oyster biomass, the individual shell length ( $L$ ) of both mussels and oysters was converted into a volumetric length ( $V$ ), representing biomass, by a fixed dimensionless shape coefficient ( $\delta_M$ ):  $V = (\delta_M \times L)^3$ . The shape coefficient is a parameter that relates the real length with the structural length in the context of the dynamic energy budget (DEB) theory (Kooijman, 2010) and is well established for oysters (0.175, van der Veer et al., 2006), as well as for mussels (0.297, Saraiva and van der Meer, 2011). Based on the assumption, that the density of bivalve flesh approaches the one of water, the volumetric length was further converted into a measure of biomass (wet weight in kg). The precise body condition of mussels was estimated by measuring the ash-free dry mass of the soft tissue (AFDM<sub>flesh</sub>). To do this, mussels were sorted to discrete shell length classes (every 2.5 ± 0.5 mm beginning with a length of 5 mm, e.g. 5, 7.5, 10, etc.), the soft parts of a random sample of individuals from each length class (max. 15 individuals) was pooled and dried to constant weight, weighed, incinerated and weighed again to obtain by subtraction the AFDM<sub>flesh</sub>.

Moreover, the tidal elevation of the bivalve beds (m below mean tide level, MTL) was obtained based on the bivalve bed contours and a bathymetric grid ( $20 \times 20 \text{ m}$ ) of the Dutch Wadden Sea provided by Rijkswaterstaat (Dutch Ministry of Infrastructure and Environment; 'vaklodgingen'; <http://opendap.deltares.nl>). For each bivalve bed, the mean tidal elevation of all grid-points overlapping with the bed contours was calculated.

### 2.2. Bird abundance on bivalve beds

All bird species within the contours of the bivalve beds were counted. Counts were usually performed in intervals covering about half of a tidal cycle (from high tide, over outgoing tide to low tide, or from low tide over incoming tide to high tide). Due to logistical reasons or bad

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