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Habitat change by the formation of alien *Crassostrea*-reefs in the Wadden Sea and its role as feeding sites for waterbirds

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ABSTRACT

Non-indigenous Pacific oysters (*Crassostrea gigas*) have been invading the central Wadden Sea since 1998, predominantly settling on intertidal blue mussel (*Mytilus edulis*) beds which are increasingly transformed into *Crassostrea*-reefs. Pacific oysters are strong ecosystem engineers and the habitat change is considered to be a threat for waterbirds losing important feeding sites in the intertidal of the Wadden Sea. This study has increased our understanding of the use of foraging habitats by birds according to changing food resources.

During the spring and autumn migration period in 2007, we recorded bird densities at two reef types varying in Pacific oyster density and at the adjacent sand flat as a reference site. We also recorded feeding behaviour, choice of prey and assessed peck and intake rate of three target species: Eurasian oystercatcher *Haematopus ostralegus*, Eurasian curlew *Numenius arquata* and European herring gull *Larus argentatus*. To evaluate the use of the *Crassostrea*-reef in the central Wadden Sea, we compared bird densities of the target species at different intertidal feeding habitats in various regions and compared the biomass intake of Eurasian oystercatcher feeding on different prey species. We show that Eurasian oystercatcher and Eurasian curlew have adapted to the new situation and learned to exploit the food supply offered by *Crassostrea*-reefs. While foraging mainly on Pacific oysters, Eurasian oystercatchers attained sustainable intake rates even though food resource at *dense reef* during autumn was very poor due to a lack in harvestable oysters. Consolidation of reefs limits the accessibility of prey for Eurasian oystercatchers whereas a successful recruitment of Pacific oysters enhances the suitability of the habitat. Eurasian curlew was promoted by the engineering effects of the Pacific oyster while feeding extensively on shore crabs at the reefs. In contrast, European herring gulls appear hampered in foraging during low tide and hereby negatively affected by the habitat change from *Mytilus*-beds to *Crassostrea*-reefs.

1. Introduction

The Wadden Sea is the most important staging site for migratory birds on the East Atlantic flyway and the most important breeding site for waders in central Europe. Annually, 10–12 million migratory waterbirds use the habitat diversity of the Wadden Sea for roosting, breeding and feeding (Meltofte et al., 1994; Laursen et al., 2010). Due to their considerably high biomass and productivity, intertidal *Mytilus*-beds are important foraging sites for waders and waterbirds (Nehls et al., 1997). In addition to common eiders (*Somateria mollissima*), Eurasian oystercatchers (*Haematopus ostralegus*) are the main avian predators of blue mussels in the Wadden Sea. Other bird species such as the European herring gull (*Larus argentatus*), Eurasian curlew (*Numenius arquata*), common redshank (*Tringa totanus*), black-headed gull (*Chroicocephalus ridibundus*) and dunlin (*Calidris alpina*) mainly feed on associated macrofauna, such as polychaetes and crustaceans living between the blue mussels (Nehls et al., 1997; Van de Kam et al., 2004). Decreasing blue mussel stocks and deteriorating body condition indices of blue mussels in most of the regions of the Wadden Sea may have decreased abundances of especially shellfish eating birds, but causes for significantly declining trends of population sizes of Eurasian oystercatcher and European herring gull during the last

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two decades in the Wadden Sea remain unclear (Ens et al., 2009; Laursen et al., 2010).

Meanwhile, the habitat type "*Mytilus*-bed" experiences novel changes throughout the entire Wadden Sea. Non-indigenous Pacific oysters (*Crassostrea gigas*) are transforming intertidal *Mytilus*-beds into *Crassostrea*-reefs. Oysters were imported for aquaculture to the Dutch Oosterschelde estuary in 1964 (Drinkwaard, 1999) (Fig. 1) and were deliberately introduced to the western Wadden Sea (The Netherlands) where wild oysters have been propagating since 1983 (Fey et al., 2010), settling predominantly on intertidal *Mytilus*-beds. In the central Wadden Sea, the first occurrence of Pacific oysters was observed in 1998, invading the area by larval drift via residual currents (Wehrmann et al., 2000). After an initial lag phase of the bioinvasion, the regional abundance of Pacific oysters increased exponentially. Since 2006, all intertidal *Mytilus*-beds in the central Wadden Sea have been colonized (Nehls et al., 2009). Juvenile oysters may grow 7 cm in their first year and reach shell lengths of up to 25 cm within only a few years (Schmidt et al., 2008). Oyster larvae prefer settling on conspecifics and the adult individual stays cemented to its substratum of settlement. Hence, shells of dead individuals contribute to the physical structure of the habitat. Increasing densities of this strong physical ecosystem engineer (Jones et al., 1994) lead to the formation of dense reefs. Both rapid growth and reef formation protects the oysters against predators and generally support invasion success (Colautti et al., 2004). In contrast to the flexible meshworks and dynamic occurrence of *Mytilus*-beds (Nehls and Thiel, 1993), Pacific oyster reefs constitute new rigid and persisting bioconstructions (Smaal et al., 2005).

The invasion and spread of the Pacific oyster overlap temporally with a long-term decline of blue mussels in the area. In the central Wadden Sea, blue mussel density is now increasing in the shelter of *Crassostrea*-reefs while habitat characteristics are mainly engineered by Pacific oysters (Nehls et al., 2009). Dense reefs may be constructed by about 2000 live and dead oysters per m^2 and may inhabit even more live blue mussels than live oysters. Blue mussel populations are built up by all size classes, especially individuals between 30 and 40 mm now contribute to the population structure in *Crassostrea*-reefs (Markert et al., 2010). Markert et al. (2010) detected an increase in biodiversity, and high abundance and biomass of associated macrofauna at areas dominated by Pacific oysters. They found prey species for birds, such as shore crabs or polychaetes, in high abundances in the reefs. However, the presence of prey does not imply accessibility at the same time, as superficial structure and habitat matrix differ essentially between *Crassostrea*-reefs and *Mytilus*-beds. Pacific oysters create complex three-dimensional rigid biogenic structures which may influence food detection as well as food accessibility for birds (Zwarts and Wanink, 1993; Zwarts et al., 1996a; Ruesink et al., 2005). Scheiffarth et al. (2007) suggested that no difference in habitat quality has to be expected for birds feeding on associated fauna but also emphasised the lack of data, especially for the Wadden Sea as the most important stop-over site for waders using the East Atlantic Flyway.

The present study aimed to increase knowledge of the intensity and quality of the use of *Crassostrea*-reefs by waterbirds. We focused on three target species (i) Eurasian oystercatcher, (ii) Eurasian curlew and (iii) European herring gull (hereafter: oystercatcher, curlew, herring gull) to answer the following questions:

- Are the birds using *Crassostrea*-reefs as feeding sites and is the ecological function of *Mytilus*-beds replaced?
- Which of the target bird species benefits or suffers from the habitat change?
- What kind of long-term effect can be expected from the habitat change?

The data for bird density are compared with different feeding habitats in various intertidal regions and with regional pre-invasion data using a BACI (Before-After/Control-Impact) approach. It is the first study on foraging behaviour and energy intake rates of oystercatcher at *Crassostrea*-reefs. The investigation increases our understanding of the impact of a non-indigenous ecosystem engineering species affecting ecosystem functions.

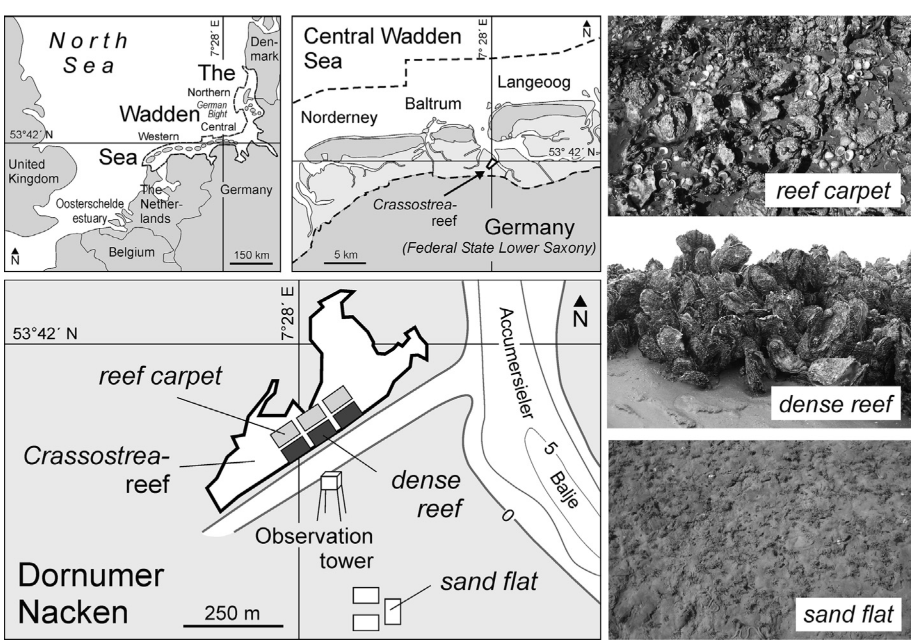

Fig. 1. Location of the Pacific oyster reef, study plots at the habitat types *dense reef*, *reef carpet* and *sand flat* (photos for details) and position of the observation tower at the *Dornumer Nacken* in the central Wadden Sea, North Sea (tidal flat area in light grey, Wadden Sea area indicated by dashed lines).