Predation on intertidal mussels

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Summary

Coastal areas are amongst the most productive ecosystems in the world. Important components of these coastal areas are reef-forming bivalves such as mussels and oysters, as they have important facilitating effects on many associated organisms through the provision of substratum, shelter or food. In the pristine Wadden Sea, intertidal beds of blue mussels (*Mytilus edulis*) and subtidal reefs of European flat oysters (*Ostrea edulis*) were common throughout the area and diversified the seascape. Extensive exploitation in the 19th century, however, led to the disappearance of the flat oyster from the Wadden Sea. As a consequence, mussels gained in importance as human food source, ultimately resulting in the introduction of commercial mussel cultures in the 1950s. Mussel beds were intensively harvested, and juvenile mussels were fished from intertidal beds for relaying to subtidal culture plots. In the early 1990s, several successive years with low recruitment and ongoing fisheries resulted in the loss of nearly all intertidal mussel beds in the Dutch Wadden Sea. Fishing restrictions subsequently allowed for the recovery of the intertidal beds. However, recovery was lower than hoped and a new potential threat emerged from the invasion of the Pacific oyster (*Crassostrea gigas*). Since the early 2000s, the alien oyster settled to an increasing degree on mussel beds, which often resulted in transformations into oyster dominated reefs, raising conservation concerns over competition with the native mussels. In order to further promote the recovery of intertidal mussel beds, restoration measures were considered. Earlier experiences indicated the difficulty of the mussel bed restoration, as most man-made beds disappeared shortly after they had been created.

In order to increase the success of mussel bed restoration measures, detailed insights in the various environmental and ecological processes affecting the survival of mussel beds were needed. The work presented in this thesis formed part of the 'Mosselwad' project, which was launched in 2010 to increase knowledge on several factors that play important roles in the survival and the stability of mussel beds. This thesis aims to investigate crucial biotic factors that act upon the survival of intertidal mussel beds. In particular, this thesis is concerned with the predation by shore crabs and mussel-feeding birds on the intertidal mussels and the impact of the recent introduction of the Pacific oyster into the Wadden Sea.

As a measure of predation pressure on mussels as well as other macrobenthic organisms among different Wadden Sea regions, waterbird distributions in relation to the extent of potential foraging habitats were explored (**Chapter 2**). Specifically, numbers of 21 waterbird species for the period 1999–2013 were investigated in relation to the surface area of six different habitats among the tidal basins of the Dutch and German Wadden Sea. The habitat areas were characterized by data on abiotic characteristics (tidal exposure and sediment structure) and on distributions of epibenthic bivalve beds. Linear regressions were used to explore bird-habitat associations, where the regression coefficients reflect bird densities in the various habitats. Most species were positively correlated with bivalve beds and intertidal areas with low tidal exposure (below 28%) and rather coarse sandy sediment (median grain size > 138.5 μm). By inspecting the regression residuals, we identified higher bird abundances of all investigated feeding guilds in the western Dutch Wadden Sea and in the south of Schleswig-Holstein, while lower abundances were found in the eastern Dutch Wadden Sea, in Lower Saxony and the north of Schleswig-Holstein. The observed regional differences in bird abundance may be related to the abundance of Peregrine Falcons, human disturbance and properties of the landscape. However, alternative explanations cannot be ruled out and further research is needed to identify the involved drivers.

Chapter 3 describes the fate of bivalve beds within the Dutch Wadden Sea for the period 1999–2013. Bed survival is analysed in relation to several covariates such orbital speed, inundation time, bed size, and bed type with respect to the bivalve composition (mussel dominated, dominated by Pacific oysters, or mixtures of both bivalve species). In general, beds were found to have a high survival when large, lying shallow, and experiencing low orbital speed. The highest effect on bed survival, however, was due to composition of bivalve species. Mixed beds had a much lower hazard rate than pure oyster or mussel beds.

In **Chapter 4**, the impact of Pacific 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 was explored. Moreover, in comparing bird densities on bivalve beds with densities expected on the total intertidal area, species exhibiting a preference for the structured habitat could be detected. 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 oyster dominance, whereas the majority of bird species was not affected by oyster occurrence. Four species were found to be negatively affected by oyster occurrence. Three of these species (Oystercatcher, Red Knot, and Common Gull) depend on intertidal mussels as food source, while the Dunlin primarily uses other food sources.

Estimating shore crab (*Carcinus maenas*) abundance on bivalve beds is challenging, since most methods common for quantifying animal abundance in marine habitats cannot be used. As abundance estimates are needed for the quantification of crab predation on mussels, the potential of two methods to quantify crab abundance on 14 epibenthic bivalve beds across the Dutch Wadden Sea was explored in **Chapter 5**. The use of the number of crabs migrating from subtidal towards intertidal areas as a proxy of abundance on bivalve beds yielded unreliable results. In contrast, crabs caught with traps on the beds were correlated with the abundance assessed on the surrounding bare flats by beam trawl and therefore provided usable results. The estimates, however, were only reliable for crabs exceeding 35 mm in carapace width (CW). The application of these estimates indicated that crab abundances on bivalve beds were influenced by the biogenic structure. Beds dominated by oysters attracted many large crabs (> 50 mm CW), whereas abundances of medium-sized crabs (35–50 mm CW) showed no relationship to the oyster occurrence.

In **Chapter 6**, the impact of Pacific oysters on the survival of different sized mussels, while being exposed to shore crab predation, was experimentally explored. Mussel survival was documented in laboratory short-term experiments. A split-plot design was followed, with differences in the three among-plot factors (acclimatization type: control and induced clumping; crab size: small (45–50 mm CW) and big crabs (60–65 mm CW); and oyster presence: presence and absence of oysters) and within-plot differences in the survival of four different mussel size classes (6, 12, 18, and 24 mm shell length). The presence of Pacific oysters reduced the mortality of unconditioned mussels as well as mussels that were acclimatized in presence of predatory cues, while being exposed to predation by crabs of two different size classes. The reduction in mortality was size-dependent both in terms of the predators and the prey. The presence of oysters notably reduced mussel mortality in presence of small crabs, while the mortality rate in presence of big crabs was less affected. Mussels that benefited the most by the presence of oysters were those of recruitment stages, smaller than 20 mm in shell length.

In **Chapter 7** and **Chapter 8**, the potential importance of parasitism in relation to predation on mussels is explored. These two chapters focus on parasite infections in brachyuran crabs in the Dutch Wadden Sea. **Chapter 7** describes an extensive field survey throughout the Dutch Wadden Sea for the rhizocephalan parasite *Sacculina carcini* infecting shore crabs. The distribution of shore crabs infected with the rhizocephalan parasite was investigated at 12 locations and in 3 adjacent habitats (intertidal mussel beds, intertidal bare sand flats and subtidal gullies) along a tidal elevation gradient. The sampling revealed that of the 27629

crabs investigated, most infected crabs were found in the subtidal gullies and almost none on intertidal bare sand flats or mussel beds at all of the 12 locations. This probably resulted from a parasite-induced manipulation of infected crabs to behave like egg-bearing females which migrate towards deeper waters, as the same pattern was observed in the distribution of non-infected ovigerous females. The prevalence of both infected crabs and ovigerous females in the gullies was significantly correlated with water depth, and both tended to increase (albeit not significantly) with increasing salinity. As water depth and salinity are expected to affect larval survival of both parasites and crabs, this suggests that the migration into subtidal habitats may result in favourable conditions for reproduction and dispersal.

In **Chapter 8**, the macroparasite richness, prevalence, and intensity among three brachyuran crab species were explored in the Western Dutch Wadden Sea. Next to the native *C. maenas*, the two invasive crabs *Hemigrapsus sanguineus* and *H. takanoi* were screened for potential parasite infection. While native shore crabs hosted three parasite groups (acanthocephalans, microphallid trematodes, rhizocephalans), the two invasive *Hemigrapsus* species were only infected with acanthocephalans. All acanthocephalans were molecularly identified (COI) as the native *Profilicollis botulus*. Prevalence and intensities of *P. botulus* were generally lower in the introduced than in the native crabs. Metacercariae of microphallid trematodes were only found in the native *C. maenas*, with mean infection levels of 100–300 metacercariae per host. Likewise, the castrating rhizocephalan *S. carcini* was only found in *C. maenas* at a few locations with low prevalences (< 3%). This first study on infection levels in invasive *Hemigrapsus* species in Europe indicates that these invasive crabs indeed experience lower infection levels than their native competitor *C. maenas*.

The integration of the information gained in this thesis indicated that the predation of mussel-eating birds and shore crabs is able to significantly affect the survival of intertidal bivalve beds (**Chapter 9**). High waterbird abundances may strongly reduce mussel biomass by preying primarily on larger mussels, whereas shore crabs of various life stages may play important roles in the survival of post-settling mussels. The juvenile mussels are of particular importance for mussel beds in order to persist over long time periods, as they rejuvenate the mussel population and compensate the losses (e.g., by bird predation) of older specimens. The introduction of Pacific oyster on the mussel beds, led to substantial decreases in the predation pressure exerted by mussel-eating birds and also resulted in reduced predation by shore crabs. This may have contributed to the overall observation that beds colonised by Pacific oysters show a higher survival than pure mussel beds. Consequently, employment of Pacific oysters in restoration measures could be a viable option to increase the likelihood that man-made bivalve beds persist over long time periods. As Pacific oysters became established in the Wadden Sea and are now ineradicable, mixed beds of oysters and mussels should be accepted as a historical contingency and should be seen as a vital addition to the habitat complexes within the Wadden Sea.