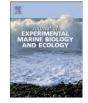
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Role of predation on sandy beaches: Predation pressure and prey selectivity estimated by laboratory experiments

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ABSTRACT

Predation is known to play an important role in structuring communities. In rocky intertidal communities, both environmental variables and the structuring role of predation determine species zonation and distribution patterns. However, on intertidal sandy beaches, little is known on the presence and the role of predation. In this study, laboratory experiments were used to examine prey consumption, prey selectivity and predation pressure of the two main epibenthic predators, being shrimp and juvenile flatfish, present on the intertidal beach at high tide. Results show that macrobenthos is important in the diet of these epibenthic predators and that prey selectivity is present. As predation pressure on the intertidal beach is high, predation is probably an important structuring factor for the sandy beach macrobenthos community. Hence, the macrobenthos zonation pattern is likely to be steered by the combination of abiotic and biotic factors: while the upper limit of a species zone is defined by the species physiological response to abiotic environmental variables, the lower limit is defined by biotic factors such as predation pressure. Furthermore, the intertidal zone functions as an important nursery area for commercially important species like shrimp and flatfish.

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1. Introduction

Predation is one of the major organizing forces within communities (e.g. Christensen and Pauly, 1998; Matson et al., 2011). The importance of predation in structuring communities has been well documented for terrestrial plant communities (e.g. Lau et al., 2008), freshwater zooplankton communities (e.g. Ibe et al., 2011) and rocky intertidal communities (e.g. Bonaviri et al., 2009; Brazão et al., 2009). The great majority of the marine studies concentrated on tidal flats, where the most important predators at high tide are juvenile flatfish and macro-crustaceans such as shrimps and crabs (Koot, 2009; Kuipers, 1977; Kuipers and Dapper, 1984). Epibenthic predators are known to be of structuring importance for the macrofauna communities on soft-bottom intertidal sediments (Evans, 1984; Kuipers and Dapper, 1981; Kuipers et al., 1981; Pihl, 1985; Pihl and Rosenberg, 1984; Reise, 1977). Richards et al. (1999) showed that crab predation on an intertidal mudflat diminished the abundances of the bivalve Macoma balthica while Kuipers and Dapper (1984) demonstrated the importance of tidal flats as nursery areas for brown shrimp. Thrush et al. (1994) showed that the negative effect of predation by birds and fish on soft bottom sediment communities was largely scale-dependent. Moreover, field enclosure or exclosure experiments are characterized by technical problems such as caging effects or scale-dependency (Thrush, 1999).

On sandy beaches, the importance of predation by epibenthic predators and the trophic relationship between these predators and the macrobenthos are far less studied. Biological interactions are believed to be of minor structuring importance in the mainly physically determined sandy beach ecosystems (Jaramillo and McLachlan, 1993; McLachlan, 1983, 2001; McLachlan et al., 1996; Schlacher et al., 2008). Despite their ecological importance during the life cycle of many marine organisms (e.g. Beyst et al., 2001; Gibson, 1973), the nurserv function of sandy beaches for epibenthic species has not been intensively studied compared to shallow water and estuarine habitats (Amara and Paul, 2003). On dissipative intertidal beaches, epibenthic predators are abundant at high tide (Beyst et al., 2001) but it is not sure whether these predators can execute a significant predation pressure on the resident fauna of intertidal dissipative beaches as the only studies on epibenthic predators did not focus on the smaller juvenile species (due to the used sampling strategy where epibenthos was collected by using a fishing net with mesh sizes of 0.5×0.5 mm) that are known to consume macrobenthos the most (Beyst et al., 1999, 2002). Furthermore, field experiments on intertidal sandy beaches are difficult to execute as this environment is highly dynamic, especially in comparison with the more benign tidal flats (McLachlan and Brown, 2006).

The high-intertidal macrobenthos community on Belgian dissipative sandy beaches consists mainly of the polychaete *Scolelepis squamata*, the two amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi* and the isopod *Eurydice pulchra* (Degraer et al., 2003). These species show a specific zonation pattern on the intertidal sandy beach (Degraer et al.,

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2003). The distribution and zonation of infaunal sandy beach organisms have been typically related to beach morphodynamical factors such as slope, wave energy, tidal range and sediment characteristics (Defeo and McLachlan, 2005; McLachlan, 1996; McLachlan and Jaramillo, 1995). Moreover, food supply has been shown to be even more important for structuring communities on sandy beaches (Dugan et al., 2003; Lastra et al., 2006; Rodil et al., 2012) but food web interactions in the sandy beach ecosystem are not yet clarified.

The epibenthic community, being temporarily present on dissipative intertidal Belgian beaches, is dominated by shrimp (*Crangon crangon*) and juvenile flatfish (especially *Pleuronectes platessa* and *Scophthalmus maximus*) (Beyst et al., 2001). Although these predators are known to have an important influence on macrofauna on intertidal flats (Kuipers and Dapper, 1984), the trophic relations between these epibenthic predators and sandy beach macrofauna on intertidal sandy beaches are not yet studied.

The aims of this study were therefore (1) to determine prey selectivity of shrimp and juvenile flatfish present on intertidal dissipative beaches, (2) to determine the prey consumption of sandy beach macrobenthos by shrimp and juvenile flatfish and (3) to estimate the predation pressure of epibenthic predators on the dominant representatives of the intertidal dissipative macrobenthos community.

The null hypothesis, tested in this study, stated that the predators had no significant effect on the survival of the prey species while prey selectivity was hypothesized not to differ from random choice.

2. Material and methods

2.1. Selection and origin of the species and specimens

Prey selectivity, prey consumption and predation pressure were investigated for all dominant members of the high-intertidal dissipative macrobenthos community of the Belgian coast: the polychaete *S. squamata*, the two amphipods *B. pilosa* and *B. sarsi* and the isopod *E. pulchra*.

On dissipative beaches, several runnels are situated where shrimps and juvenile flatfish stay behind with receding tide. *C. crangon* (brown shrimp), *S. maximus* (turbot) and *P. platessa* (plaice) are the most commonly caught epibenthic predators (Beyst et al., 1999). All predators and prey species for the laboratory experiments were collected on the Belgian dissipative beach of De Panne (2°33'24" E 51°05'42" N).

2.2. Experimental conditions

Experiments were conducted in June 2010, in a climate-controlled room at 18 °C and with a day/night regime of 16:8 h, the natural summer photoperiod in Belgium. Predators and prey were added to aquaria provided with a constant oxygen supply. Similar aquaria of 18–9–13 (l–w–h) cm were used for both experiments. These aquaria were filled with 4 cm of natural Belgian beach sediment, sieved and decanted to remove all fauna, and with 1 l of Belgian coastal sea water, sieved over 64 µm mesh size to remove all larger fauna.

Predators were collected one day before the start of the experiment by dredging shallow water with a hand operated beam trawl. Before the start of the experiments, predators were starved and acclimatized in the lab for 24 h (Hiddink et al., 2002). All prey species were collected by sieving the beach sediment over a 1 mm sieve.

The average total length of the shrimps used was 3 to 3.5 cm and the total length of the juvenile flatfish used was 3 to 5 cm since predators of these sizes are known to feed on macrobenthos (Beyst et al., 1999; Campos et al., 2008; Janssen and Kuipers, 1980). Sex of the experimental predators was not determined but predators were divided randomly over the treatments and replicates. The effects of *C. crangon* and juvenile flatfish were studied in separate aquaria since the two types of predators might also have a mutual effect on each other (Figs. 1 & 2) (Beyst et al., 1999). Although this probably resulted in a higher

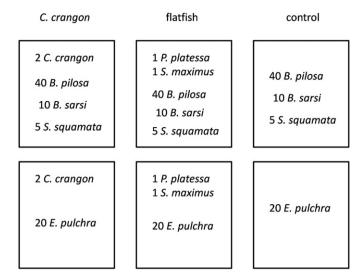


Fig. 1. Set-up experiment 1: predators Crangon crangon and the juvenile flatfish Pleuronectes platessa and Scophthalmus maximus; prey Bathyporeia pilosa, B. sarsi, Scolelepis squamata and Eurydice pulchra. All treatments were replicated seven times.

consumption estimation as compared to the field situation where predation between predators probably decreased consumption, it was the aim of this experiment to determine potential consumption without inter-predator influences. In all flatfish-treatments the same twopredator combination of one larger *P. platessa* and one smaller *S. maximus* was used (Figs. 1 & 2).

The aims of this study were examined by means of two mesocosm experiments. The first experiment aimed at testing general prey selectivity, prey consumption and predation pressure, while the second experiment focused only on prey selectivity between the amphipods *B. pilosa* and *B. sarsi*.

2.3. Set-up experiment 1

The predator impact of juvenile flatfish and shrimps was investigated on four prey species: B. pilosa, B. sarsi, S. squamata and E. pulchra (Fig. 1). Prey densities were chosen to be naturally occurring, average densities of Belgian beaches (Speybroeck, 2007). Experimental densities of B. pilosa were 1708 ind/m²(=40 ind/experimental treatment), these of the related *B. sarsi* 427 ind/m² (=10 ind/experimental treatment), these of the polychaete S. squamata 213 ind/m² (= ind/experimental treatment), and finally these of the isopod *E. pulchra* 856 ind/m² (= 20 ind/ experimental treatment). The latter density is ten-fold higher compared to natural densities (Vandewalle, 2009) since at natural Eurydice abundances, the number of experimental isopods would be too low to guarantee a reliable estimation of the predator impact. Although densities of predators are known to strongly fluctuate on the beach with every tidal cycle, a predator density of 85 ind/m² (= 2 ind/experimental treatment) was used in the current study, based on the study by Beukema (1992). As E. pulchra itself is a predator, who feeds on the other species, the predation impact of shrimps and flatfish on E. pulchra was tested separately from the other prey species (Fig. 1).

The prey species were added in the aquaria prior to the predators in above-mentioned natural densities, to mimic the field situation at upcoming tide and give a reliable estimation of field predation pressure. The prey selection experiment lasted for 72 h and all treatments were replicated seven times (Fig. 1).

2.4. Set-up experiment 2

The second experiment focused on the prey selectivity of the epibenthic predators between the two congeneric amphipods

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