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Impact of predation on the polychaete *Hediste diversicolor* in estuarine intertidal flats

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Abstract

In estuarine sediment flats benthic macroinvertebrates are intensively consumed by a variety of predators, such as aquatic birds and nekton (mostly fish and crustaceans). However, there is still a lack of conclusive studies that evaluate if this predation has a relevant impact on the populations of those invertebrates, which are a key element of the estuarine food chain. In the Tagus estuary we experimentally tested and quantified the impact of predation on the polychaete *Hediste diversicolor*, one of the most important prey for a variety of predators in many estuaries. Using an exclusion experiment, we compared the seasonal variation in the densities of *H. diversicolor* from February to November in sediment plots (1) available to both bird and nekton predators, (2) just to nekton, and (3) without predators. We also followed changes in the abundance of potential predators throughout the study. The lowest densities were systematically observed in the plots accessible to all predators, followed by those which excluded just birds, and finally by those that excluded all predators. The exclosures were in place for 9 months, at the end of which the average density of *H. diversicolor* in the plots protected from all predators was eight times greater than in those without any protection. These results demonstrate that predation had a major impact on the densities of *H. diversicolor*. The relative importance of bird and nekton predation varied along the study, and this seems to be determined by different peaks of abundance of the two types of predators. However, when present in high densities, birds and nekton seem to have a similar impact on *H. diversicolor*. Our results suggest that predation is a key factor on the population dynamics of *H. diversicolor*. In addition, the levels of predation that we observed suggest that this polychaete can be a limited resource, and this could have major ecological consequences for predators for which it is a key prey.

Keywords: *Hediste diversicolor*; intertidal mudflat; Tagus estuary; predation; waders; nekton

1. Introduction

Benthic macroinvertebrates are key prey in estuarine food webs, supporting a wide range of predators, such as crabs, shrimps, fishes and birds (e.g. Kalejta and Hockey, 1991; Sprung, 1994; Barry et al., 1996; Moreira, 1997; Baeta et al., 2006). Polychaetes are particularly important prey for many predators (e.g. Moreira, 1999; Cabral, 2000; Baeta et al., 2006) because they have high nutritional value compared with other estuarine macroinvertebrates (Cummins and Wuycheck, 1971).

Several studies have tested whether birds, fish and other estuarine predators can have a significant impact on the composition and structure of benthic macroinvertebrate communities of intertidal flats (Quammen, 1984; Raffaelli and Milne, 1987; Sewell, 1996; Hindell et al., 2001; Hiddink et al., 2002; Como et al., 2004; Hamer et al., 2006; Mendonça et al., 2007). This impact potentially depresses the densities of prey species, and

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thus affecting the structure and dynamics of benthic invertebrate communities (Thrush, 1999).

In general the biomass removed by predation on benthic invertebrates in estuaries is only a relatively small fraction of the biomass available (Scheiffarth and Nehls, 1997; Hampel et al., 2005). However, in locations with high predator densities, and/or in periods of the year when their energetic needs are particularly high, such as when waders are preparing for migration, predation pressure may cause depletion of prey, with several ecological consequences (Schneider and Harrington, 1981). Facing food shortage, predators may be forced to find alternative food items (Beukema, 1993; Piersma et al., 1993) or feeding locations (Goss-Custard et al., 1996). In these situations prey may become a limited resource, causing competition among the species that depend on them (Hamer et al., 2006).

A common approach to study the impact of predators on benthic invertebrates is the use of exclusion experiments, in which areas exposed to predation are compared with plots where access to predators is experimentally blocked. The results of these experiments have been rather variable (e.g. Quammen, 1984; Raffaelli and Milne, 1987), but most failed to detect evidence of impacts of predation on macroinvertebrate densities (e.g. Sewell, 1996; Hindell et al., 2001; Hamer et al., 2006). However, several authors have identified three major weaknesses in the design of most experiments carried out so far: (1) the small size of samples and experimental plots (e.g. Raffaelli and Milne, 1987), (2) the lack of consideration of size-specific predation (Hamer et al., 2006), and (3) the influence of the experimental manipulations on the sediment characteristics and thus on invertebrate response (e.g. Sewell, 1996).

In fact, most studies were based on relatively modest sample sizes and small experimental areas (e.g. Raffaelli and Milne, 1987), and this may justify why predation effects could not be detected. Densities of invertebrates before and after the exclusion manipulations are usually estimated by sampling the sediment with cylindrical cores. However, the small area covered by each core, and the high variance of the results among cores may contribute for the failure to detect significant decreases in invertebrate numbers (Sewell, 1996).

Another potential reason for the failure to detect an impact of predation is the pooling of all the species and sizes present in the sediment, especially in the case of bivalves. In fact, not all invertebrate species are consumed, and some predators only take some size classes of the consumed species (e.g. Piersma et al., 1993; Moreira, 1994; Santos et al., 2005).

Finally, experimental artefacts may also limit the success of exclusion experiments. Some authors claim that the treatments may change sediment properties (Piersma, 1987), and other environmental parameters (Hindell et al., 2001), making it difficult to assure that predation is the only factor varying among treatments. In spite of these shortcomings, exclusion experiments remain the best method for measuring predation potential (Aronson and Heck, 1995), but it is essential to control the influence of experimental artefacts.

The polychaete *Hediste diversicolor* is one of the most important prey items for waders and fish in European estuaries (e.g. Chambers and Milne, 1975; García-Arberas and Rallo, 2002; Hampel et al., 2005). It is generally consumed whole, which contributes to make it a good model to test the impact of predation by estuarine organisms. Indeed, the impact on some other important prey is confounded by the fact that they may survive predation, because they are only partially eaten. This is the case of the bivalve *Scrobicularia plana*, which often has its siphons harvested by predators (Zwarts and Wanink, 1989; Moreira, 1999).

In this study we experimentally tested and quantified the impact of predation on the polychaete *Hediste diversicolor*, using predator exclosures. The experimental design, which minimized the main described shortcomings of exclusion manipulations, also allowed us to distinguish the impact of nekton (here mostly fish and crustaceans) and bird predators.

2. Methods

2.1. Study area

This study was carried out in the Tagus estuary (38°45′ N, 09°02′ W, Fig. 1), one of the most important wetland areas for wintering and migratory waders in Western Europe. It is also an important nursery area for several commercially important fish species, like the flatfish (Cabral et al., 2007). The Tagus estuary is classified as a Nature Reserve, and a Special Protection Area under the European Birds Directive.

In this estuary the tides are semi-diurnal and have amplitude ranging from 1 to 3.8 m in neap and spring tides, respectively. Most of the intertidal flats are muddy, with comparatively small sandy areas and scattered (dead) oyster banks (Rodrigues et al., 2006). We selected a homogeneous study area with a mud content of about 95%, in an area known to be intensively used by waders during the winter and migratory periods (Dias et al., 2006; Granadeiro et al., 2006). The most abundant macroinvertebrates were the bivalve *Scrobicularia plana*, the gastropod *Hydrobia ulvae* and the polychaete *Hediste diversicolor* (unpublished data). The epifauna of the estuary is also rich and species like shrimps, crabs and smaller fish occur in high densities (Costa and Bruxelas, 1989). For sake of simplicity all these groups will be referred to as nekton.

Most of the waterbird and nekton community feed on the polychaete *Hediste diversicolor*. The nekton and bird species known to occur in the study area consume the entire size range (and age-classes, Cabral et al., unpublished, Lourenço et al., 2005), although individual species may select specific sizes (e.g. Moreira, 1994; Scheiffarth, 2001; Santos et al., 2005). *Hediste diversicolor* is the macrofauna polychaete with greatest density and biomass in the whole Tagus estuary (Rodrigues et al., 2006), and consequently is a very important species in its food web. The recruitment events of *H. diversicolor* are highly variable among estuaries, but generally there are two main recruitment periods during the year (Chambers and Milne, 1975; García-Arberas and Rallo, 2002). In the Tagus estuary recruitment events were detected between early spring and late summer (Silva et al., 2006). This species is