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The effect of macrofaunal disturbance on *Cerastoderma edule* post-larvae

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ABSTRACT

Populations of the Common European cockle (*Cerastoderma edule*) often have highly patchy distributions and variable recruitment success. One of the proposed reasons is that high densities of filter feeders and/or bioturbators are thought to reduce the success of larval settlement and post-settlement survival, but the direct causal processes driving these observations are not clearly identified and validated. Through combined field and laboratory experiments, we test the hypothesis that macrofauna cause decreases in post-larval density through feeding and movement activities. The effect of excluding the bioturbating lugworm *Arenicola marina* and filter-feeding adult cockles on post-larval cockle densities was estimated in separate field experiments at two locations from the time of initial larval settlement in May 2012 to late summer August 2012. Lugworm exclusion led to a significant increase in cockle post-larval densities whereas the opposite was true for adult cockles, where exclusion led to a reduction in *C. edule* post-larval density. Although clear effects were observed in the field, experiments conducted in the laboratory failed to detect changes in mortality or byssus drifting of post-larvae as a consequence of macrofaunal activity. This study demonstrates that the presence of macrofauna can have both positive and negative effects on post-settlement density of *C. edule* post-larvae. Thus the density, distribution and identity of macrofauna have significant effects on the density and spatial distribution of *C. edule* post-larvae during the post-settlement period. These observations have implications for conservation and fishery management of this species.

1. Introduction

Identifying processes influencing the success and spatial distribution of recruitment in populations is important for our understanding of ecosystems (Sutherland et al., 2013). Ascertaining and disentangling key processes driving recruitment in intertidal soft sediment systems are challenging due to the highly mobile early life stages of many species, and the importance of biological interactions (Reise, 2002; Rhoads and Young, 1970). The common European cockle *Cerastoderma edule* is an important species on North East Atlantic soft-sediment tidal flats, both commercially (Hicken, 2008) and ecologically (Flach, 1996). The cohort strength and distribution of adults is largely determined during the post-settlement stage (0-group), which is considered as the period from larval settlement through to survival of their first winter (Beukema and Dekker, 2005). The occurrence of high *C. edule* post-settlement mortality due to predation (Jensen and Jensen, 1985; Whitton et al., 2012) and their ability to migrate, using a byssus thread to increase hydrodynamic drag, during this post-settlement period is understood to influence subsequent adult densities and spatial patterns (Armonies, 1994). However, interactions with other fauna may also be influential. Habitat engineering (Reise, 2002) through sediment surface disturbance by deposit feeders, burrowers and bioturbators may prevent larvae and post-larvae colonising affected areas, creating discrete patches in some species (Woodin, 1976). The importance of such interactions in soft sediments and the importance of the post-larval stage in *C. edule* for recruitment success (Beukema and Dekker, 2005), suggest that such processes could create spatial patterns in adult density.

Adults of the lugworm *Arenicola marina* (a burrowing deposit-feeding polychaete) and *C. edule* (a shallow burrowing surface-dwelling suspension-feeding mollusc) can make major contributions, 18.8 and 16.2% respectively (Beukema, 1976), to the macrofaunal biomass in north western European intertidal flats (Beukema, 1976). They are both considered bioturbators because they modify the physical and biological characteristics of sediment, through the physical disturbance of their surroundings (Flach and de Bruin, 1994; Flach, 1996). This bioturbation occurs when lugworm cause surface sediment to enter their burrow at the feeding depression, and deposit sediment onto the sediment surface when defecating. When lugworms are excluded from an area the biological and physical habitat is likely to change. For example abundances in microbes can increase (Lei et al., 2010), meiofauna have been shown to decrease (Reise, 1985), and some macrofauna species (Flach, 1992; Volkenborn et al., 2009) and halophytic plants (Van Wesenbeeck et al., 2007) that depend on more stable sediment appear or increase in density. These biological responses are often due to the loss of the feeding burrows affecting

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oxygen penetration and the associated sediment reworking (Reise, 1985; Wendelboe et al., 2013). Although a less active bioturbator, *C. edule* also disturbs the surrounding sediment when closing its shell valves, and when making horizontal and vertical movements (Flach, 1996).

Habitat modification by cockles and lugworm may influence the suitability of areas for *C. edule* post-larval settlement. Lugworm can reduce densities of post-larval *C. edule* when excluded from sediment (Flach, 2003, 1992). Similarly exclusion of *C. edule* has been shown to modify post-larval density (Flach, 2003, 1996), but outcomes have been variable. These studies found no effect or even an increase in post-larval density (de Montaudouin and Bachelet, 1996; Van Colen et al., 2013), temporally variable outcomes (Andre and Rosenberg, 1991) and in general there is little evidence of a negative linear relationship between adult cockle density and post-larval density. Interestingly, recent studies have demonstrated that adult cockles may facilitate settlement success through sediment stabilisation under certain conditions (Donadi et al., 2014, 2013b), and so uncertainty remains about the direction and predictability of adult/post-larval interactions in cockles.

Interactions between macrofauna and *C. edule* post-larvae may be operating directly or indirectly. Direct interactions may include ingestion of the post-larvae by macrofauna (Hiddink et al., 2002b), and mortality or emigration as a consequence of disturbance caused by bioturbatory activities (Armonies, 1996). Indirectly the presence of macrofauna may increase post-larval mortality through predation, by increasing their vulnerability as they are disturbed and become exposed at the sediment surface or through increasing their movement (Flach and de Bruin, 1994; Flach, 2003).

The overarching question of this study was what effect macrofauna are having on *C. edule* post-larval densities. To address the question combined field and laboratory experiments were conducted. The field experiment conducted tested the effect of macrofauna on natural settlement and post-settlement densities, with the laboratory studies seeking to investigate the poorly understood causative processes. In the field, we tested the hypothesis that the presence of *A. marina* and adult *C. edule* independently decreases post-larval density compared to lugworm and cockle free areas. It is expected that the predicted effect will increase in magnitude over time due to increasing interaction events with macrofauna. In the laboratory experiments were established to assess both direct effects of adult *A. marina* (ingestion, smothering and disturbance due to feeding activities) and adult *C. edule* (smothering and disturbance due to the movements of adult *C. edule*) *and the role of refugia in modifying disturbance effects*. In addition using a flume, we investigated whether the presence of macrofauna increased the number of *C. edule* post-larvae undertaking byssus drifting compared with those in macrofauna free sediment. Byssus drifting has a high potential to create spatial patterns and density changes post-settlement. If certain conditions that vary in space and time trigger migrations, such as macrofauna presence, then spatial patterns could change significantly over a few tidal cycles (Armonies, 1994).

2. Methods

2.1. Field experiment general approach

To observe the possible effects of adult cockles *C. edule* and lugworm *A. marina* on colonisation of *C. edule* post-larvae, separate field experiments were undertaken in the Dee estuary, on the English–Welsh border (53°20′52 N, 03°10′38 W) (Fig. 1A), and Traeth Melynog on the Isle of Anglesey, North Wales (53°08′22 N, 04°19′47 W) (Fig. 1B). In the Dee estuary cockles were excluded from experimental plots and at Traeth Melynog lugworm were excluded, as each location was best suited to manipulating only one of the macrofauna species. 18 plots were established at each location comprising a 3 × 6 grid of 1 m^2 plots, with a 10 m separation between each plot (Fig. 1). Three treatments were randomly allocated across the 18 plots at each site: 1) an untouched control 2) an exclusion treatment where either lugworm or adult cockles were excluded and 3) a procedural control to account for the disturbance of excluding these macrofauna. The corners of each plot were marked with a bamboo stake that extended less than 10 cm above the sediment, to minimise drag and the chance of algae accumulating on the markers. The plots were sampled following the first detection of larval settlement (May to June) for 3 to 4 months, to understand how densities of post-larval cockles changed temporally among the treatments. *C. edule* post-larvae were quantitatively sampled using a 64 mm diameter corer (3217 mm^2) to a depth of 15 mm. Random replicate cores were taken from each plot and the number of post-larvae counted and pooled.

2.1.1. Adult C. edule exclusion field experiment, Dee estuary

Individuals of *C. edule* over 15 mm in length were removed from the 1 m^2 experimental exclusion plots on 9th May 2012. Plots were raked to a depth of 15 cm and the sediment placed into a mesh bag. This allowed the sediment to pass through but retained cockles. The procedural control plots were raked in the same way, but instead of sieving the sediment the cockles that were retained by the rake were redistributed in the plot and allowed to re-burrow. Control plots were left undisturbed. Underlying patchiness in standing water pools and microphytobenthos among the plots was observed, but not quantified. Plots were sampled on three occasions using three pooled cores per plot (<1% of total plot area) on 17th May, 19th June and the 2nd July 2012. Sampling was not conducted after 2nd of July because this marked the beginning of the cockle fishing season in the Dee estuary, when the chance of human disturbance to experimental plots was high. On the final sampling occasion sediment from a 0.1 m^2 quadrat was removed to a depth of 5 cm in the centre of each plot and sieved over 2 mm mesh to ascertain if there were any large cockles (>2 mm) in the experimental plots that had either escaped the initial raking procedure, or migrated into the plots afterwards.

2.1.2. Lugworm exclusion field experiment, Traeth Melynog

Lugworm in the experimental plots were excluded by digging out the sediment in the plots to a depth of at least 10 cm. Subsequent immigration of lugworms into the plots was prevented by burying a horizontal 1 m^2 square of plastic mesh (2 × 2 mm mesh) at a depth of 10 cm in the sediment, and returning the excavated sediment onto the mesh (Fig. 2). This method has been successfully used in other studies to exclude lugworm from sediment (Volkenborn and Reise, 2007, 2006; Volkenborn et al., 2009). The procedural control plots were created by digging and turning over the sediment to a depth of 10 cm in the same way as the exclusion plots, but without any mesh being placed before the sediment was returned. Plots were dug on 18th April 2012 to allow enough time (29 days) for recovery of the sediment structure from disturbance before sampling for *C. edule* post-larvae on 16th May, 18th June, 20th July, 26th July and 23rd of August 2012. During the first three sampling events three cores were taken per plot and pooled, but from July to August eight cores were taken per plot due to decreasing densities of post-larvae. On the 20th July the number of lugworm feeding depressions and faecal casts present within three 0.1 m^2 quadrats per plot were recorded. Build-up of loose macro-algae around the plot markers was removed on each sampling occasion from both the Dee estuary and Traeth Melynog locations (Fig. 2A and B).

2.2. Laboratory experiments

2.2.1. Aquarium study

2.2.1.1. Macrofauna presence and density. To determine the effect of macrofauna identity and density on post-larval cockle survival and growth, a two-way factorial design was used. The factor 'macrofauna' had three levels: adult cockles present; lugworms present and a control with no