Journal of Experimental Marine Biology and Ecology 331 (2006) 91–98

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*

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Received 4 July 2005; received in revised form 4 October 2005; accepted 10 October 2005

Abstract

The responses of the burrowing bivalves *Macoma balthica* and *Cerastoderma edule* to chemical cues emitted by feeding shore crabs *Carcinus maenas* were investigated. *M. balthica* held in the laboratory and exposed to chemical signals in effluent water discharging from tanks containing *C. maenas* fed 20 *M. balthica* day^{-1} reacted by increasing their burial depths from approximately 30 mm to depths of >60 mm, over a period of several days. When the signal was removed the bivalves gradually returned to their original depth over 5 days. *C. edule* similarly exposed to effluent from crabs feeding on conspecifics showed no response. In an attempt to identify the signal inducing this burrowing response, *M. balthica* were exposed to a variety of chemical signals. Crabs fed *M. balthica* elicited the strongest response, followed by crabs fed *C. edule*. There were also small responses to effluent from crabs fed on fish, crabs previously fed on *M. balthica* and to crab faeces, but no responses to starved crabs, crushed *M. balthica*, or controls. We conclude that increased burrowing depth of *M. balthica* is induced by some as yet unidentified chemical cue produced by feeding crabs and is strongest when the crabs were fed on *M. balthica*. Unexpectedly, neither the presence of crabs themselves, nor of damaged conspecifics, was effective in eliciting a burrowing response. The mortality rates of *M. balthica* and *C. edule* selected by crabs when burrowed at normal depths and after exposure to effluent from feeding crabs were different. Crabs selected 1.5 times more *C. edule* than *M. balthica* when both species were burrowed at their normal depths, but 15 times more after the tanks had been exposed to effluent from feeding crabs for 5 days. The burrowing response of *M. balthica* thus appears to reduce mortality significantly by displacing predation pressure on to the more accessible *C. edule*.

Keywords: Alarm signals; Burrowing behaviour; *Cerastoderma edule*; *Macoma balthica*; Predator avoidance

1. Introduction

Chemically mediated defence responses are widespread in both freshwater and marine ecosystems (for review see Harvell, 1990; Tollrian and Harvell, 1999). Such responses are triggered by water-borne alarm substances, which can be released by the predator, or by damaged prey, and may result in either morphological or behavioural responses by the prey species, such that their vulnerability to predation is reduced (see Wisenden, 2000). The advantage of such inducible responses, over purely genetic ones, is that of flexibility, since the costs associated with defence are only incurred when the threat of predation is high (Harvell, 1990; Behrens Yamada et al., 1998). Many marine

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doi:10.1016/j.jembe.2005.10.002

invertebrates exhibit such responses, including the induction of protective spines in bryozoans (Harvell, 1984), extension and opening of pedicellaria in sea urchins (Phillips, 1978) and changes in shell morphology in barnacles (Lively, 1986). The greatest range of responses has, however, been reported amongst molluscs. Chemically mediated defence responses within the Gastropoda include morphological adaptations, such as reduced growth or reproductive output and thickening of the shell lip in whelks (Appleton and Palmer, 1988; Palmer, 1990; Rawlings, 1994) and littorinid snails (Behrens Yamada et al., 1998), as well as behavioural ones, such as predator avoidance behaviour in periwinkles (Phillips, 1978; Behrens Yamada et al., 1998; Jacobsen and Stabell, 1999; Keppel and Scrosati, 2004) and mud snails (Ashkenas and Atema, 1978).

To date the only work on chemically mediated defence responses in bivalves has focussed on the mussel, *Mytilus edulis*. Responses reported in this species include the development of enlarged adductor muscles and thickening of the shell (Reimer and Tedengren, 1996; Leonard et al., 1999), production of additional byssus (Cote, 1995; Dolmer, 1998; Leonard et al., 1999; Smith and Jennings, 2000) and clumping behaviour (Cote and Jelnikar, 1999). To our knowledge no studies have demonstrated chemically mediated predator avoidance responses in soft sediment bivalves, despite the fact that such species are heavily exploited by a variety of predators, notably crabs, birds and fish (for review see Seed, 1993). Burrowing bivalves can reduce the risks of predator-induced mortality in a variety of ways (Vermeij, 1978), including the colonisation of spatial refuges, such as the high intertidal, or regions of extreme or fluctuating salinity, the development of structural defences, such as large body size, thickened or ornamented shells or by employing avoidance responses (Seed, 1993). The most commonly used avoidance response is to increase burrowing depth, which is known to provide protection against both bird and crab predators (Blundon and Kennedy, 1982; Haddon et al., 1987; Zwarts and Wanink, 1989).

The extensive intertidal sand and mudflats of Europe support dense populations of burrowing bivalves, such as the cockle, *Cerastoderma edule* and the tellinid clam *Macoma balthica*. These species are subject to intense predation pressure from birds, especially oystercatchers, which feed and select large individuals (>20 mm) high on the shore, and from shore crabs *Carcinus maenas*, which prey mostly on smaller individuals (<15 mm) at lower tidal levels (Sanchez-Salazar et al., 1987b). As a result the density, size and spatial distributions of these bivalve populations are largely determined by the seasonality and spatial pattern of predation pressure (Sanchez-Salazar et al., 1987b; Richards et al., 1999). *C. edule* has a robust and globular shell, which is relatively resistant to crab predation (Sanchez-Salazar et al., 1987a). As a result crabs selectively take only small cockles in the size range 5–15 mm and larger cockles exhibit a 'refuge in size' in which they are relatively immune to attack by *C. maenas* (Sanchez-Salazar et al., 1987a). Conversely since *C. edule* is an obligate suspension feeder, with short siphons, it is obliged to remain close to the sediment surface. By contract *M. balthica* is a smaller species, attaining a size of ~20 mm in European waters, with a slender, lightly built shell and long feeding siphons and is capable of switching between suspension and deposit feeding. Increased burrowing depth in *M. balthica* provides protection from epi-benthic predators, but imposes a cost involved in employing this strategy in that deeper burial leads to a decrease in the feeding radius of the siphons and in turn a reduction in growth rate (Zwarts and Wanink, 1989; Zwarts et al., 1994; De Goeij and Luttikhuizen, 1998). The optimal behaviour pattern in this species would thus appear to be to increase burial depth when the risk of predation is high, but return close to the surface to feed when the risk declines.

In this study we examine for the first time whether burrowing bivalves show a chemically mediated predator avoidance response and attempt to identify the nature of the signal inducing such a response. Finally, we determine whether chemically mediated increases in burrowing depth in *M. balthica* contribute to significant reductions in predation.

2. Methods

M. balthica and *C. edule* were collected during July and August from the mid to upper intertidal zone in Red Wharf Bay, Anglesey, UK, by removing the top 5–10 cm of sediment with a spade and sieving it through 2 mm mesh. Shore crabs *C. maenas* (carapace widths 50–60 mm) were collected using a hoop net baited with fish deployed from Menai Bridge pier, Anglesey. Obtaining crabs using fish bait ensured they were all actively feeding before the predation experiments were undertaken. Upon collection all the experimental animals were maintained in flowing seawater. Bivalves were held in open plastic buckets containing a 10 cm depth of sediment from the collection site, whilst the crabs were kept in similar buckets, without sediment, but with weighted perspex lids, and were fed daily with a mixture of *C. edule* and *M. balthica*.