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Breaking and entering: Examining the role of stress and aerial exposure in predator–prey relationships between the common shore crab (*Carcinus maenas*) and cultivated blue mussels (*Mytilus edulis*)

Julia Calderwood [a,b,*], Nessa E. O'Connor [a,b,c], Dai Roberts [a,b]

[a] Queen's University Marine Laboratory, 12-13 The Strand, Portaferry, Co. Down, Northern Ireland, BT22 1PF, UK
[b] School of Biological Sciences, Medical Biology Centre, Queen's University Belfast, 97 Lisburn Road, Belfast, BT9 7BL, UK
[c] Institute of Global Food Security, Queen's University Belfast, 18-30 Malone Road, Belfast, BT9 5BN, UK

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ABSTRACT

During benthic cultivation *Mytilus edulis* (blue mussels) are subject to predation pressure from a number of predators including *Carcinus maenas* (shore crabs). This predator can be responsible for substantial losses of mussels from the fishery and a full understanding of the predator–prey relationship between *M. edulis* and *C. maenas* is required to ensure attempts that reduce predatory pressure and subsequent commercial loss are successful. Whilst much work has examined the prey–predator size relationships between *C. maenas* and *M. edulis*, far less research has investigated how stress, such as periods of extended aerial exposure, may affect these relationships. We tested whether profit in terms of calories gained by crabs consuming mussels stressed by aerial exposure for 48 h differed from that of mussels at ambient conditions and whether being stressed affected the mussel's likelihood of predation. We also tested whether the size relationship between predators and their prey differed when mussels were stressed. We found that the profitability of prey (calories gained per second of handling time) did not vary between stressed and unstressed mussels. Handling times for stressed and unstressed mussels were similar, even when crabs were presented with mussels of the maximum size that they are able to consume. Small crabs were more likely to reject a mussel of preferred size if it was unstressed, suggesting that crabs may be able to assess that these mussels would require extra effort to break into and consume. Our findings suggest that the predator–prey relationship between mussels and crabs is not altered when mussels are stressed. *C. maenas* remains a voracious predator and regardless of the condition of mussels laid on commercial beds there is a need to control this predator in attempt to reduce losses in the benthic fishery.

Statement of relevance: This work is directly relevant to those involved in the benthic cultivation of mussels. Whilst extensive research has investigated sized-based predator–prey relationships but very little is known about how stress may alter the relationship between *Carcinus maenas* and *Mytilus edulis*. Our findings have particular relevance to the on-growing of mussels in benthic cultivation and demonstrate that efforts made during handling and transportation processes to maintain mussel condition do not increase their resilience to predation. This research can be used to inform producers on the impacts of predators on their crop and highlights the continued need to monitor and control them to reduce losses and ensure monetary profit.

1. Introduction

Intensive monoculture of marine biota occurs throughout the world with aquaculture representing the fastest-growing animal food producing sector globally (Beadman et al., 2004). World aquaculture production reached a high of 60 million tonnes in 2010 with an estimated value of $119 billion (FAO, 2012a). Of this total 1.8 million tonnes of mussels were produced by aquaculture in 2010 with a market value of greater than $1.5 billion (FAO, 2012b). Mussels provide an ideal group of organisms for mariculture owing to their high fecundity coupled with a relatively fast growth rate (Newell, 1989). Mussels are cultivated throughout the world using various techniques including bouchot culture, where mussels are grown on poles set in the intertidal zone, suspended culture, where mussels are grown on ropes suspended in the water column and benthic cultivation, where mussels are grown on the sea bed (Spencer, 2002). Benthic mussel cultivation is practised commonly in Europe (Smaal, 2002) and involves transplantation of wild 'seed' mussels from natural beds, where high densities result in poor growth, to culture sites where mussels are relaid at low densities. Culture sites are usually located in sheltered in-shore waters with a good food supply allowing mussels to grow to a marketable size in

* Corresponding author at: Queen's University Marine Laboratory, 12-13 The Strand, Portaferry, Co. Down, Northern Ireland, BT22 1PF, UK.
E-mail address: jcalderwood05@qub.ac.uk (J. Calderwood).

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two years or less. With this method of aquaculture, cultured animals are subject to the same predatory pressures as wild populations. Predators such as starfish, crabs, gastropods and birds can, therefore, play a major role in the mortality of cultivated molluscs feeding on them both intertidally and subtidally (Beadman et al., 2003; Hickman, 1992; Spencer, 2002). As a consequence, the mechanisms of predation and factors affecting predation rates are of particular interest to mussel cultivators who can lose a substantial proportion of their crop to predators, thus, reducing the economic output of such fisheries (Beadman et al., 2003; Dare and Edwards, 1976).

The shore crab *Carcinus maenas* is an opportunistic feeder with a varied diet, largely determined by the availability of different prey species, although it is thought to prefer molluscan prey (Baeta et al., 2006; Levinton, 2001; Murray et al., 2007). The feeding preferences of *C. maenas* have indeed been shown to result in a negative effect on a number of inshore commercial shellfish species globally (Klassen and Locke, 2007; Leignel et al., 2014; Lowe et al., 2000; O'Connor et al., 2013; Walton et al., 2002). In addition, as an invasive species, *C. maenas* had a detrimental impact on clam fisheries in Australia as well as clam, oyster and mussel fisheries in North America and Canada (Jamieson et al., 1998; Miron et al., 2005; Walton et al., 2002). Within its native range in Europe, *C. maenas* is a significant predator of subtidal mussels and has been reported to have a considerable impact on cultivated stocks of *Mytilus edulis* (DARD, 2008; Miron et al., 2005; Murray et al., 2007; Spencer, 2002). For example, it has been estimated that *C. maenas* is responsible for losses of greater than 10% of mussels from benthic cultivation plots in the Menai Straits, Wales (Murray et al., 2007). The vulnerability of an individual mussel to crab predation is influenced by numerous mechanisms and may vary with the profitability of individual prey items and the density of adjacent prey (Brousseau et al., 2001) and may be size-specific (Elner and Hughes, 1978; Elner, 1980; Smallegange et al., 2008). *C. maenas* has been shown to forage optimally on mussels by choosing sizes that maximise the rate of energy intake in relation to time spent foraging, although constraints such as the potential for claw damage, can result in a preference for smaller sub-optimal prey items (Elner and Hughes, 1978; Elner, 1980; Hughes, 1980; Smallegange and Van Der Meer, 2003).

Whilst a significant amount of research has been performed on the effect of size on predator–prey interactions, there is an additional need to consider how such species interactions may vary under extreme conditions (Sanford, 2002). Although a number of studies have considered how stressful environmental conditions may affect the behaviour and functional role of consumers (Menge and Farrell, 1989; Menge and Sutherland, 1976; O'Connor et al., 2011; Petes et al., 2008), comparatively less research has addressed how stress imposed on their prey may alter predator–prey interactions. Stressors, such as elevated body temperature, have been shown to result in a reduction in the valve sealing efficiency of a mussel which could reduce its ability to withstand attack from a predator (Dowd and Somero, 2013). Aquaculture practises introduce additional stressors to marine communities through practises such as the handling, transportation and sorting of organisms (Lacoste et al., 2001; Calderwood et al., 2014). It is of interest to those involved in the benthic production of mussels to understand how a reduction in mussel condition, as a result of specific stressors, may affect their vulnerability to predation. This study tested whether the size relationship between predators (crabs) and their prey (mussels) was affected when the prey organism was stressed. By examining controlled predator–prey interactions between *C. maenas* and *M. edulis*, we tested the hypotheses that: (a) stressed mussels will be more profitable to eat than unstressed mussels; (b) predator–prey size relationships will differ between stressed and unstressed mussels, with crabs eating more stressed mussels at the top end of their consumable size range than unstressed mussels; (c) stressed mussels will be more prone to predation than unstressed mussels, and (d) the feeding rate of *C. maenas* presented with increasing densities of *M. edulis* (i.e. functional response) will differ between stressed and unstressed mussels.

2. Materials and methods

2.1. Experimental set-up

Two experiments were carried out at Queen's University Marine Laboratory in Portaferry, Northern Ireland, between 4th July and 27th September 2013. For both experiments a total of 300 shore crabs (*C. maenas*; mean carapace width = 59.2 mm (± 0.3 S.E.)) were collected using baited pots at Strangford Lough (54° 23′ 26.89″ N; 5° 34′ 8.17″ W) and kept in holding tanks until required. Only undamaged, male crabs were used for experiments to eliminate variation that may result from differences in morphology and predation behaviour between males and females (Barbeau et al., 1998; Elner and Hughes, 1978; Smallegange et al., 2008; Flynn et al., 2015). Crabs were fed to satiation on mussel flesh before being transferred to individual 6 L aquaria where they were starved for 72 h prior to the start of the experiments to standardise hunger levels (Alexander et al., 2015; Micheli, 1995).

The first experiment assessed prey profitability and examined predator–prey size relationships and prey vulnerability, using 160 mussels (*M. edulis*; mean shell length = 26.0 mm (± 0.3 S.E.)) collected at low tide from Strangford Lough, Northern Ireland taking care to cut byssus threads to avoid causing internal damage and unnecessary stress to mussels(54° 29′ 21.73″ N; 5° 32′ 27.22″ W). Prior to the start of the experiments, all mussels were cleaned of epibionts and acclimatised for 7 days in 430 L holding tanks, supplied with a constant flow of sand-filtered seawater pumped from Strangford Lough at a rate to 1.25 L min^{-1} (Maire et al., 2010; Shepard et al., 2000). Mussels used were either 'unstressed' and transferred directly from holding tanks to the experimental aquaria where they remained immersed at all times, or were 'stressed' by being emersed in a temperature controlled room at 9.8 °C (+/−0.4 °C) for 48 h prior to the start of the experiments. The 48-h period of emersion was chosen based on the results of a previous study (Calderwood et al., 2014), which showed that transportation periods of 48 h, as experienced during the transportation of mussels from seed beds to on-growing plots, had a detrimental effect on the physiology and subsequent behaviour of *M. edulis*.

The calorific value of mussel tissue was quantified to estimate whether the value of the prey for the predator differed between stressed and unstressed mussels. Total wet biomass, length, width and girth of stressed and unstressed mussels ($n = 20$) was recorded before whole tissue was dissected from the shells and dried at 60 °C for 48 h. The calorific content of dried tissue samples was determined with the use of an oxygen bomb calorimeter (Parr, Illinois, USA).

To examine predator–prey size relationships and prey vulnerability crabs were divided into two size classes (small crabs = 50 mm ≤ 60 mm; large crabs = 60 mm ≤ 70 mm carapace width). Individual crabs from each of the two size classes, were placed in an individual aquarium and allocated a single stressed or unstressed mussel of either their preferred or maximum size. Mussels were selected to ensure that the shell length of each (whether of preferred or maximum size) was scaled to the size of each crab based on carapace width (Murray et al., 2007), resulting in a total of eight experimental treatments, each being replicated 20 times. Ten individual feeding trials were run per day in a randomised design, with all trials being completed within 3 weeks. Each feeding trial took place under low-level lighting with the observer positioned to the side of the experimental aquarium to avoid visual disturbances to the crab. After a mussel was added to an aquaria containing a crab, the different stages of predation were timed following Elner and Hughes (1978): 'attack time' (time taken from mussel entering the aquarium to first contact between the crab with the mussel); 'breaking time' (time taken from crab first making contact with the mussel, through breaking the shell open, to taking a first bite of flesh); 'eating time' (the period between taking the first bit of flesh to abandoning the shell, which could include further breaking and entering attempts in order to extract all flesh from the shell); and 'handling time' (breaking and eating time combined). Profitability was