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BEHAVIOURAL ADAPTATIONS OF MUSSELS TO VARYING LEVELS OF FOOD AVAILABILITY AND PREDATION RISK

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ABSTRACT

Blue mussels Mytilus edulis (n = 14) were studied in the laboratory using Hall sensor systems to record their gaping behaviour when exposed to varying food rations and levels of predation risk. Mussel response to increasing daily algal ration was to increase mean gape angle per day and was associated with copious pseudofaeces production at excessive initial algal concentrations, e.g. 250 cells/μL. Mean gape angle decreased (backward S-shaped curve) when fed a fixed algal ration per day where simulated predation risk (introduced fresh mussel homogenate) increased in the water, presumably as an anti-predation strategy. However, this behaviour is presumed to lower feeding rates. There was a general positive relationship between both gape angle and the extent of valve movement (adduction/abduction) per event and valve movement speed. However, the fastest valve adduction events, which resulted in valve closure, were recorded independent of gape angle and only when mussels were first exposed to high perceived predation risk. We interpret this as an appropriate response, with high energetic cost, as a first line of defence from predators such as starfish and crabs. Overall, mussel response to predation appears graded and complex, indicating a trade-off between maximizing feeding/pseudofaeces production and minimizing predation risk.

INTRODUCTION

Adult bivalves are often sessile or minimally motile and therefore generally cannot choose where they feed. However, they still face trade-offs between maximizing feeding rate and minimizing risks that vary over time as their environment changes around them. Bivalves such as mussels and oysters must open their hard, protective shells in order for their ciliary filter-feeding system to extract particulate and dissolve matter from the water column, with a greater angle of shell gape (aperture) generally allowing a greater flow of water through the bivalve and hence a higher rate of matter extraction (e.g. Nagai et al., 2006). However, a mussel’s first line of defence from predators such as starfish (Asteroidae) and crabs (Decapoda) is to close, preventing entry. It thus seems likely that a wider shell gape increases the chance of their shell being breached by these predators and by others such as oystercatchers (Haematopus ostralegus). Once the shell is closed the risk of predation by starfish and crabs is then dependent on other factors such as shell thickness, compressive strength, shell lip thickness, adductor muscle strength and byssus attachment strength (Leonard, Bertness & Yund, 1999; Readman et al., 2003).

The nervous system of blue mussels Mytilus edulis (see Stefano, 1990) has a suite of sensory systems including mechanoreceptors (e.g. LaCourse & Northrop, 1977) and olfactory receptors (reviewed in Kats & Dill, 1998) that can presumably detect the movements and chemical cues of both predators and food (cf. Rovero, Hughes & Chelazzi, 1999). We examined the possibility that mussels exhibit appropriate, complex responses by weighing up their need to feed against and the likelihood of predation. Specifically, we hypothesize that mussel feeding rate should generally decrease with perceived predation risk (cf. Leonard et al., 1999). Data were collected using Hall sensor systems (Wilson, Reuter & Wahl, 2003; Robson et al., 2009) to record mussel gape angle in the laboratory. Gape angle was used as a proxy for feeding (Dolmer, 2000; Wilson et al., 2005; Saurel et al., 2007) and general mussel activity (Robson et al., 2009).

MATERIAL AND METHODS

Overall experimental design

To make measurements of valve gape relative between bivalves of different lengths, we modified the methods developed by Wilson et al. (2005) to quantify gape angle in blue mussels (Robson et al., 2009). Briefly, this involved quantifying bivalve gape angle (°) using a Hall sensor (a transducer for magnetic field strength) attached to one shell valve reacting to a magnet attached to the other shell valve. Variation in gape extent produced a corresponding variation in the magnetic field strength perceived by the Hall sensor (cf. Wilson et al., 2002). This was recorded by an archival logger. Since Hall sensor output is proportional to magnetic field strength and angle of impingement, the sensor output has to be calibrated by comparing shell gape angle with sensor output, over a wide range of angles. To do this, at the end of experiments, the posterior adductor muscle of each mussel was severed with a knife to allow comparison of all possible gape angles with sensor output. Gape angle calibration took about 5 min per mussel. Subsequently, data from sensor output were regressed nonlinearly against gape angle (for details see Wilson et al., 2002, 2005; Wilson & Liebsch, 2003; Robson, Wilson & Garcia de Leaniz, 2007) to allow determination of gape angle from the sensor output recorded during the course of the experiments.
The archival logger used for the work was a 15-channel JUV-Log (Juv Elektronik, Borstel, Germany), equipped with 12 Hall-sensor (Honeywell, SS99E) channels and one temperature channel, each with 22-bit resolution, recording gape angle at better than 0.01°. The unit had a 1 GB RA memory and could record at a maximum frequency of 2 Hz. The magnets used were 5 × 5 × 2 mm neodymium boron.

Collection and maintenance of mussels for aquarium experiments

Mussels were collected from Swansea Bay, Wales, UK (LR SS630875), at low tide by cutting their byssus threads and transferred to a flow-through aquarium system within 2 h. Magnets and Hall sensors were glued to the exterior of each mussel shell using Aquarium Sealant (Geocel, Plymouth, UK). The equipped mussels were then replaced in an aerated flow-through aquarium system containing seston-laden seawater from Swansea Bay, Wales, UK, for at least a week before being subjected to standard conditions (see below). Experiments with mussels in aquaria took place from July to December 2006.

Mussels in standard conditions

Fourteen mussels with an initial mean length of 42.5 mm ± SD 0.3 and mean whole wet weight 11.03 ± SD 0.84 were kept in separate, well-aerated tanks filled with 121 l of 0.45-μm filtered seawater. Mussel (pseudo)-faeces and seawater were removed from tanks and replaced with fresh 0.45-μm-filtered seawater once every 24 h. Mussels were subject to a daily light regime of 13 h light and 11 h dark (water temperature 16.2°C ± 0.4), and each fed a mixed algal diet of ~100 × 106 Tetraselmis suecica and ~100 × 107 Thalassiosira weissflogii cells/day.

Mussel response to varying algal ration

Mussels were subject to the same light regime as in standard conditions (above) with the logger recording gape angle at 2 Hz throughout the experiments described below. The 14 mussels were removed from standard conditions and were food-deprived for 48 h in individual, well-aerated tanks filled with 121 l of 0.45-μm filtered seawater before being fed 1 of 11 different daily algal rations at random: 0, 0.2 × 107, 0.8 × 107, 2.5 × 107, 2.75 × 107, 3 × 107, 25 × 107, 60 × 107, 120 × 107, 240 × 107 and 300 × 107 Thalassiosira weissflogii cells/day at an initial concentration of 200 cells/μl and simultaneously exposed to random to one of nine different concentrations of fresh mussel homogenate: 0, 0.01 × 107, 0.04 × 107, 0.21 × 107, 0.42 × 107, 0.83 × 107, 2.08 × 107, 4.17 × 107 and 8.33 × 107 g/ml of fresh mussel homogenate, to simulate predation risk. The homogenate was produced from the towed-dried flesh of freshly killed blue mussels blended for 90 s at high speed in a Waring blender (Waring Products Division, New Hartford, CT, USA). After being exposed to one level of simulated predation risk, mussels were maintained in standard conditions for 2 weeks (to mitigate against any possible habituation to simulated predation risk) before being subjected to a different level of simulated predation risk. The process was repeated until all mussels had been in experiments with the nine different levels of simulated predation risk.

Calculation of change in gape angle per second

Gape angle data for six mussels under standard conditions were collected over 1 week and plotted against the rate of change in gape angle (converted to standardized units of °/s, but measured over intervals of 0.5 s) to produce a characteristic pattern for each mussel represented by the change in gape angle per second (CHIGA) pattern (for details see Robson et al., 2007). Two nonlinear curves [one corresponding to mussel valve abduction (positive CHIGA) and the other to mussel valve adduction (negative CHIGA)] were fitted to describe the edge contours indicating maximum CHIGA for each of the six mussels using TableCurve (Systat Software Inc., Richmond, CA, USA) (in each case, R2 > 0.99). Values of the edge contours indicating maximum CHIGA for both valve abduction and adduction were taken for every 0.5° increase in gape angle for each of the six mussels and an average taken for each CHIGA value (Fig. 1). The best-fit relationship between the mean maximum CHIGA to define the edge contours via rate of change of gape angle (y) and gape angle (x) for both valve abduction and adduction followed an eighth order polynomial (edge contour equations); y = (a + bx + cx2 + dx3 + ex4 + fx5 + gx6 + hx7 + ix8). Mussel valve abduction constants were: a 0.05835, b 0.89554, c -0.39952, d 0.08777, e -0.02341, f 0.00973, g 0.00237, h 0.00026 and i -0.00001. Mussel valve adduction constants were: a -0.02844, b -0.46223, c -0.30656, d 0.21954, e -0.08372, f 0.02116, g 0.00026 and i -0.00001.

<table>
<thead>
<tr>
<th>Gape angle (°)</th>
<th>Change in gape angle</th>
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<tr>
<td>0</td>
<td>-1</td>
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<tr>
<td>1</td>
<td>-0.5</td>
</tr>
<tr>
<td>2</td>
<td>-0.1</td>
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<td>3</td>
<td>0.0</td>
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<td>4</td>
<td>0.5</td>
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Figure 1. Mean maximum CHIGA ± SE indicated by a line of best-fit around the highest and lowest y values (edge contours) at 0.5° intervals calculated from six mussels 42.50 mm long ± SD 0.26 using data acquired over 7 days at a rate of 2 Hz (see text for details). The mussels were held in standard conditions (see text for details). Positive y values delineate the mean maximum CHIGA during valve abduction and negative y values maximum CHIGA during valve adduction.
Calculation of relative valve adduction and abduction speed ($\dot{p}$)

Relative valve adduction and abduction speeds ($\dot{p}$) (Robson et al., 2007) were used to measure the valve movement behaviour of the 14 mussels in aquarium experiments. Briefly, in order to work out how the observed speed of valve adduction or adduction events related to maximum rates of valve adduction or adduction, the first observed gape angle ($A_0$) in a valve adduction or adduction event was taken and the next angle ($A_0 + 1$) predicted ($A_0 + 1$) according to the boundary equations (see the Calculation of change in gape angle per second section). The difference ($D$) between the next observed ($A_0 + 1$) and next predicted ($A_0 + 1$) angle was calculated. The process was then repeated using the next gape angle in the abduction or adduction sequence. This process was repeated for the entire abduction or adduction event and $\Sigma D$ calculated (an integral with units $s^{-2}/0.5s$). In order to correct for gape angle-dependent CHIGA (cf. Fig. 1), this integral $\times 2$ (units $s^{-2}/s$) was subsequently divided by the total movement in degrees of the valve adduction or adduction event, to give a final value for the probability of the adduction or adduction event to the maximum. This value, $\dot{p}$ (units $s^{-1}/s$), is an arbitrary, but relative, scale that allows comparison between mussels that abduct and adduct their valves at different maximum rates. The closer $\dot{p}$ is to zero the faster the valve movement. For full details including a worked example of calculating $\dot{p}$ see Robson et al. (2007).

Statistical analysis

Minitab 14 (Minitab Inc., State College, PA, USA) was used to test for autocorrelations in the mussel gape data. Where appropriate, the raw time series for each mussel was systematically reduced using a line delete program (LINEDEL, Jensen Software Systems, Germany) until the remaining data were within the 95% confidence intervals for the autocorrelations. Mean gape angle was then calculated from nonautocorrelated data.

Mussel response to varying algal ration and predation risk

A one-way repeated-measures ANOVA and post hoc tests with Bonferroni’s correction was used to test for pair-wise differences in mean gape angle with daily algal ration. A one-way repeated-measures ANOVA and post hoc tests with Bonferroni’s correction was used to test for pair-wise differences in mean gape angle with simulated predation risk. Gaping < 1° was defined as ‘valve closure’ and is probably associated with a period of relative quiescence because only at $\geq 1°$ gape is it possible to see a visible inhalant/exhalant siphon opening within the two shell valves.

Comparison of valve movement speed between conditions

One-way repeated-measures ANOVAs and post hoc tests with Bonferroni’s correction were used to test for pair-wise differences in mean $\dot{p}$. Valve abduction and adduction $\dot{p}$ data were square root- or log-transformed to satisfy the assumption of normality in the repeated-measures ANOVAs. Linear regression was used to look for a relationship between mean gape angle and mean $\dot{p}$, and a relationship between mean valve movement (abduction and adduction events combined) and mean $\dot{p}$. Mean $\dot{p}$ was log-transformed to satisfy the assumption of normality in both regression analyses.

Paired t-tests were used to test for any difference between the $\dot{p}$ of the fastest valve adduction event of mussels when fed $240 \times 10^7$ Thalassiosira weissflogii cells/day and the $\dot{p}$ of the first valve adduction event after mussels were simultaneously exposed to high simulated predation risk ($3.33 \times 10^{-4}$ g/ml of fresh mussel homogenate) and $240 \times 10^7$ Thalassiosira weissflogii cells/day. Paired t-tests were only undertaken on the 10 mussels gaping > 1° when they were fed.

RESULTS

Mussel response to varying algal ration

In general, mean mussel gape significantly increased as daily algal ration increased ($F_{10,130} = 2683.696$, $P < 0.001$; Fig. 2) and was associated with copious pseudofaecal production at excessive initial algal concentrations, e.g. 250 cells/µl.

Mussel response to varying simulated predation risk

When fed $240 \times 10^7$ Thalassiosira weissflogii day$^{-1}$ and simultaneously exposed to varying levels of simulated predation risk; there was a significant effect of simulated predation on mussel gape ($F_{5,101} = 1240.325$, $P < 0.001$). Mean gape angle generally decreased, approximating as a decay curve, as the degree of simulated predation risk increased from 0.01 $\times 10^{-4}$ to $8.33 \times 10^{-4}$ g/ml of mussel homogenate (Fig. 3). No homogenate (control) and just 0.01 $\times 10^{-4}$ g/ml of homogenate had no measurable effect on gape behaviour (Fig. 4A, B; cf. Fig. 3). Homogenate introduced at levels of 0.42 and $8.33 \times 10^{-4}$ g/ml had an increasingly negative effect on normal gape behaviour (Fig. 4C, D).

Comparison of valve movement speed between conditions

In general, both mean abduction and adduction $\dot{p}$ increased as daily algal ration increased (Fig. 5A: $F_{10,130} = 88.710$, $P < 0.001$ and Fig. 5B: $F_{10,130} = 37.384$, $P < 0.001$, respectively) and, overall, both mean abduction and adduction $\dot{p}$ decreased as simulated predation risk increased at a fixed daily algal ration of $240 \times 10^7$ Thalassiosira weissflogii cells/day (Fig. 5C: $F_{5,101} = 128.057$, $P < 0.001$, Fig. 5D: $F_{5,101} = 26.272$, $P < 0.001$, respectively). Thus, in general there was a significant

Figure 2. The relationship between mean gape angle (±SE) of mussels and log daily algal ration. Daily algal ration bins not sharing a letter are significantly different.
positive relationship between mean gape angle and mean \( \beta \) from each data bin in Fig. 5 (see Fig. 6: \( F_{1,38} = 107.07, P < 0.001, \gamma = -0.206x + 1.518, R^2 = 0.739 \)). Beyond this, the greater the gape angle, the greater the amount the valve movement per event (Fig. 6). There was a significant positive relationship between mean valve movement per event (abduction and adduction events combined) and mean \( \beta \) from each data bin in Fig. 5 (Fig. 6: \( F_{1,38} = 566.51, P < 0.001, \gamma = -0.424x + 1.869, R^2 = 0.935 \)). The fastest adduction \( \beta \) of mussels fed \( 240 \times 10^7 \) Thalassiosira weissflogii cells/day was significantly slower than the first valve adduction event after the mussels were fed \( 240 \times 10^7 \) Thalassiosira weissflogii day\(^{-1} \) and simultaneously exposed to high simulated predation risk (8.33 \( \times 10^4 \) g/ml of mussel homogenate) (mean \( \beta + SE = -2.92 \pm 0.16 \) and \(-0.24 \pm 0.20 \), respectively, \( n = 10, t = 10.88, P < 0.001 \)). The fastest valve adduction \( \beta \) of mussels fed \( 240 \times 10^7 \) Thalassiosira weissflogii day\(^{-1} \) started from gape angles in the range \( 2^\circ - 4.5^\circ \) and always resulted in valve closure.

**DISCUSSION**

**Mussel response simulated predation risk**

Mean gape angle decreased in a backward S-shaped (type III) behavioural response curve (Holling, 1959a, b) as the amount of simulated predation risk increased in the seawater. We conclude that, above a background level of simulated predation risk (somewhere between \( 0.01 \times 10^{-2} \) and \( 0.04 \times 10^{-2} \) g/ml of mussel homogenate), the greater the simulated predation risk in the water the greater the threat 'perceived' by the mussel and thus the lower the gape angle. Presumably, the lower the shell gape angle, the less the chance of the shell being breached by predators such as oystercatchers which 'stab' gaping mussels (Norton-Griffiths, 1967), or the claws of crabs entering the gap between the shell valves and damaging the soft parts. The reduced gape angle (Fig. 3) obviously reduced the ability of the mussels to filter-feed and take up oxygen (Famme, 1980) compared with mussels fed the same daily ration without simulated predation risk (Fig. 2). These results show that the response of mussels to predation is graded and complex and indicates that they adjust their behaviour in a trade-off.
between effective feeding/pseudofaeces production and the likelihood of predation.

Valve movement speed

The present study has highlighted considerable variance in the mussel abduction and adduction speed, which adds to initial findings by Robson et al. (2007) and Robson (2008). In general, the speed of valve abduction and adduction events increased as both gape angle and the amount of valve movement per event increased (Fig. 6). High food availability (daily algal ration) was associated with high gape angle and a fast valve abduction speed to that gape angle, probably to maximize feeding rate while the food availability was good. Conversely, lower food availability was associated with lower gape angles and slower valve abduction speeds. During opening to low gape angles, valve abduction speed was probably regulated more by muscle action potentials which slowed down the rate of relaxation in the posterior adductor muscle (Lowy, 1953; Hoyle & Lowy, 1956).

It appears that, in general, greater food availability incited a greater gape angle (a proxy for activity including pseudofaeces production) (Fig. 2) within our experimental context, which allowed the mussels to adduct their valves further and was associated with a faster addiction rate per event (Fig. 6) at relatively high energetic cost (Ruppert, Fox & Barnes, 2004). The increase in magnitude and speed of valve addiction per event with increasing gape angle and hence activity is possibly related to the increasing degree to which the mussels need to excrete waste (Nagai et al., 2006; García-March, Sanchis Solsona & García-Carrascosa, 2008) and/or enhance perfusion of the tissues by newly reoxygenated haemolymph (Shick et al., 1986; Shick, Widdows & Gnaiger, 1988) as feeding rate increases.

High perceived predation risk was associated with smaller gape angles during feeding periods (Figs 3, 4), presumably as an anti-predation strategy. Furthermore, mussels under increasing threat of predation became less responsive to food, opening more slowly with increasing perceived predation. We assume that this behaviour will have resulted in lower feeding rates. In contrast to the general positive relationship between gape angle/valve movement per event and speed, the fastest valve adduction events resulting in valve closure were recorded (starting from a range of gape angles; 2°–4.5°) only when mussels were first exposed to high perceived predation risk and probably involved the greatest use of the fastest contracting muscle fibres (Huang & Satterlie, 1989). One might reasonably suppose that mussels close their shell valves as fast as possible when the threat of predation is first applied, independent of gape angle and the high energetic cost of rapid closure (Ruppert et al., 2004), as a first line of defence from some predators. In general a closed shell has a lower predation risk than an open one, although the specific defence by mussels against dogwhelks (Naucella lapillus) is to gape in order to protrude their foot to immobilize the gastropod with byssus threads (Seed & Suchanek, 1992).

We suggest that in order to identify the reasons for every valve abduction and adduction event, many more parameters of mussels and their environment will need measuring and at high temporal resolution. Examples of this would be: aspects of neurobiology, including muscle action potentials (Lowy, 1953), video endoscopy of the gill filter-feeding and rejection tracts (e.g. Beninger & St Jean, 1997), oxygen uptake, haemolymph PO2 (Shick et al., 1986), heat dissipation (Shick et al., 1986), mussels’ prey and their environment. A primary finding of the work conducted here is that the response of mussels to predation is graded and complex and indicates that mussels trade-off between maximizing feeding/pseudofaeces production and minimizing predation risk.

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