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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 (abduction/adduction) 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 some predators such as starfish (Asteroidea) 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; Beadman *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, 2005; 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 13-channel JUV-Log (Juv Elektronik, Borstel, Germany), equipped with 12 Hall-sensor (Honeywell, SS59E) 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 g ± SD 0.84 were kept in separate, well-aerated tanks filled with 12 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 $\sim 100 \times 10^6$ *Tetraselmis suecica* and $\sim 100 \times 10^7$ *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 12 l of 0.45-μm filtered seawater before being fed 1 of 11 different daily algal rations at random: 0, 0.2×10^7, 0.8×10^7, 2.5×10^7, 2.75×10^7, 3×10^7, 25×10^7, 60×10^7, 120×10^7, 240×10^7 and 300×10^7 *Thalassiosira weissflogii* cells/day at concentrations of 0, 0.17, 0.67, 2.08, 2.29, 2.5, 20.8, 50, 100, 200 and 250 cells/μl, respectively, at one moment in time. Thus, after the algal cells had been added to each tank, the cell concentration decreased as mussels removed algae from the water. Mussel gape angle was recorded for 24 h after the initial addition of the algae. After being in one algal ration experiment, mussels were maintained in standard conditions for 2 weeks before being subjected to a different daily algal ration experiment. The process was repeated until all mussels had been in the 11 different daily algal rations experiments.

Mussel response to varying simulated predation risk

The same mussels as used in the previous experiment were subject to the standard conditions light regime with the logger recording gape angle at 2 Hz throughout the experiments described below. Fourteen mussels were food-deprived for 48 h in individual, well-aerated tanks filled with 12 l of 0.45-μm filtered seawater and fed 240×10^7 *Thalassiosira weissflogii* cells/day (an initial concentration of 200 cells/μl) and simultaneously exposed at random to one of nine different concentrations of fresh mussel homogenate: 0, 0.01×10^{-4}, 0.04×10^{-4}, 0.21×10^{-4}, 0.42×10^{-4}, 0.83×10^{-4}, 2.08×10^{-4}, 4.17×10^{-4} and 8.33×10^{-4} g/ml of fresh mussel homogenate, to simulate predation risk. The homogenate was produced from the towel-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, $R^2 > 0.99$). 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); $y = (a + bx + cx^2 + dx^3 + ex^4 + fx^5 + gx^6 + hx^7 + ix^8)$. 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,

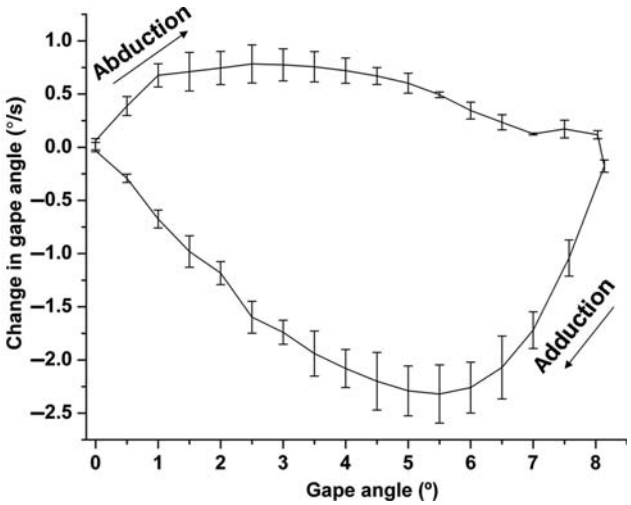

Figure 1. Mean maximum CHIGA ± SE indicated by a line of best-fit around the highest and lowest y values (edge contours) at 0.5° intervals calculated from six mussels 42.50 mm long ± SD 0.26 using data acquired over 7 days at a rate of 2 Hz (see text for details). The mussels were held in standard conditions (see text for details). Positive y values delineate the mean maximum CHIGA during valve abduction and negative y values maximum CHIGA during valve adduction.

g −0.00333, h 0.00029 and i −0.00001. These equations were used to predict the maximum CHIGA of the 14 mussels in the aquarium experiments for any gape angle during both valve abduction and adduction events.

Calculation of relative valve adduction and abduction speed (Þ)

Relative valve abduction and adduction speeds (Þ) (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 abduction or adduction events related to maximum rates of valve abduction or adduction, the first observed gape angle (a_n) in a valve abduction or adduction event was taken and the next angle ($a_n + 1$) predicted ($A_n + 1$) according to the boundary equations (see the Calculation of change in gape angle per second section). The difference (D) between the next observed ($a_n + 1$) and next predicted ($A_n + 1$) 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 ΣD calculated (an integral with units $^{\circ 2}$/0.5 s). In order to correct for gape angle-dependent CHIGA (cf. Fig. 1), this integral × 2 (units $^{\circ 2}$/s) was subsequently divided by the total movement in degrees of the valve abduction or adduction event, to give a final value for the proximity of the abduction or adduction event to the maximum. This value, Þ (units °/s), is an arbitrary, but relative, scale that allows comparison between mussels that abduct and adduct their valves at different maximum rates. The closer Þ is to zero the faster the valve movement. For full details including a worked example of calculating Þ 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 ≥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 Þ. Valve abduction and adduction Þ 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 Þ, and a relationship between mean valve movement (abduction and adduction events combined) and mean Þ. Mean Þ 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 Þ of the fastest valve adduction event of mussels when fed 240×10^7 *Thalassiosira weissflogii* cells/day and the Þ of the first valve adduction event after mussels were simultaneously exposed to high simulated predation risk (8.33×10^{-4} g/ml of fresh mussel homogenate) and 240×10^7 *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 240×10^7 *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 ($F_{8,104} = 1240.325$, $P < 0.001$). Mean gape angle generally decreased, approximating as a decay curve, as the degree of simulated predation risk increased from 0.01×10^{-4} to 8.33×10^{-4} g/ml of mussel homogenate (Fig. 3). No homogenate (control) and just 0.01×10^{-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 8.33×10^{-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 Þ 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 Þ decreased as simulated predation risk increased at a fixed daily algal ration of 240×10^7 *Thalassiosira weissflogii* cells/day (Fig. 5C: $F_{8,104} = 128.057$, $P < 0.001$, Fig. 5D: $F_{8,104} = 26.272$, $P < 0.001$, respectively). Thus, in general there was a significant

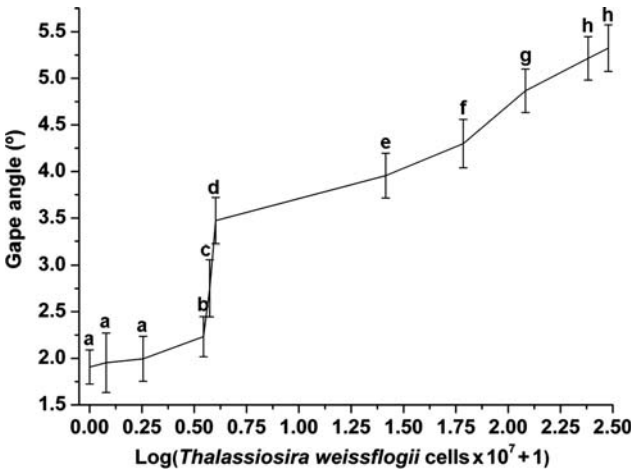

Figure 2. The relationship between mean gape angle (±SE) of mussels and log daily algal ration. Daily algal ration bins not sharing a letter are significantly different.

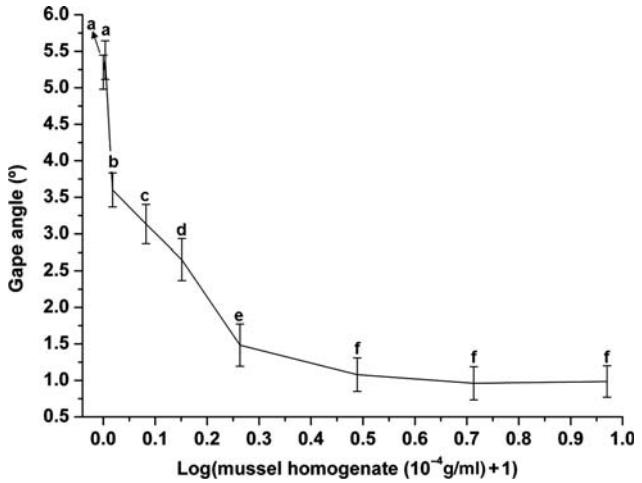

Figure 3. The relationship between mean gape angle (°) (±SE) and simulated predation risk (mussel homogenate × 10^{-4} g/ml) when mussels were fed 240 × 10^7 *Thalassiosira weissflogii* cells/day. Mussel homogenate bins not sharing a letter are significantly different.

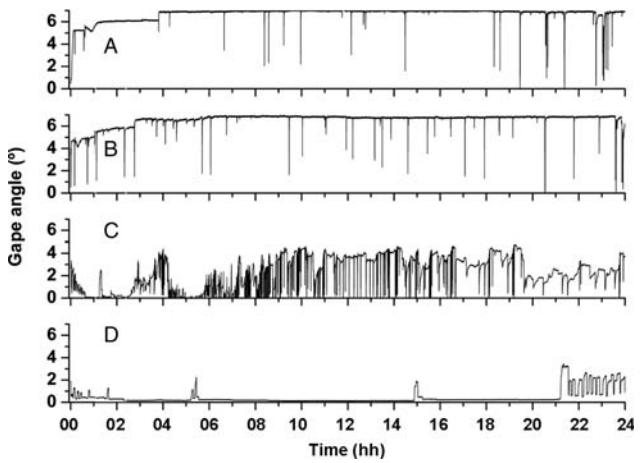

Figure 4. Valve gape angle (°) of a 42.6 mm long mussel over 24 h when fed 240 × 10^7 *Thalassiosira weissflogii* cells/day and simultaneously exposed to simulated predation risk (**A**) 0 (control), (**B**) 0.01, (**C**) 0.42 and (**D**) 8.33 × 10^{-4} g/ml of mussel homogenate.

positive relationship between mean gape angle and mean Þ from each data bin in Fig. 5 (see Fig. 6: $F_{1,38}$= 107.07, $P<$ 0.001, $y = -0.206x + 1.518$, $R^2 = 0.739$). 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 Þ from each data bin in Fig. 5 (Fig. 6: $F_{1,38} = 566.51$, $P < 0.001$, $y = -0.424x + 1.869$, $R^2 = 0.935$). The fastest adduction Þ of mussels fed 240 × 10^7 *Thalassiosira weissflogii* cells/day was significantly slower than the first valve adduction event after the mussels were fed 240 × 10^7 *Thalassiosira weissflogii* day^{-1} and simultaneously exposed to high simulated predation risk (8.33 × 10^{-4} g/ml of fresh mussel homogenate) (mean Þ ± SE = −2.92 ± 0.16 and −0.24 s^{-1} ± 0.20, respectively, n = 10, $t = -10.88$, $P < 0.001$). The fastest valve adduction Þ of mussels fed 240 × 10^7 *Thalassiosira weissflogii* day^{-1} started from gape angles in the range 5.5°–6.5° and always resulted in valve closure. The first valve adduction event Þ after the mussels were fed 240 × 10^7 *Thalassiosira weissflogii* day^{-1}, and simultaneously exposed to high simulated predation risk,

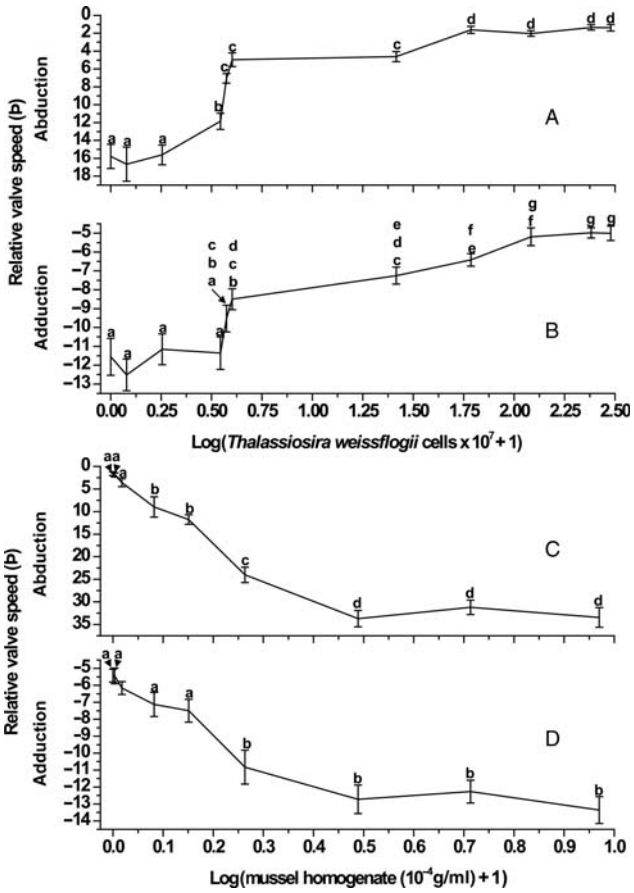

Figure 5. The relationship between daily algal ration and mean relative valve movement speed (Þ) during (**A**) valve abduction and (**B**) valve adduction. The relationship between simulated predation risk (mussel homogenate) when simultaneously fed 240 × 10^7 *Thalassiosira weissflogii* cells/day and mean Þ during (**C**) valve abduction and (**D**) valve adduction. Note that the closer Þ is to 0 the faster the valve movement. Daily algal ration and mussel homogenate bins not sharing a letter are significantly different.

started from gape angles in the range 2°–4.5° 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 × 10^{-4} and 0.04 × 10^{-4} 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

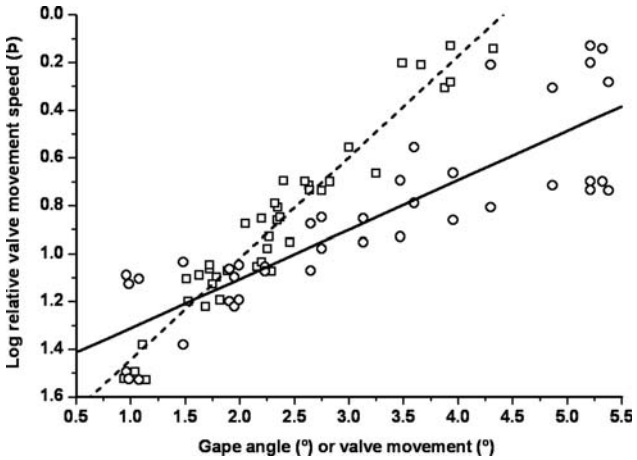

Figure 6. The positive relationship between mean gape angle and mean relative valve movement speed (Þ) from each data bin in Figure 5 (circles and solid regression line, $n = 40$, $y = -0.206x + 1.518$, $R^2 = 0.739$, $P < 0.001$), and the positive relationship between mean valve movement per event (abduction and adduction events combined) and mean Þ from each data bin in Figure 5 (squares and dashed regression line, $n = 40$, $y = -0.424x + 1.869$, $R^2 = 0.935$, $P < 0.001$). The valve adduction Þ values were made positive so the relationship could be displayed in one figure. Note that the closer Þ is to 0, the faster the valve movement.

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 Þ, 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 adduction rate per event (Fig. 6) at relatively high energetic cost (Ruppert, Fox & Barnes, 2004). The increase in magnitude and speed of valve adduction 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; Garcia-March, Sanchís 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 Þ, 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 (*Nucella 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 PO_2 (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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REFERENCES

BEADMAN, H.A., CALDOW, R.W.G., KAISER, M.J. & WILLOWS, R.I. 2003. How to toughen up your mussels: using mussel shell morphological plasticity to reduce predation losses. *Marine Biology Research*, **142**: 487–494.

BENINGER, P.G. & ST JEAN, S.D. 1997. The role of mucus in particle processing by suspension-feeding marine bivalves: unifying principles. *Marine Biology*, **129**: 389–397.

DOLMER, P. 2000. Feeding activity of mussels *Mytilus edulis* related to near-bed currents and phytoplankton biomass. *Journal of Sea Research*, **44**: 221–231.

FAMME, P. 1980. Effect of shell valve closure by the mussel *Mytilus edulis* L. on the rate of oxygen consumption in declining oxygen-tension. *Comparative Biochemistry and Physiology, Part A: Physiology*, **67A**: 167–170.

GARCIA-MARCH, J.R., SANCHÍS SOLSONA, M. & GARCÍA-CARRASCOSA, A.M. 2008. Shell gaping behaviour of *Pinna nobilis* L., 1758: circadian and circalunar rhythms revealed by in situ monitoring. *Marine Biology*, **153**: 689–698.

HOLLING, C.S. 1959a. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist*, **91**: 293–320.

HOLLING, C.S. 1959b. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, **91**: 385–398.

HOYLE, G. & LOWY, J. 1956. The paradox of *Mytilus* muscle. A new interpretation. *Journal of Experimental Biology*, **33**: 295–310.

HUANG, Z. & SATTERLIE, R.A. 1989. Smooth muscle fiber types and a novel pattern of thick filaments in the wing of the pteropod mollusc *Clione limacina*. *Cell and Tissue Research*, **257**: 405–414.

KATS, L.B. & DILL, L.M. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**: 361–394.

LACOURSE, J.R. & NORTHROP, R.B. 1977. Mechanoreceptors within the anterior byssus retractor muscle of *Mytilus edulis* L. *American Zoologist*, **17**: 969.

LEONARD, G.H., BERTNESS, M.D. & YUND, P.O. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology*, **80**: 1–14.

LOWY, J. 1953. Contraction and relaxation in the adductor muscles of *Mytilus edulis*. *Journal of Physiology*, **120**: 129–140.

NAGAI, K., HONJO, T., GO, J., YAMASHITA, H. & OH, S.J. 2006. Detecting the shellfish killer *Heterocapsa circularisquama* (Dinophyeeae) by measuring bivalve valve activity with a Hall element sensor. *Aquaculture*, **255**: 395–401.

NORTON-GRIFFITHS, M. 1967. Some ecological aspects of the feeding behaviour of the oystercatcher *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. *Ibis*, **109**: 412–424.

ROBSON, A.A. 2008. *Gaping at environmental variability: how do bivalves react to changing circumstance?* PhD thesis, Swansea University, UK.

ROBSON, A.A., THOMAS, G.R., GARCIA DE LEANIZ, C. & WILSON, R.P. 2009. Valve gape and exhalant pumping in bivalves: optimization of measurement. *Aquatic Biology*, **6**: 191–200.

ROBSON, A., WILSON, R. & GARCIA DE LEANIZ, C. 2007. Mussels flexing their muscles: a new method for quantifying bivalve behaviour. *Marine Biology*, **151**: 1195–1204.

ROVERO, F., HUGHES, R.N. & CHELAZZI, G. 1999. Cardiac and behavioural responses of mussels to risk of predation by dogwhelks. *Animal Behaviour*, **58**: 707–714.

RUPPERT, E.E., FOX, R.S. & BARNES, R.D. 2004. *Invertebrate zoology: a functional evolutionary approach*. Brooks Cole Thomson, Belmont.

SAUREL, C., GASCOIGNE, J.C., PALMER, M.R. & KAISER, M.J. 2007. In situ mussel feeding behavior in relation to multiple environmental factors: regulation through food concentration and tidal conditions. *Limnology and Oceanography*, 52: 1919–1929.

SEED, R. & SUCHANEK, T.H. 1992. Population and community ecology of *Mytilus*. In: *The mussel* Mytilus*: ecology, physiology, genetics and culture* (E. Gosling, ed.) pp. 87–169. Elsevier, Amsterdam.

SHICK, J.M., GNAIGER, E., WIDDOWS, J., BAYNE, B.L. & DEZWAAN, A. 1986. Activity and metabolism in the mussel *Mytilus edulis* (L) during intertidal hypoxia and aerobic recovery. *Physiological Zoology*, **59**: 627–642.

SHICK, J.M., WIDDOWS, J. & GNAIGER, E. 1988. Calorimetric studies of behavior, metabolism and energetics of sessile intertidal animals. *American Zoologist*, **28**: 161–181.

STEFANO, G.B. 1990. *Neurobiology of Mytilus edulis*. Manchester University Press.

WILSON, R.P. & LIEBSCH, N. 2003. Up-beat motion in swinging limbs: new insights into assessing movement in free-living aquatic vertebrates. *Marine Biology*, **142**: 537–547.

WILSON, R., REUTER, P. & WAHL, M. 2005. Muscling in on mussels: new insights into bivalve behaviour using vertebrate remote-sensing technology. *Marine Biology*, **147**: 1165–1172.

WILSON, R.P., STEINFURTH, A., ROPERT-COUDERT, Y., KATO, A. & KURITA, M. 2002. Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology*, **140**: 17–27.