Mar Biol (2007) 151:1195–1204
DOI 10.1007/s00227-006-0566-z

RESEARCH ARTICLE

Mussels flexing their muscles: a new method for quantifying bivalve behaviour

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Received: 16 August 2006 / Accepted: 17 November 2006 / Published online: 12 December 2006

Abstract We employed a novel technique to quantify how blue mussels *Mytilus edulis* react to predation risk in their environment by quantifying mussel gape using a Hall sensor attached to one shell valve reacting to a magnet attached to the other. Change in gape angle per second (CHIGA) versus gape angle plots resulted in a distribution with a boundary, which defined the maximum CHIGA of a mussel at all gape angles. CHIGA boundary plots for all individual mussels were similar in form. However, the CHIGA boundary increased in extent with mussel length (maximum CHIGA for mussel valve closures for mussels 2.98 and 79.6 mm long were −1.5 and −11°s^{-1}, respectively), showing that larger mussels opened and closed most rapidly. Mussel extract added to the seawater, a factor believed to signal predation, caused mussels to close significantly faster than otherwise ($P < 0.001$). This approach for assessing how mussels react to their environment indicates that mussel response to predation is graded and complex and may well indicate animal-based assessments of the trade-off between effective feeding and the likelihood of predation.

Communicated by A. Atkinson, Cambridge.

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Introduction

Animal behaviour (e.g., Scott 2004) is normally assumed to lead to maximized lifetime reproductive success (e.g., Clutton-Brock et al. 2004) and specific reactions to environmental variability constitute a part of this behaviour. Documentation of behaviour with survival value is common in vertebrates (e.g., Vilensky 1987; Bertram et al. 1997; Sandercock and Heckman 1997) but reports are notably lacking in sessile molluscs, primarily due to the difficulty of quantification of behaviours that occur in these generally small animals whose behaviour is characterized by minimal movement carried out over comparatively long time periods. Such movement may, however, be critical in survival and its quantification may provide insights into strategies and environmental conditions of consequence for this important animal group.

There is significant commercial mussel production in over 40 countries world-wide (FAO 1999) and mussels, particularly *Mytilus edulis*, have been proposed as potent bioindicators. However, this is largely based on assessment of changes in animal body composition and is thus only undertaken when the animals are sacrificed (e.g., Fisher et al. 1996). However, DeZwart et al. (1995) did employ mussels as bioindicators using remote-sensing technology, but see Wilson et al. (2005) for criticism of the DeZwart et al. (1995) "mosselmonitor". We propose that appropriate assessment of behaviours denoting mussel well-being should help improve mussel cultivation and may increase the utility of mussels as bioindicators of environmental conditions (e.g., Fisher et al. 1996). Accordingly, we show here how new sensor and logging tag methodology (Wilson et al. 2005) can be used to quantify mussel

gape and the change in gape angle per second in live blue mussels *M. edulis* in order to elucidate how these animals react to changes in their environment.

Materials and methods

Overall experimental design

We used the methods developed by Wilson et al. (2005) to quantify gape angle in blue mussels *M. edulis*. Briefly, this involved using a Hall sensor (a transducer for magnetic field strength) attached to one mussel valve and a small magnet attached to the other valve. Variance in gaping extent produced a corresponding variance in the magnetic field strength perceived by the Hall sensor. This was recorded by a logger. Since Hall sensor output is proportional to magnetic field strength and angle of impingement, the transducer output has to be calibrated by comparing shell gape angle with sensor output, over a wide variety of angles, and curve-fitting the data (for details see Wilson et al. 2002, 2005; Wilson and Liebsch 2003). This curve-fit can then be used to determine any gape angle by converting the transducer output accordingly.

The logger used for the work was a 13-channel JUV-Log, equipped with 12 Hall-sensor (Siemens KSY 10) channels and one temperature channel, each with 22 bit resolution. The unit had a 512 Mbyte RA memory and could record at rates of up to 2 Hz. The magnets used were $5 \times 5 \times 2$ mm neodymium boron magnets.

Collection and maintenance of mussels

Inter-tidal mussels were collected from LR SS630875 Swansea Bay, Wales, UK at low tide and transferred to a flow-through aquarium system within 2 h. Magnets and Hall sensors were glued to mussel shells using Aquarium Sealant (Geocel, Plymouth, UK) before the mussels were replaced in an aerated flow-through aquarium system for at least a week before being used in experiments. Experiments with mussels took place from October 2005 to June 2006.

Measuring gape angle in standard conditions

In order to determine how six mussels (mussel length see Table 1) reacted to standard conditions, the logger recorded gape angle at 2 Hz for multiple periods of ~5 days. At this time the individual mussels were kept in separate aquaria. Mussels were subject to a daily regime of 13 h light and 11 h dark, water temperature 16 ± 0.3°C and each fed a mixed algal diet of ~100 million *Tetraselmis suecica* and ~1,000 million *Thalassiosira weissflogii* cells day^{-1} at $40 \pm$ SD 3.1 cells µl^{-1}.

Measuring gape angle in non-standard conditions

Mussels were subject to the same daily feeding and light regime as in standard conditions. The reaction of six mussels to the chemical stimulus of an injured *M. edulis* was recorded by the logger while a damaged (shell cracked) 55 mm long conspecific was placed in a 1.5 l tank supplied with filtered, aerated seawater draining into a 50 l tank containing six mussels equipped with Hall sensors. Loggers recorded for ~4 days before and after the application of the injured mussel and the procedure was repeated six times with both fresh filtered seawater and a new injured mussel.

Calculation of CHIGA

The Hall sensor data were converted into gape angle and plotted against the change in gape angle (converted to standardized units of degrees per second, but measured over intervals of 0.5 s) to produce a characteristic pattern, which we shall subsequently refer to as the CHIGA (CHange In Gape Angle per second) pattern (Fig. 1). The density of the points within the CHIGA pattern reflects the incidence of the particular conditions of change in gape angle per second as a function of gape angle, but the boundaries represent limits in the change in gape angle per second (Fig. 1). The ease with which these boundaries could be detected depended on the length of the data set and the conditions under which the mussel was held (see Fig. 4 and Results). Two non-linear curves were fitted to describe these boundaries using Table-curve (giving r^2 better than 0.99), one which corresponded to mussel opening (solid line in Fig. 1) and one for mussel closure (dashed line in Fig. 1) (see Table 1). These equations were used to predict the maximum CHIGA for any gape angle during both opening and closing events.

We reasoned that proximity of any particular temporal sequence of points describing a change in valve gaping during opening or closure events to the boundaries (defined by our equations in Table 1) indicated the extent to which the mussel was relaxing (abducting) or contracting (adducting) its adductor muscles in relation to the maximum rate of change achievable. Since the shell opening process is passive, mediated by the elasticity of the hinge (Ruppert et al. 2004), the most relaxed adductor muscles (anterior and posterior) results in fastest opening. Conversely, since shell gape

Table 1 Best-fit relationship between change in gape angle per second (CHIGA) ($°s^{-1}$) to define the boundary (y) and gape angle (x) (see calculation of CHIGA in Materials and methods)

Mussel length (mm)	Valve movement	Relationship
29.8	Opening	$y = (a + bx + c/x + dx^2 + e/x^2 + fx^3 + g/x^3 + hx^4)$ a 1.5888486 b −0.52408928 c −0.35121223 d 0.19131119 e 0.029613084 f −2.80E−02 g −8.63E−04 h 1.22E−03
	Closing	$y = (a + bx + cx^2\ln x + dx^3 + ee^x)$ a 0.058736807 b −0.55896575 c 0.1513833 d −0.037638453 e 0.000702693
34.6	Opening	$y = (a + bx0.5 + cx + dx1.5 + ex^2 + fx^{2.5} + gx^3 + hx^{3.5} + ix^4 + jx^{4.5} + kx^5)$ a −3.2201826 b 28.261003 c −98.470003 d 192.8207 e −231.32861 f 1.79E + 02 g −9.21E + 01 h 3.11E + 01 i 6.66E + 006 j 8.17E−01 k −4.37E−02
	Closing	$y = (a + cx + ex^2 + gx^3 + ix^4)/(1 + bx + dx^2 + fx^3 + hx^4 + jx^5)$ a 0.03826436 b −0.30557562 c −0.3008307 d 0.054804004 e 0.063870721 f −5.85E−03 g −4.58E−03 h 2.99E−04 i 1.10E−04 j −5.27E−06
38.7	Opening	$y = (a + bx + cx^2 + dx^3 + ex^4 + fx^5 + gx^6 + hx^7 + ix^8)$ a −0.029847969 b 1.3726608 c −1.435414 d 0.91228114 e −0.37543336 f 9.52E−02 g −1.40E−02 h 1.10E−03 i −3.48E−05
	Closing	$y = (a + bx + cx^2 + dx^3 + ex^4 + fx^5)$ a 0.017766632 b −0.50999977 c −0.090428403 d 0.094381006 e −0.019634252 f 1.25E−03
44.7	Opening	$y = (a + cx + ex^2 + gx^3 + ix^4)/(1 + bx + dx^2 + fx^3 + hx^4)$ a −0.09611428 b 0.051349164 c 0.68877847 d −0.013542099 e −0.12260023 f 4.14E−04 g 7.69E−03 h 2.90E−06 i −1.65E−04
	Closing	$y = (a + bx + cx^2 + dx^3 + ex^4 + fx^5 + gx^6 + hx^7 + ix^8 + jx^9 + kx^{10}$ a 0.11750452 b −1.147895 c 1.6774392 d −1.4270188 e 0.57351823 f −1.27E−01 g 1.66E−02 h −1.31E−03 i 6.22E−05 j −1.61E−06 k 1.76E−08
54.6	Opening	$y = (a + cx + ex^2)/(1 + bx + dx^2 + fx^3)$ a −0.009530934 b 0.48840935 c 0.47804793 d −0.046097521 e −0.053146559 f −2.10E−03
	Closing	$y = (a + cx + ex^2 + gx^3 + ix^4)/(1 + bx + dx^2 + fx^3 + hx^4 + jx^5)$ a −0.017200221 b 0.36103367 c −1.278371 d −0.38897404 e 0.80373711 f 8.35E−02 g −1.72E−01 h −5.01E−03 i 1.09E−02 j 1.08E−05
79.6	Opening	$y = (a + bx + cx^2 + dx^3 + ex^4 + fx^5 + gx^6 + hx^7 + ix^8)$ a 0.03040645 b 1.0774803 c −0.35758174 d 0.069764735 e −0.00723012 f 4.21E−04 g −1.39E−05 h 2.45E−07 i −1.79E−09
	Closing	$y = (a + bx + cx^2 + dx^3 + ex^4 + fx^5 + gx^6 + hx^7 + ix^8)$ a 0.19715819 b −1.3270658 c 0.43059846 d −0.1084851 e 0.013337685 f −8.59E−04 g 2.97E−05 h −5.20E−07 i 3.63E−09

closure is active, the faster the adductor muscles contract, the closer the CHIGA approaches the boundary defined by the equations.

Calculation of Þ

In order to work out how quickly mussel opening or closing events related to maximum rates of opening or closure, the first observed gape angle (a_n) in an opening or closure event was taken and the next angle ($a_n + 1$) predicted ($A_n + 1$) according to the boundary equation (see Table 1). 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 opening or closure sequence. This process was repeated for the entire opening or closure event and $\sum D$ calculated (an integral units $^{\circ 2}0.5\ s^{-1}$).

In order to correct for gape angle-dependent CHIGA (cf. Fig. 1), this integral × 2 (units $^{\circ 2}s^{-1}$) was subsequently divided by the total movement in degrees of the closure or opening event, to give a final value for the proximity of the closure or opening event to the maximum. This value termed Þ (units $°s^{-1}$) (see Table 2 for a worked example of calculating Þ) is an arbitrary but relative scale. Þ permits comparison between mussels that open and close at different maximum rates. Þ avoids the bias that bigger mussels close quicker than smaller mussels (see Results). CHIGA was recorded at 2 Hz to capture the form and accurate speed of the fastest closures.

Statistical analysis

(Paired) t-tests were carried out to test for significant ($P < 0.05$) differences in valve closure rates of six mussels before and after exposure to a chemical signal from an injured conspecific.

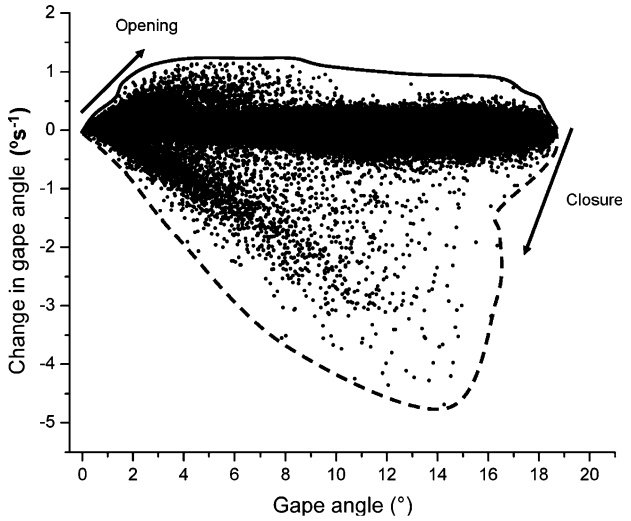

Fig. 1 Change in gape angle per second (CHIGA) versus gape angle for a single 44.7 mm long mussel using data acquired over a period of 7 days at a rate of 2 Hz. The mussel was held in standard conditions (see Measuring gape angle in standard conditions) and stressed by calibration (see Overall experimental design and see Results). The *solid line* delineates the edge contours indicating maximum CHIGA during opening, the *dashed line* that during closure

Results

Mussels were substantially disturbed during and for at least 24 h after calibration of gape angle. However, calibration of gape angle against Hall sensor output proved unproblematic although ten to fourteen calibration readings over a wide range of gape angles were needed to produce best-fit functions with correlation coefficients in excess of 0.97. Blue mussels gaped in the range of 0–24°. The vast majority of mussel gape closure (>97%) and subsequent opening (>98%) events followed a specific, recognizable pattern consisting of a relatively rapid closure followed by a slower opening, this latter having a roughly logarithmic form (Fig. 2). In the examples of mussel closures (Fig. 3a) the variance in rate of valve closure was most reduced between about 4.3 and 2.9° and valve opening (Fig. 3b) between about 1.3 and 2.3°

The logging time required to acquire well-defined boundaries to the CHIGA pattern varied considerably between mussels. For example, the time taken to reach the boundary at a gape angle of 5° for six different mussels varied between 8 and 94 h (Fig. 4). CHIGA boundary plots for all mussels were similar in form. However, the extent of the CHIGA boundary increased with mussel length (maximum CHIGA for mussel valve closures for 29.8 and 79.6 mm long mussels were −1.5 and $-11°s^{-1}$, respectively, while openings were 1.0 and $3.6°s^{-1}$, respectively).

Contour plots of the incidence (frequency) of CHIGA versus gape angle indicated the prevalence of particular responses (e.g., Fig. 5). For instance, over 5 days the mussel in Fig. 5 was closed or nearly closed for between 0 and 1° 6% of the time and spent 89% of the time open 6 between 6 and 11° (Fig. 6). This particular animal spent only 5% of its time gaping between 1 and 5°.

From 0 to 48 h after calibration of gape angle, 18% of openings had Þ-values of ≥7.43 (Fig. 7a) and 24% of closures had Þ-values $\leq -0.04°s^{-1}$ (Fig. 7b) (data derived from a 54.6 mm long mussel). No valve opening occurred between Þ-values of 2.59° and $7.43°s^{-1}$ and no valve closure between Þ-values of −0.04° and $-0.186°s^{-1}$.

Mussels closed rapidly and almost instantaneously upon exposure to the chemical stimulus of an injured conspecific (e.g., Fig. 8). The mussels closure Þ-values were significantly higher (i.e., indicating slower closure rates) (t −10.21, $P < 0.001$) immediately prior to exposure to the seawater in which the injured conspecific was housed (mean Þ-values = $-0.772°s^{-1} \pm$ SD 0.441) than immediately after (mean Þ-values = $-0.021°s^{-1} \pm$ SD 0.012). In other words mussels closed slower in a predation risk free environment than in an environment where predation of conspecifics was simulated.

Table 2 Worked example of the calculation of Þ for a closure event from a 44.7 mm long mussel

Observed closing 0.5 s^{-1} (°)	Predicted maximum CHIGA ($°s^{-1}$) from equations (see Table 1)	Predicted next angle 0.5 s^{-1} if closing at maximum rate (°)	Difference between predicted next maximum angle 0.5 s^{-1} and observed next angle 0.5 s^{-1} (D)
5	−2.097498429	3.951	−0.55
4.5	−1.998271261	3.501	−0.5
4	−1.893258608	3.053	0.053
3	−1.510913916	2.245	−0.26
2.5	−1.203356009	1.898	−0.1
2	−0.855283769		
Total closure 5–2 = 3°			$\sum D = -1.357°^2 0.5\ s^{-1}$
			Þ = $\sum D \times 2 \div$ total closure (°) = $-0.905°s^{-1}$

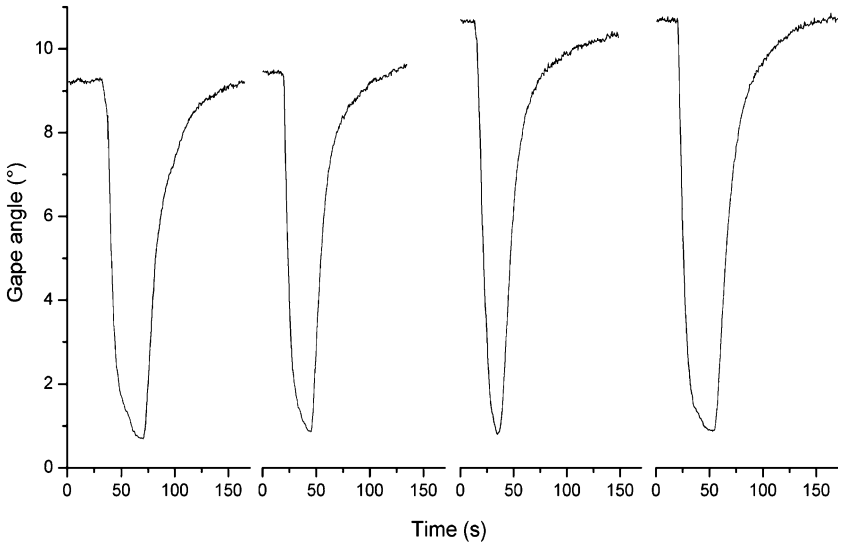

Fig. 2 Examples of the most common form of mussel valve closure and subsequent opening events. Note the faster rate of closure compared to opening with the rate decreasing near the endpoints of both closure and opening events

Detailed examination of mussel response after simulated proximate predation typically showed a short period of rapid opening and closure over a small range of gape angles (0–2°) before one or several long slow openings (e.g., inset of Fig. 8). In an environment without injured conspecifics, opening Þ-value for the 34.6 mm long mussel was $0.949°s^{-1}$, while stressed opening had Þ-value of $20.531°s^{-1}$.

Discussion

This work takes a previously described methodology, developed to examine mussel behaviour via changes in mussel gape (Wilson et al. 2005) and proposes an analytical treatment which further enhances our ability to quantify how mussels react to their environment. The results obtained in this study concur broadly with those presented by Wilson et al. (2005). For example, the individuals used in this current study showed frequent closure events and these were most likely due to the elimination of faeces and pseudo-faeces from the exhalant siphon (e.g., Gosling 2003). However, from our observations we speculate that mussels may also close to create a water current to try and remove the build up of faeces and pseudo-faeces around their gape, which may be restricting water flow into the inhalant siphon. We note that mussels are also known to close as a response to suboptimal algal concentrations for efficient filtration, to prevent desiccation, in response to sudden changes in salinity and as a mechanism against predators e.g., Gosling (2003). Mussels open primarily to filter feed, absorb oxygen and eliminate waste. Although the incidence of opening and closure events was documented to some degree by Wilson et al. (2005) these authors made no mention of the variability in the rate at which mussel gape angle changed and the present study shows how important this is in assessment of mussel behaviour.

Ruppert et al. (2004) reviews the mechanisms used by bilaterally symmetrical shellfish to close or open shell halves. The mechanism is ostensibly simple, consisting of closure brought about by contraction of the adductor muscle(s) while opening is passive, the force being derived from the elastic hinge, we speculate modulated by relaxation in the adductor muscle. Our results clearly show that opening and closure events have highly variable rates according to circumstance although, generally, the variation in the rate of valve closure and opening appears greatest at the beginning and end of the closure (Fig. 3a) or opening (Fig. 3b) event. Some variation in muscle contraction speed in molluscs can be attributed to muscle fibre types. Ruppert et al. (2004) note that the use of "quick" muscles produces a rapid closure, but one that causes fatigue within a short period. Where mussels are to remain closed for extended periods, the use of "catch muscles" is apparently energetically more appropriate although contraction speed is slow. Our work does not allow us to determine the extent to which different muscle fibre types might be used in the contraction process but we propose that the intra-individual variability in closure and opening rates has survival value. Consequently, assessment of the rate of change of gape angle can provide a measure of an animal's assessment of the environment.

Reduced rates of gape closure, which are exemplified by high Þ-values, were greatest during low-risk periods (no stimulus in the water relating to predation) and likely to be caused mainly by contraction of

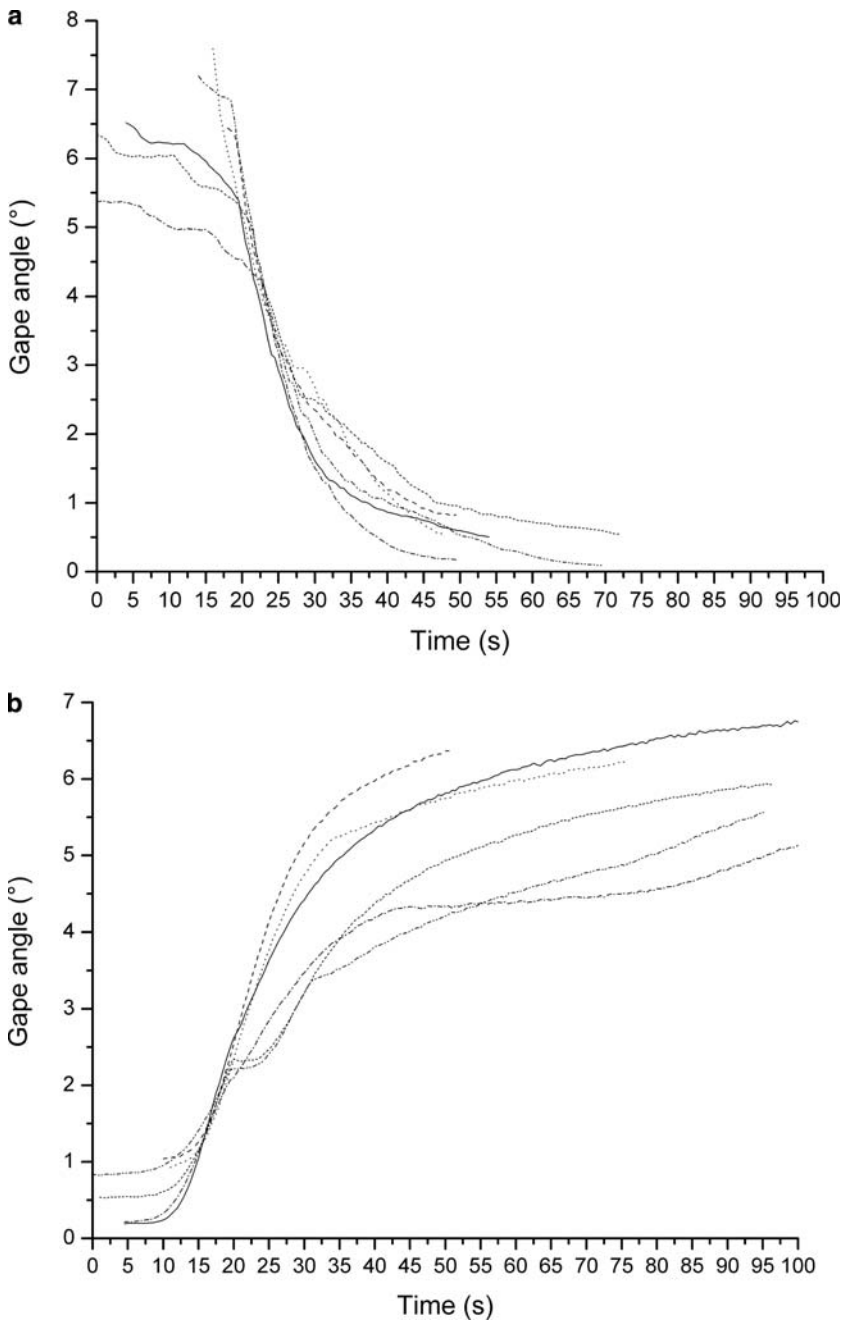

Fig. 3 Six detailed examples of the form of mussel valve closure **a** and opening **b** events from **a** 44.7 mm long mussel

"catch" muscles, especially before periods of extended closure. Þ-values were lowest (with highest rates of closure) during conditions, which might be construed as high risk (as exemplified by the presence of an injured conspecific) and is likely to be caused by contraction of "quick" muscles in response to perceived danger. This reaction is supported by the literature, which documents that mussels rapidly close their valves when threatened (Ruppert et al. 2004) by predators including eider ducks, crabs, starfish, octopus and whelks (Spencer 2002).

In general, therefore, we propose that for any given period during which multiple closure and opening events occur, the higher the percentage of opening events with Þ-values in excess of $7.43°s^{-1}$, the more stressed the mussels will have been. The lower the percentage of data with Þ-values greater than $-0.04°s^{-1}$ the more stressed the mussels will have been during closing. Consideration of all values together should give an overall picture of how the animal perceives its environment for the period under consideration (Fig. 7). Cases where Þ-values are positive for a closure

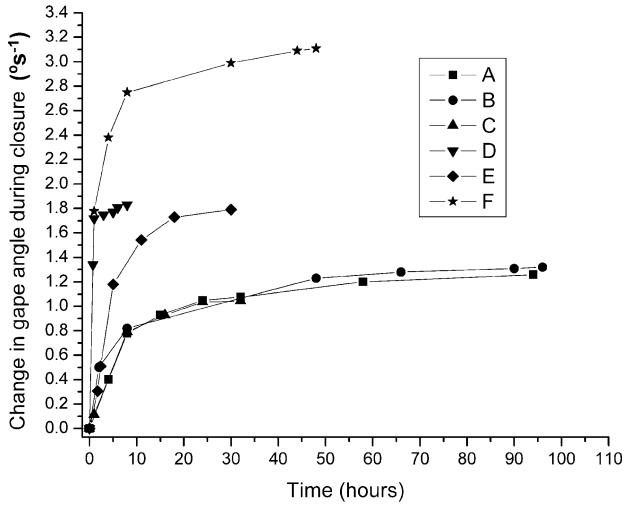

Fig. 4 Maximum recorded closure speed ($°s^{-1}$) at a gape angle of 5° as a function of time for six different individual mussels (delineated by different letters). Mussel length (mm) *A* 29.8, *B* 34.6, *C* 38.7, *D* 44.7, *E* 54.6, *F* 79.6

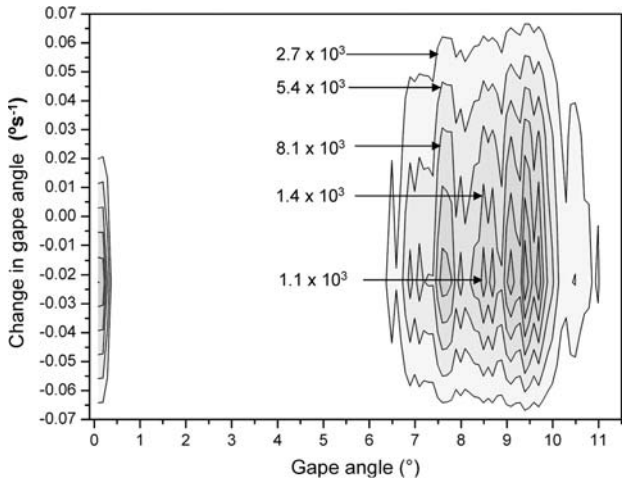

Fig. 5 Contour plot illustrating the relative incidence of CHIGA versus gape angle for a 54.6 mm long mussel over 5 days. Units of contour values is the number of observations

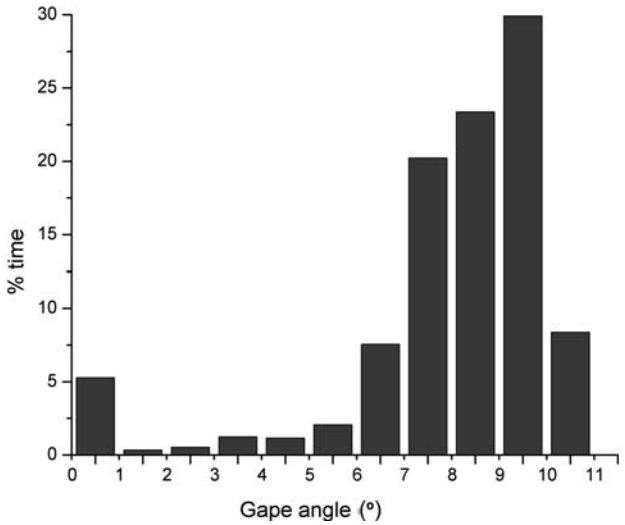

Fig. 6 Gape angle versus percentage time plot for a 54.6 mm long mussel over 5 days

event or negative for an opening event indicate that the change in gape angle per second has exceeded the defined CHIGA boundary. This can either be treated by recalculating this boundary using a greater volume of data (see below) or by simply accepting the value as an extreme measure.

The extent to which the Þ-values recorded here can be used as standard for *M. edulis* from any environment depends critically on our ability to define the CHIGA boundary. This boundary is best approached during closure by having animals that are stressed but, conversely, best approached during opening by having animals that are maximally relaxed. Obviously, both these conditions have to occur during the calibration period. The periods of no stress and stress must be sufficiently spread apart to ensure mussels have recovered from any previous periods of stress. From this study it is recommended that CHIGA boundaries should be obtained from recording mussel gape angle over a period of >4 days with the act of calibration of gape angle against Hall sensor output acting as the induced stressor at the end of the period of data logging. Clearly, the longer the recording time, the more likely the boundary will be well defined at its maximum CHIGA (Figs. 1, 4). However, we note that CHIGA increased as mussels grew (but insignificantly over 3 weeks) so this needs to be taken into account. Further work might allow us to define standard CHIGA boundaries as a function of mussel length, which would preclude the onerous 4 day calibration period proposed above, although it is likely that boundaries may vary with a wide variety of environmental conditions including temperature, food, salinity and oxygen levels.

A primary finding of the work conducted here is that mussel gaping and closure does not represent a binary behavioural state. Rather, that both gape angle and the change in gape angle per second vary extensively and that the ability to vary these presumably has survival value. Mussels cannot feed unless they are gaping, and increased extent of gaping leads to an enhanced ability to feed (e.g., Jørgensen 1990). However, gaping mussels are more susceptible to predation so it would seem appropriate for animals to weigh up the balance of advantages of food acquisition with the likelihood of predation (cf. Perez-Tris et al. 2004). Mussels have a suite of sensory systems such as pallial tentacles with

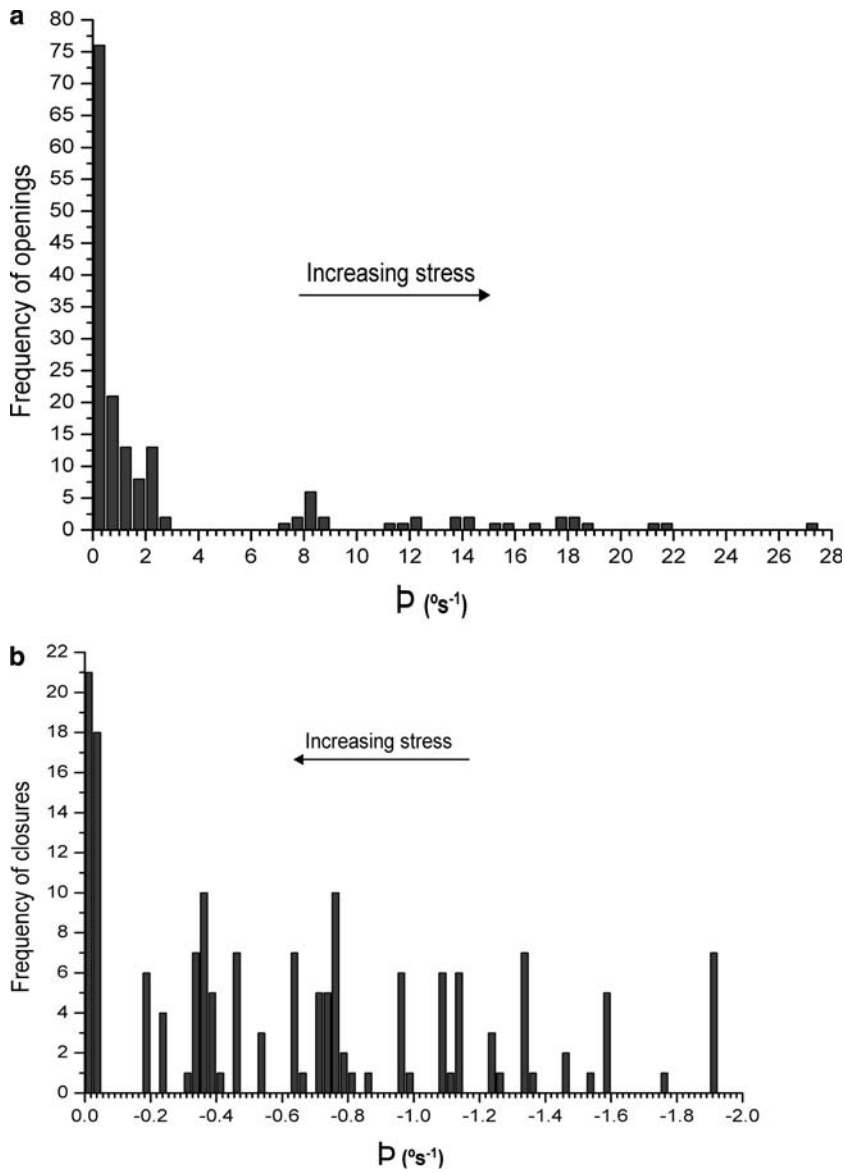

Fig. 7 Frequency of openings **a** and closures **b** versus Þ-value plot for a 54.6 mm long mussel from 0 to 48 h after calibration of gape angle

primary ciliary receptor cells as mechanoreceptors (Ruppert et al. 2004), pallial eyes (ocelli), cerebral eyes (cephalic eyes) and chemoreceptors, possibly including osphradia (Ruppert et al. 2004; Leonard 1999), which may be used to assess environmental quality so it is appropriate that these animals display an appropriately complex behavioural response.

Precise measurement of mussel response to environmental conditions is not only useful in an animal life history strategic sense, but also has real value in a bio-indicator sense. Both Curtis et al. (2000) and DeZwart et al. (1995) proposed using mussels for examining the effects of pollution using shell movements although since this publication, no formal procedure has been developed. The system presented here allows mussel response to be measured in real time without the need to kill the bivalve. This contrasts with many other methods, which include measuring stress proteins e.g., HSP70 (e.g., Snyder et al. 2001) and immune changes (Lacoste et al. 2002) where stress cannot be measured in real time, or at the instant the stressor is applied.

The work presented here adds to the methodologies already being used to quantify mussel response to the environment. Typically, these are based on visual observation techniques (e.g., Riisgård et al. 2003) which have particular biases depending on e.g., water turbidity or parallax errors, or the use of electrical coils (e.g., Kádár et al. 2005) which give a binary output for "open" or "shut" animals. Our work shows, however, that changes in gape angle can be resolved finely and that this information gives another quantifiable dimension of animal response to the environment. Further

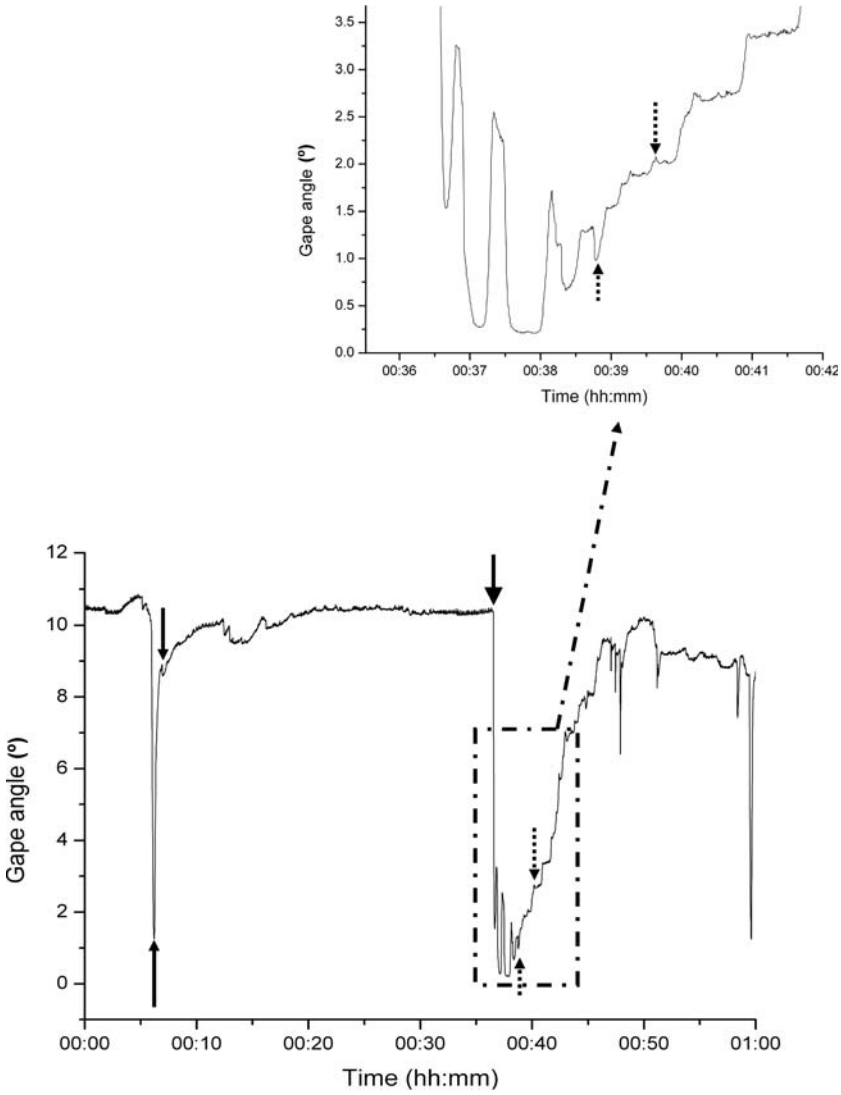

Fig. 8 Mussel gape angle versus time for 34.6 mm long mussel. The *large arrow* indicates the time when the mussel was stressed by being exposed to water in which a damaged conspecific was housed. Closure Þ-value for this was $-0.009°s^{-1}$. The inset shows greater detail of how the mussel responded to the stressor. Unstressed opening indicated by *small arrows* and stressed opening indicated by *dashed arrows*

study is required in the laboratory to determine how mussels react to particular conditions of food or predation and to examine how mussels in the wild react. Determination of Þ-values has direct commercial value as a tool to measure the performance of mussels in suspended and bottom culture in terms of mussel wellbeing and growth. Þ-values also have considerable commercial potential when used on bivalve hatchery broodstock where the environment can be manipulated to produce optimal conditions for gamete production. Þ-values used in conjunction with a technique currently being developed for measuring filtration rates using pressure micro-sensors and the current techniques for measuring bivalve heart rates (Depledge and Andersen 1990; Rovero et al. 1999) and pumping behaviour (Mouabad 2001) have the potential to revolutionize our understanding of mussel behaviour.

Acknowledgments The authors express their thanks to Nikolai Liebsch, Jay Daniels, Keith Naylor, Deep Dock Ltd and the European Social Fund for financing this work. All experiments performed comply with current UK law.

References

Bertram JEA, Lee DV, Todhunter RJ, Foels WS, Williams AJ, Lust G (1997) Multiple force platform analysis of the canine trot: a new approach to assessing basic characteristics of locomotion. Vet Comp Orthopaed 10:160–169

Clutton-Brock TH, Russell AF, Sharpe LL (2004) Behavioural tactics of breeders in cooperative meerkats. Anim Behav 68:1029–1040 DOI 10.1016/j.anbehav.2003.10.024

Curtis TM, Williamson R, Depledge MH (2000) Simultaneous, long-term monitoring of valve and cardiac activity in the blue mussel *Mytilus edulis* exposed to copper. Mar Biol 136:837–846 DOI 10.1007/s002270000297

Depledge MH, Andersen BB (1990) A computer-aided physiological monitoring-system for continuous, long-term recording

of cardiac activity in selected invertebrates. Comp Biochem Physiol 96A:473–477 DOI 10.1016/0300–9629(90)90664-E

DeZwart D, Kramer KJM, Jenner HA (1995) Practical experiences with the biological early warning system mosselmonitor. Environ Toxicol Water Qual 10:237–247

FAO (1999) Yearbook of fishery statistics for 1997, vol 84. Food and Agriculture Organisation of the United Nations, Rome

Fisher NS, Teyssie JL, Fowler SW, Wang WX (1996) Accumulation and retention of metals in mussels from food and water: a comparison under field and laboratory conditions. Environ Sci Technol 30:3232–3242

Gosling E (ed) (2003) Bivalve molluscs: biology, ecology, and culture. Blackwell Publishing, Oxford

Jørgensen CB (1990) Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen and Olsen, Fredensborg

Kádár E, Costa V, Santos RS, Lopes H (2005) Behavioural response to the bioavailability of inorganic mercury in the hydrothermal mussel *Bathymodiolus azoricus*. J Exp Biol 208:505–513 DOI 10.1242/jeb.01415

Lacoste A, Malham SK, Gelebart F, Gélébart F, Cueff A, Poulet SA (2002) Stress-induced immune changes in the oyster Crassostrea gigas. Dev Comp Immunol 26:1–9 DOI 10.1016/S0145–305X(01)00067–2

Leonard GH, Bertness MD, Yund PO (1999) Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. Ecology 80:1–14

Mouabad A, Ait Fdil M, Maarouf A and Pihan JC (2001) Pumping behaviour and filtration rate of the freshwater mussel *Potomida littoralis* as a tool for rapid detection of water contamination. Aquat Ecol 35:51–60 DOI 10.1023/A:1011499325045

Perez-Tris J, Diaz JA, Telleria JL (2004) Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape? Anim Behav 67:511–521 DOI 10.1016/j.anbehav.2003.06.008

Riisgård HU, Kittner C, Seerup DF (2003) Regulation of opening state and filtration rate in filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, *Mya arenaria*) in response to low algal concentration. J Exp Mar Biol Ecol 284:105–126 DOI 10.1016/S0022–0981(02)00496–3

Rovero F, Hughes RN, Chelazzi C (1999) Cardiac and behavioural responses of mussels to risk of predation by dogwhelks. Anim Behav 58:707–714 DOI 10.1006/anbe.1999.1176

Ruppert EE, Fox RS, Barnes RD (2004) Invertebrate zoology: a functional evolutionary approach 7th edn. Brooks Cole Thomson, Belmont

Sandercock TG, Heckman CJ (1997) Force from cat soleus muscle during imposed locomotor-like movements: experimental data versus hill-type model predictions. J Neurophysiol 77:1538–1552

Scott G (2004) Essential animal behaviour. Blackwell Science, UK

Snyder MJ, Girvetz E, Mulder EP (2001) Induction of marine mollusc stress proteins by chemical or physical stress. Arch Environ Contam Toxicol 41:22–29

Spencer BE (2002) Molluscan shellfish farming. Blackwell Science, UK, pp 204–219

Vilensky JA (1987) Locomotor behaviour and control in humans and non-human primates: comparisons with cats and dogs. Neurosci Biobehav Rev 11:263–274 DOI 10.1016/S0149–7634(87)80013–1

Wilson RP, Liebsch N (2003) Up-beat motion in swinging limbs: new insights into assessing movement in free-living aquatic vertebrates. Mar Biol 142:537–547

Wilson RP, 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. Mar Biol 140:17–27 DOI 10.1007/s002270100659

Wilson R, Reuter P, Wahl M (2005) Muscling in on mussels: new insights into bivalve behaviour using vertebrate remote-sensing technology. Mar Biol 147:1165–1172 DOI 10.1007/s00227–005–0021–6