Small actions, big costs: the behavioural energetics of a commercially important invertebrate

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Anthropogenic disturbance of farmed animals can be detrimental by adversely affecting behaviours and metabolic rate, potentially reducing their commercial value. However, relatively little is known about the normal behavioural time budgets and associated metabolism of many such species, particularly for example pectinid bivalves, which use anaerobic metabolism during periods of short-burst activity. In the present study, we used the accelerometry technique to measure scallop overall dynamic body acceleration in combination with respirometry in order to obtain and compare the behavioural time budgets and associated metabolism of 10 scallops, Pecten maximus, in an aquaculture hatchery and 10 in the wild. Scallops in the wild typically spent only 0.1 per cent of the time moving (less than 2 min d⁻¹), yet, on average, the estimated metabolism of such movement represented 16.8 per cent of daily energy expenditure. Furthermore, owing to their reliance on anaerobic pathways during such activity, movement resulted in the wild scallops having a raised metabolic rate for, on average, an estimated 7.8 per cent of the time, during which oxygen debts accumulated during movement were paid off. Hatchery scallops also typically spent only 0.1 per cent of the time moving but estimated metabolism of such movement represented 41.8 per cent of daily energy expenditure. Estimated mean daily metabolism of scallops in the hatchery was significantly higher than scallops in the wild (169.1 versus 120.7 mg O₂ d⁻¹) because anthropogenic disturbance in the hatchery caused energetically costly non-feeding behaviours. Consequently, hatchery scallops also spent a far greater amount of time with a raised metabolic rate (an estimated 26.6% of the time) than wild scallops. While short-term bursts of movement in pectinid bivalves may appear innocuous, they result in large expenditures of energy and an oxygen debt that is paid off over long periods of time that together limit further movement. These findings have implications for the farming industry; mitigating anthropogenic disturbances to farmed colonies may minimize non-feeding behaviours and hence maximize growth rates by reducing the costs of such movements and increasing the opportunity to feed.

Keywords: accelerometry; overall dynamic body acceleration; bivalve; metabolic rate; excess post-exercise oxygen consumption; anthropogenic

1. INTRODUCTION

Research on the detailed ecology of edible organisms is needed to aid both their conservation because of over-exploitation [1] and their sustainable farming. Fished and farmed species, for instance, can suffer considerable anthropogenic disturbance, for example on account of working practices that expose them to unnatural vibrations, light and shadows. Indeed, disturbance associated with observing tanks of non-experimental, commercially grown aquatic species can cause some animals to perform unnatural or anti-predator behaviours that can be energetically costly. Repeated disturbance is known to have negative (e.g. decreased growth rate) or even fatal effects on species [2] and thus an important energy-based issue to investigate in commercially important aquatic organisms concerns whether anthropogenic...
Aquatic living resources are exploited by mankind worldwide. There are about 400 pectinid species, with around 33 species exploited commercially. The commercial pectinid scallops have a combined value of about US$ 1.7 billion worldwide [4]. The ecological energy budgets of scallops have been determined in relation to seasonal changes in temperature [5], food availability [6] and reproductive stage [7], but not in concert with the analysis of scallop movement, although there has been research into the dynamics and energetics of a single scallop movement—swimming [8–11]. Scallop movement and orientation in response to water flow have been studied under laboratory conditions but not to the level of detail required to provide a behavioural time budget [12]. Indeed, excluding studies on scallop escape reactions and subsequent recovery, the amount of time that scallops spend quiescent versus moving has not been quantified. For example, the daily cost of scallop valve movement (which includes active behaviours such as valve closure, digging and jumping [13,14]) has not been measured, and thus whether it constitutes a significant proportion of daily energy expenditure is unclear. Thus, relatively little is known about the normal behavioural time budgets and associated metabolism of scallops, either in aquaculture or in the wild.

The accelerometry technique, which measures body motion to estimate behaviours and associated metabolic rate, is starting to establish itself as a valuable method for obtaining behavioural time and/or energy budgets of a range of animals [15–20]. Gleiss’ theoretical paper gives detailed physical explanations as to why the method should work [21], but key is that strong relationships are found across a range of animals between the rate of energy expenditure and acceleration measurements. The method generally involves firstly calibrating a derivative of acceleration (typically ODBA; overall dynamic body acceleration; [16]) with metabolic rate. To date, the latter has been measured as the rate of oxygen consumption ($\dot{V}O_2$) during the behaviour(s) of interest via respirometry [21,22], which assumes that metabolism is fuelled by entirely aerobic processes [23]. However, anaerobic metabolism occurs in the muscles of many aerobic species during unsustainable, short-term movement such as fast running [24,25], fast swimming [26,27] and combative behaviours [28,29], and can sometimes even represent the source of the great majority of energy expenditure during these behaviours [30].

Anaerobic metabolism also predominates during scallop movement [3,31], which occurs over short time periods usually less than 1–10 s in duration [32]. Subsequent to such short-burst activity, a recovery period after movement is required for restoration of the phosphoarginine pool and ATP pool (energy reservoirs) [33,34], with recuperation relying upon ATP production by mitochondria within the muscle fibres [34]. These recovery periods are represented by oxygen consumption after exercise over and above oxygen consumption representing routine metabolic rate, i.e. oxygen uptake known as excess post-exercise oxygen consumption (EPOC [35]). When measuring metabolic rate as the rate of oxygen consumption, where anaerobic metabolism is prominent, including EPOC is often considered to at least approximately account for the anaerobic metabolic component, such that measured oxygen consumption during the movement plus the subsequent EPOC is a reasonable representation of metabolism during that movement [30]. When movement durations are short, EPOC comprises a large percentage of the total oxygen consumed as a result of the movement because the oxygen consumed during the brief period of movement is small [30].

In the present study, we relate metabolic rate with ODBA in scallops, Pecten maximus (Linnaeus 1758), estimating metabolic rate as total oxygen consumption (total $\dot{V}O_2$) during the movement of interest plus the subsequent EPOC. This enabled the generation of ODBA-based prediction equations to estimate scallop, P. maximus, energetics. Further, we document the ODBA signatures that indicate each of the major scallop behaviours. These metabolism and behaviour calibrations allowed us to compare in detail the behavioural time budgets and associated metabolic rates of scallops, P. maximus, in a hatchery and in the wild. We hypothesize that anthropogenic disturbance will cause hatchery scallops to display a different behavioural time budget to wild scallops and expend more energy overall. We further hypothesize that since anaerobic metabolism in scallops is used for short bursts of movement but is unsustainable and reduces the energy reserves available to escape (swim) from predators, scallops will generally fully recover from a movement event, denoted by a return of $\dot{V}O_2$ to resting levels, before undertaking another movement event.

2. MATERIAL AND METHODS
All research detailed below was conducted in accordance with institutional, national and international guidelines relating to the use of bivalves in research.

Ten scallops in the Rade de Brest were caught by divers near l’Écluse du Tinduff (48.3024 N, −4.4477 W), Port Du Tinduff, 29470, France. They were placed in a single hatchery tank filled with natural, unfiltered sea water (3 × 1.4 × 0.55 m deep) at l’Écluse du Tinduff. The tank had a coarse shell and gravel bottom and the sea water in the tank was continuously exchanged with fresh sea water from the Rade de Brest. Thus, scallops in the hatchery had a natural seston diet. An infrared camera recorded all scallop movements while in the hatchery.

The scallops were maintained within the tank for 6 days and then each was instrumented with a custom-built accelerometer logger (JUV Elektronik, Borstel, Germany), replaced in the tank and left untouched for 7 days (‘observation experiments’). Recording time was limited by battery capacity, which supplied sufficient voltage for around 36 h. The accelerometer logger recorded for the final 24 h of the observation experiments at which point with the accelerometer logger still recording, each scallop was placed alone inside a respirometry chamber submerged in the tank described above for 12 h, during which time accelerometer logger behaviour and metabolic rate-calibration data were obtained.
Soon afterwards, the accelerometer logger was removed. Then scallop dimensions and mass were measured.

A further 10 scallops were caught in the same area in the Rade de Brest, immediately instrumented with accelerometer loggers and returned to the location where they had been caught. The accelerometer loggers started recording data 6 days after deployment and they were removed after about 36 h of recording. Scallop dimensions and mass were measured at this time. These wild scallops were not involved in respirometry experiments.

2.1. Accelerometer loggers

The accelerometer loggers were set to record acceleration in three axes (0–6 g), gape angle (°) via a calibrated Hall sensor [36], depth (m) and temperature (°C) at 16 Hz with 22-bit resolution onto a 1 Gb RA memory card. This recording frequency is sufficiently high to use measures of scallop acceleration as a proxy for metabolic rate [37] and to ascertain unique signatures for each scallop behaviour. Preset accelerometer loggers were heat-sealed into a polyethylene film. After epibionts were removed from the outer shell surface, a sealed accelerometer logger was glued to the outer shell of the upper (left/flat) valve of each scallop using glue (Araldite 90 s epoxy, Huntsman Advanced Materials) and waterproof tape (Tesa tape No. 4651, Hamburg, Germany).

The accelerometer loggers employed were smaller and lighter than those used in previous studies measuring ODBA [16,19]. Including the memory card, the accelerometer loggers were 4.0 × 1.7 × 1.1 cm maximum dimensions and the Hall sensor, including the associated wire, had maximum dimensions of 3.0 × 0.4 × 0.3 cm. Including the memory card, Hall sensor and one-half AA 3.6 V lithium battery, the package deployed had a mass of 21.1 g. The air inside the polyethylene film made the accelerometer loggers neutrally buoyant in sea water.

Data from the accelerometer loggers were downloaded onto a PC using custom-made software. The z-axis of the accelerometer logger measured sway, the y-axis measured surge and the x-axis measured heave (see [17] for more details). From the downloaded accelerometer logger data, an approximation of absolute acceleration (g) resulting only from dynamic acceleration in each of the three dimensions was extracted from each axis following removal of the static acceleration using a running mean of 3 s (cf. [38]). These values were then summed to produce ODBA (see [16,38] for more details). Valve movements were recorded and quantified from the valve gape data.

2.2. Observation experiments

Scallops in the hatchery were continuously exposed to indirect artificial light and periodic anthropogenic shadows and vibrations caused by the workings of a scallop hatchery manned 24 h d⁻¹. Ten scallops were equipped with accelerometer loggers on 14 May 2010 which recorded data in observation experiments from 09.00 h on 20 May for 24 h. Mean hatchery scallop ash-free dry tissue mass (dry mass) = 10.9 g, range 9.0–13.6 g; see table 1; shell height (maximum distance from umbo to shell edge) 108.0 mm ± s.e.m. 2.1, maximum shell width 129.3 ± 1.5, sea water temperature 15.3–16.6°C, salinity 32–33%.

The 10 scallops studied in the wild were instrumented on 1 July 2010, with the accelerometer loggers programmed to record data 6 days after deployment at 09.00 h for approximately 36 h. Observation experiments in the wild when the accelerometer logger recorded data were for 24 h (or 36 h where specifically stated) from the 09.00 h start time of data logging. Mean wild scallop dry mass = 11.4 g, range 9.3–13.6 g; shell height 111.8 mm ± s.e.m. 1.4, maximum shell width 131.1 ± 1.2, sea water temperature 15.1–16.2°C, salinity 32–33%, depth 7.0–13.1 m.

2.3. Respirometry experiments

A closed-circuit respirometry system was used to measure scallop metabolic rate via calculations of VO₂. The respirometer chamber was cylindrical, flat-bottomed (internal diameter 15 cm, height 26.1 cm) and contained sterilized sand to a depth of 8 cm. The respirometer chamber contained 3.2 l of sea water when no scallop was present and water flow in the chamber was 2 l min⁻¹, allowing stable measurement of oxygen concentration by a dissolved oxygen probe (YSI 66562 Rapid Pulse Sensor) once per second [39,40]. Scallops were placed in the respirometer chamber at approximately 09.00 h on 21 May 2010 by which time they had made neither valve movements for at least 15 min nor swum for at least 6 days. Metabolic rate of scallops and controls (no scallop) was determined which time they had made neither valve movements for 30 min, a steady routine metabolic rate (the metabolic rate of a quiescent, undisturbed animal which can include feeding behaviour but specifically no valve adduction or rapid (<0.5 s per event) valve abduction [41]) was measured over 1 h. For each scallop, the three measurements of routine metabolic rate were combined, averaged and the standard deviation calculated.

Movement was defined as valve adduction at any speed (all <0.5 s per event) or rapid (<0.5 s per event) valve abduction (active and rapid relaxation of the smooth adductor muscle [42,43]) occurring after the glide period [32] of spinning and swimming. Movement also included the glide period during spinning and swimming, EPOC (VO₂ after exercise over and above VO₂ representing routine metabolic rate) started immediately after a period of movement and the end-point of EPOC was defined as when VO₂ returned to within +1 s.d. of routine VO₂. Periods without movement were defined as periods without valve adduction, rapid valve abduction or gliding. During periods without movement when there is no EPOC, VO₂ should be an accurate measure of routine metabolic rate. In contrast, during movement a large proportion of scallop
Table 1. Summary of the 24 h behavioural time budgets and associated metabolic rate of hatchery and wild scallops. Standard error of the mean are provided for measured values, while standard error of the estimate are provided for estimated values.

<table>
<thead>
<tr>
<th>Hatchery scallop ID</th>
<th>Dry mass (g)</th>
<th>Mean ODBA during movement within a 24 h period (g)</th>
<th>Mean estimated VO$_2$ per 24 h (mg O$_2$ d$^{-1}$)</th>
<th>Mean estimated duration of raised metabolic rate per 24 h period (h)</th>
<th>Time spent on movement per 24 h period (s)</th>
<th>Proportion of time spent on movement (%)</th>
<th>Proportion of time spent on movement + EPOC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>12.0</td>
<td>0.5185</td>
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<td></td>
<td>254.1</td>
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<td>2</td>
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<td>3</td>
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<td>0.22</td>
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<tr>
<td>4</td>
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<td></td>
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<td>55.3</td>
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<td></td>
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<tr>
<td>10</td>
<td>12.6</td>
<td>0.7093</td>
<td></td>
<td></td>
<td>119.4</td>
<td>0.14</td>
<td></td>
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<tr>
<td>Mean ± s.e.m./s.e.e.</td>
<td>10.9 ± 0.5</td>
<td>0.6792 ± 0.0332</td>
<td>169.1 ± 10.7</td>
<td>6.38 ± 0.90</td>
<td>111.8 ± 20.5</td>
<td>0.13 ± 0.02</td>
<td>26.6 ± 3.8</td>
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</table>

<table>
<thead>
<tr>
<th>Wild scallop ID</th>
<th>Dry mass (g)</th>
<th>Mean ODBA during movement within a 24 h period (g)</th>
<th>Mean estimated VO$_2$ per 24 h (mg O$_2$ d$^{-1}$)</th>
<th>Mean estimated duration of raised metabolic rate per 24 h period (h)</th>
<th>Time spent on movement per 24 h period (s)</th>
<th>Proportion of time spent on movement (%)</th>
<th>Proportion of time spent on movement + EPOC (%)</th>
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<td></td>
<td>98.1</td>
<td>0.11</td>
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<tr>
<td>9</td>
<td>10.1</td>
<td>0.1936</td>
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<td>58.0</td>
<td>0.07</td>
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</tr>
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<td>0.1821</td>
<td></td>
<td></td>
<td>48.1</td>
<td>0.06</td>
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</tr>
<tr>
<td>Mean ± s.e.m./s.e.e.</td>
<td>11.4 ± 0.4</td>
<td>0.2509 ± 0.0249</td>
<td>120.7 ± 4.8</td>
<td>1.88 ± 0.32</td>
<td>88.1 ± 17.6</td>
<td>0.10 ± 0.02</td>
<td>7.8 ± 1.3</td>
</tr>
</tbody>
</table>
metabolism is anaerobic and thus cannot be measured as VO₂ during that movement. However, measuring the EPOC associated with movement reasonably accounts for the anaerobic element of metabolism [30]. Therefore, in the present study, the estimated metabolic rate of a scallop during a period of movement was measured as: 

\[
\frac{[\text{VO}_2 \text{ during movement} \times \text{movement duration}) + ([\text{VO}_2 \text{ during period of EPOC} – \text{routine } \text{VO}_2] \times \text{EPOC duration})]}{\text{movement duration}}
\]

Daily metabolism was calculated by summing estimates of routine metabolic rate during periods without movement and estimates of metabolic rate during movement over a 24 h period. Estimated total VO₂ per day associated with a type of movement was calculated as the estimated metabolic rate during such movement multiplied by the total duration of that movement over the day.

### 2.4. Data analysis

Using the infrared camera recordings, scallop movements were classified as the following:

- a ‘cough’—a rapid valve adduction associated with the expulsion of faeces and other substances from the mantle cavity [13,42];
- digging—creating a self-formed depression in the seafloor sediment, using only infrequent rapid valve adductions (valve abdution is very gradual (>4 s) between each digging adduction), so that the scallop lies recessed with the flat valve roughly in the plane of the substrate [13];
- a ‘turn’—a rapid valve adduction causing less than or equal to about one full rotation on the substrate;
- spinning—rapid valve adduction followed by abduction events (2–3 s⁻¹) causing multiple rotations on the substrate;
- swimming—rapid valve adduction followed by abduction events (2–3 s⁻¹) causing the scallop to lift off the substrate.

The infrared camera recording of each type of movement in the hatchery confirmed a unique ODBA trace as a function of time (cf. [17]; OriginPro v. 7.5, OriginLab Corporation, USA). Then, by manually identifying and quantifying the duration of each scallop behaviour from the ODBA traces, the behavioural time budgets of the scallops were calculated.

All data included in statistical analyses met the necessary parametric assumptions; certain variables were transformed to make them normally distributed. A relationship to predict routine metabolic rate from dry mass was generated from a single linear regression using data from the 10 instrumented scallops in a hatchery. This equation was used to estimate the metabolic rate of scallops in the hatchery and in the wild during movement.

The mean whole wet mass of a scallop with epibionts on the outer shell surface (n = 20) was 278.8 ± 7.9 g (range 224.8–332.8 g) and was significantly greater than for the same scallops with the epibionts removed and instrumented with an accelerometer logger (mean 210.0 ± 6.6 g, range 168.9–279.9 g, t = 9.76, p ≤ 0.001). Each scallop behaviour provided a consistently unique acceleration

3. RESULTS

The mean whole wet mass of a scallop with epibionts on the outer shell surface (n = 20) was 278.8 ± 7.9 g (range 224.8–332.8 g) and was significantly greater than for the same scallops with the epibionts removed and instrumented with an accelerometer logger (mean 210.0 ± 6.6 g, range 168.9–279.9 g, t = 9.76, p ≤ 0.001). Each scallop behaviour provided a consistently unique acceleration
3.1. Metabolic rate prediction equations

Mean routine metabolic rate of the 10 hatchery scallops in the respirometer was 0.066 mg O$_2$ min$^{-1} \pm 0.003$ at 16°C. Based on the respirometry data, the linear regression equation for predicting routine metabolic rate of a scallop from dry mass was significant ($p < 0.001$; figure 3):

$$\text{routine metabolic rate (mg O}_2\text{ min}^{-1}) = (0.0056 \times \text{dry mass (g)}) + 0.0058 \quad (r^2 = 0.85).$$

(3.1)

The equation generated for predicting metabolic rate of a scallop during movement from ODBA (figure 4) and dry mass was also significant ($p < 0.001$):

$$\text{estimated metabolic rate (mg O}_2\text{ min}^{-1}) = (62.27 \times \text{ODBA (g)}) + (-0.5034 \times \text{dry mass (g)}) + 5.107 \quad (r^2 = 0.82).$$

(3.2)

as was the equation generated for predicting the duration of raised metabolic rate of a scallop from total ODBA (figure 5) and dry mass ($p < 0.001$):

$$\text{square root of the duration of raised metabolic rate (min)} = (16.88 \times \text{square root of total ODBA (g x min)}) + (0.0895 \times \text{dry mass (g)}) - 0.915 \quad (r^2 = 0.87).$$

(3.3)

In the respirometry chamber, after one or multiple valve movements, measurements of VO$_2$ always returned to routine VO$_2$ for at least 5 min before another valve movement.

3.2. Comparing scallops in the hatchery and in the wild

The morphology of the hatchery and wild scallops was similar. There was no significant difference between the dry mass of the two groups of scallops after the experiments (mean dry mass: 10.9 $\pm$ 0.5 g and 11.4 $\pm$ 0.4 g, for hatchery and wild scallops, respectively; $t_{18} = -0.73$, $p = 0.473$). Furthermore, there was no significant difference in the estimated total routine metabolism per 24 h (mean = 96.0 mg O$_2$ $\pm$ 3.8 and 99.9 mg O$_2$ $\pm$ 3.5 for the hatchery and wild scallops, respectively; $z = -0.74$, $n = 20$, $p = 0.460$ (table 2)). For each 24 h, for both groups of scallops, routine behaviour was estimated to be undertaken during a
Figure 2. Examples of valve gape and ODBA of various scallop behaviours: (a) coughing, (b) digging, (c) turning and (d) spinning behaviours.

Figure 3. Routine metabolic rate (measured as rate of oxygen consumption, VO₂: mg O₂ min⁻¹) against hatchery scallop ash-free dry tissue mass (g). The best-fit regression line (solid line) and 95% prediction intervals (dashed lines) are shown.

Figure 4. Estimated metabolic rate (measured as rate of oxygen consumption, VO₂: mg O₂ min⁻¹) against ODBA (g) for each hatchery scallop (denoted by different symbols) during a range of movements. The best-fit regression line (solid line) and 95% prediction intervals (dashed lines) are shown.
Figure 5. Square root of the duration of raised metabolic rate (min) associated with movement against the square root of total ODBA (mean ODBA for a movement × duration of movement) during the movement for each hatchery scallop (denoted by different symbols) during a range of movements. The best-fit regression line (solid line) and 95% prediction intervals (dashed lines) are shown.

more time and energy digging and turning compared with scallops in the wild (time digging: \( t_{d} = 2.33, p = 0.032 \); time turning: \( t_{t} = 2.20, p = 0.041 \)); energy digging: \( z = 2.59, n = 20, p = 0.010 \); energy turning: \( z = 2.06, n = 20, p = 0.040 \). All 10 scallops in the hatchery swam during the course of 1 day (table 2) but no spinning behaviour was recorded in any scallops in the wild during the entirety of the 36 h recording period. Only two scallops in the wild swam when the accelerometer logger was recording; both just once and for a short period (ca 5 s). Estimated metabolic rate during these swims was 84.2 ± 2.4 mg O\(_{2}\) min\(^{-1}\) (\( n = 2 \)) and the estimated total VO\(_{2}\) associated with swimming (total VO\(_{2}\) during swimming + EPOC) per day was 7.1 ± 0.4 mg O\(_{2}\) (\( n = 2 \); cf. table 2). Visual inspection of the data suggested no influence of tidal cycles or circadian rhythms on the movement and associated metabolic rate of scallops in the hatchery or in the wild.

Calculations made using equation (3.3) estimated that if a scallop of 11 g dry mass swam for a total of 218 s d\(^{-1}\), composed of many short swims averaging 5 s, it would have a constantly raised metabolic rate.

4. DISCUSSION

The present study shows that although scallops undertake active behaviours infrequently and lasting just fractions of a second to a few seconds at a time, those behaviours nonetheless incur large energetic costs. In total, the time scallops moved in the present study was typically less than 2 min d\(^{-1}\) yet on average an estimated 29.3 per cent of daily energy expenditure was spent on such movement. Furthermore, owing to their reliance on anaerobic pathways during such activity, movement resulted in the scallops having a raised metabolic rate for on average an estimated 17.2 per cent of the time, during which rapidly accumulated oxygen debts were paid off. Validity of these results is provided by comparison with previous studies. For example, in the respirometry experiments of the present study, maximum ODBA was produced by a spin involving six rapid valve adduction–abduction events at a rate of 2–3 s\(^{-1}\) although this resulted in a relatively small subsequent EPOC of less than 30 min (figure 5). This finding is similar to the results of Livingstone et al. [33], who recorded a recovery period of approximately 30 min after five rapid valve adduction, followed by abduction events at a rate of 2–3 s\(^{-1}\) in the giant scallop, *Placopecten magellanicus* (cf. recovery period of scallops after valve movements causing complete exhaustion [33,47,48]).

4.1. The accelerometry method

The present study is the first to apply the accelerometry technique for investigating the behavioural energetics of a bivalve; by far, the smallest species studied by this method to date. As found in previous studies calibrating metabolic rate with ODBA [16,49], the relationship for scallops was strong (figure 4). Thus, within the body mass and temperature range included in the present study, using equations (3.1) and (3.2), the detailed behaviour and the estimated metabolic rate of a group of scallops can be obtained (estimates for individual

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Table 2. Detailed 24 h behavioural time budgets and associated metabolic rates of hatchery and wild scallops. Standard error of the mean are provided for measured values, while standard error of the estimate are provided for estimated values.

<table>
<thead>
<tr>
<th></th>
<th>hatchery scallop mean ± s.e.m/s.e.e.</th>
<th>wild scallop mean ± s.e.m/s.e.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>cough mean ODBA (g)</td>
<td>dig mean ODBA (g)</td>
</tr>
<tr>
<td>hatchery scallop</td>
<td>0.1941 ± 0.0144</td>
<td>0.6519 ± 0.0417</td>
</tr>
<tr>
<td>wild scallop</td>
<td>0.1625 ± 0.0126</td>
<td>0.6707 ± 0.0680</td>
</tr>
<tr>
<td>proportion of time spent coughing (%)</td>
<td>0.025 ± 0.004</td>
<td>0.056 ± 0.019</td>
</tr>
<tr>
<td>proportion of time spent digging (%)</td>
<td>0.019 ± 0.003</td>
<td>0.011 ± 0.004</td>
</tr>
</tbody>
</table>
animals will often be inaccurate [22]. Furthermore, equation (3.3) (figure 5) enables estimates of the time for complete recovery from oxygen debt subsequent to movement, which is a key metabolic parameter for scallops as periods of EPOC constrain their behaviours.

Instrumentation of a scallop with an accelerometer logger did not seem to limit their behavioural options because scallops in the present study were able to perform all the movement types previously reported [8,13,14,50]. Accelerating the accelerometer is a cost to the scallop but accelerating the epibionts is likely an even greater cost to the animal, or at the least similar to the cost of the accelerometer, because epibiont mass removed was greater than logger mass. Indeed, we specifically picked scallops with significant biofouling such that its removal would counter the mass and volume of the logger, and significant biofouling is the norm for scallops at least in the Rade de Brest area. All the instrumented scallops had a significant biofouling is the norm for scallops at least in the Rade de Brest area. All the instrumented scallops had a

4.2. Comparing scallops in the hatchery and in the wild

Measuring the behavioural time budgets and associated metabolic rate of an animal in different environments provides valuable data to empirically determine if the variation in the environment affects their ecology. The present scallop data are the most detailed behaviour and energetics data yet obtained using the accelerometry technique.

There was neither difference in the time spent on movement in the two environments nor in the estimated metabolic cost of the coughing, digging and turning behaviours. However, the behavioural budgets of the periods spent moving differed. Wild scallops performed either digging or turning, or both behaviours, so some daily change in orientation, possibly towards optimum feeding conditions [12,52] was possible since the infrared camera recording showed that both digging and turning can result in a change in orientation. Hatchery scallops also exhibited digging and turning behaviours, but spent more time and energy on these behaviours than the wild scallops. Furthermore, spinning was exhibited by every scallop in the hatchery but was not recorded at all in the wild. This stark contrast is probably owing to anthropogenic disturbance (vibrations, artificial light and shadows) in the working scallop hatchery, resulting in anti-predatory behaviour [3]. In contrast, scallops in the wild spent more time and energy on the relatively low-energy cough, indicating that they were feeding more. Indeed, more time and energy was spent on the cough than any other movement type in the wild, while in the hatchery, more time and energy was spent on digging, turning and spinning. Hatchery scallops likely exhibited lower feeding rates not only because of time spent on anti-predator behaviours but also because these behaviours reduced the energy available for feeding; hatchery scallops spent a far greater amount of time with a raised metabolic rate (an estimated 26.6% versus 7.8%). We conclude that the estimated metabolic costs per day were significantly higher for scallops in the hatchery compared with the wild because of the type, and not the duration, of movement performed per day.

These findings have implications for the farming industry; mitigating anthropogenic disturbances to farmed colonies may minimize energetically costly

Table 3. Details of movement behaviours exhibited over 24 h by hatchery and wild scallops. Standard error of the mean are provided for measured values.

<table>
<thead>
<tr>
<th></th>
<th>hatchery scallop</th>
<th>wild scallop</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean ± s.e.m.</td>
<td>mean ± s.e.m.</td>
</tr>
<tr>
<td>duration of one cough (s)</td>
<td>0.31 ± 0.03</td>
<td>0.32 ± 0.03</td>
</tr>
<tr>
<td>(n = 8)</td>
<td>0.26 ± 0.01</td>
<td>0.25 ± 0.01</td>
</tr>
<tr>
<td>duration of one dig (s)</td>
<td>22 ± 3 (29 min ± 8)</td>
<td>18 ± 2 (25 min ± 7)</td>
</tr>
<tr>
<td>self-formed depression</td>
<td>(n = 8)</td>
<td>(n = 8)</td>
</tr>
<tr>
<td>in sediment</td>
<td>0.22 ± 0.01</td>
<td>0.24 ± 0.01</td>
</tr>
<tr>
<td>duration of one turn (s)</td>
<td>1.44 ± 0.08</td>
<td>n.a.</td>
</tr>
<tr>
<td>(n = 8)</td>
<td>n.a.</td>
<td>5.04 ± 0.14</td>
</tr>
<tr>
<td>number of cough events per day</td>
<td>0.03 0.08</td>
<td>0.08 n.a.</td>
</tr>
<tr>
<td>number of digging</td>
<td>69 ± 10</td>
<td>233 ± 39</td>
</tr>
<tr>
<td>events per day</td>
<td>181 ± 58</td>
<td>36 ± 9</td>
</tr>
<tr>
<td>number of self-formed</td>
<td>8 ± 3</td>
<td>2 ± 1</td>
</tr>
<tr>
<td>depressions made per day</td>
<td>30 ± 6</td>
<td>13 ± 4</td>
</tr>
<tr>
<td>number of turn events per day</td>
<td>25 ± 4</td>
<td>0</td>
</tr>
<tr>
<td>number of spinning</td>
<td>0</td>
<td>0.2 (i.e. &lt;1)</td>
</tr>
<tr>
<td>events per day</td>
<td>n.a.</td>
<td>0</td>
</tr>
<tr>
<td>number of swims per day</td>
<td>n.a.</td>
<td>n.a.</td>
</tr>
</tbody>
</table>

*One rapid valve adduction associated with digging.
non-feeding behaviours and hence maximize growth rates by reducing the costs of such activities and increasing the opportunity to feed.

4.3. Recovery and excess post-exercise oxygen consumption

Our results highlight that scallops increase oxygen uptake immediately after movement [33] and almost always fully metabolically recover from that movement before another movement event (based on equation (3.3)). While anthropogenic touch stimulation can cause scallops to perform movement during periods of EPOC [42,53], in the present study, where there was no touch stimulation, the scallops rarely moved until their oxygen debt had been repaid. None of the scallops in the present study displayed apparent exhaustion after valve movement(s) in the form of a complete lack of oxygen uptake [3,41].

Full recovery may be strategic because during EPOC, behavioural options are limited because of the reduced amount and rate of energy expenditure possible. For example, scallops exhibiting EPOC will be more limited in their ability to swim away from predators or dig themselves into sediment.

Anthropogenic stimulation of scallops to swim until exhaustion clearly results in a rapid accumulation of oxygen debt [33,54]. It was estimated that if the average scallop (11 g dry mass) swam for a total of 218 s (3.6 min) per day (cf. typical time moving—coughing, digging, turning, spinning and swimming—totalling less than 2 min d⁻¹; tables 1–3), it would have a constantly raised metabolic rate. While likely a theoretical scenario, a constantly raised metabolic rate may represent the limiting factor on the amounts of scallop movement that can be undertaken.

5. CONCLUSIONS

The accelerometry technique has provided unprecedented information about the typical behavioural time budgets and associated metabolic rate of a commercially important invertebrate both in the hatchery and in the wild. While short-term bursts of scallop movement may appear innocuous, they result in large expenditures of energy and an oxygen debt that is paid off over long periods of time that together limit further scallop movement. So, for an animal that relies on unsustainable, short-term activity for movement, undertaking a small movement has serious implications, perhaps most importantly that for a significant period of time subsequently, these animals are likely less able to escape predation and less able to feed. The latter issue probably has consequences for somatic growth rates and gamete production in farmed colonies where anthropogenic disturbance can cause animals to elicit a range of energetically costly behaviours. While this finding may well be generalizable to other cephalopod species, the total activity budget of an endotherm is much smaller than that of an ectotherm overall as a proportion of total metabolic costs owing to the dominance of basal metabolic costs in endotherms. Thus, anthropogenic disturbances increasing the occurrence of energetically costly anaerobic activities are likely to impact the bottom line of an alligator, frog, turtle, salmon or scallop farm much more than a cattle farm.

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REFERENCES

Energetics of a commercial invertebrate  A. A. Robson et al.  1497


