

Metabolic rate depression in a marine pulmonate snail: pre-adaptation for a terrestrial existence?

David J. Marshall and Christopher D. McQuaid

Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140, South Africa

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Summary. Terrestrial and freshwater pulmonate snails exhibit a marked depression of aerobic metabolism during estivation. This is an adaptation for existence in periodically harsh environments and, though marine gastropods may undergo anaerobic metabolism, they have not been shown to adaptively depress aerobic metabolic rate. We compared the metabolic response to progressive aerial exposure of two intertidal gastropod limpets, a prosobranch and a pulmonate. The prosobranch *Patella granularis* maintained a constant heart rate until shortly before death. In contrast, the pulmonate *Siphonaria oculus* underwent facultative depression of heart rate, accompanied by a decline in oxygen consumption. Both heart rate and oxygen consumption returned to normal levels on reimmersion in water. Metabolic rate depression is energy conserving, and may account for the ability of *S. oculus* to extend higher up the shore than *P. granularis*, into areas where food availability is low. *S. oculus* is a primitive, marine pulmonate, periodically subject to harsh conditions, and its capacity for metabolic rate depression may represent a pre-adaptation for life on land.

Key words: Limpets – Intertidal – *Siphonaria* – *Patella* – Metabolic rate depression

Many terrestrial and freshwater pulmonate snails survive unfavourable environmental conditions (food and water deprivation, low temperatures) by their remarkable capacity for depression of metabolic rate (McMahon 1983; Barnhart and McMahon 1987; Storey and Storey 1990). Although a few marine pulmonate species exist, there are no reports of depression of aerobic metabolism by marine gastropods (Storey and Storey 1990). We compared the metabolic response to continual aerial exposure, of two intertidal limpets, a prosobranch and a pulmonate, and report that, while the prosobranch

showed no metabolic control, the pulmonate was capable of facultative metabolic rate depression. Comparisons were made between two upper-shore limpet species of distant phylogenetic relationship, *Patella granularis* L. (Gastropoda: Prosobranchia) and *Siphonaria oculus* Krauss (Gastropoda: Pulmonata). Conveniently, they have similar shell shapes and sizes, and thus water relation properties (Lowell 1984).

Methods

Limpets (mean dry weight \pm SD: 161 ± 38 mg; $n=37$) collected from Port Alfred ($33^{\circ}36'S$; $26^{\circ}53'E$), South Africa, were held under constant laboratory conditions of temperature ($25 \pm 0.5^{\circ}C$; $\bar{n} \pm$ SD; typical diurnal air temperature in summer), salinity (35‰) and subdued illumination, for 5 days prior to experimentation. A tidal cycle of 12 : 12 h air : water, was maintained. Metabolic rate response was inferred from recordings of heart rate.

Heart beat was monitored by impedance pneumography (True-man 1967), by coupling a transducer (Z135/Bioscience) and strain gauge (FC 135/Bioscience), with a twin-channel George Washington oscillograph (MD 400). To prepare limpets for experiments, two holes were drilled through the shell near the heart, and a platinum electrode (0.3 mm diameter) with connecting lead, was inserted into each hole. Electrodes were set in position using dental wax and epoxy glue. After a settling period of at least 12 h in seawater, limpets were exposed to air ($25 \pm 0.5^{\circ}C$; $80 \pm 5\%$ R.H.; $\bar{x} \pm$ SD) for 72 h, during which aerial heart rate (f_h) was recorded at 12 h intervals. Individual heart rates (beats/min) were determined from recording traces. In the event of variability, a mean was derived from fifteen 1-min intervals.

Results and discussion

Long-term aerial exposure induced different heart rate responses in the limpet species (Fig. 1). The mean heart rate of *P. granularis* remained relatively constant (50–60 beats/min) for the duration of the exposure period. High mortality of this limpet was observed after 48 h aerial exposure and only a single individual survived 72 h in air. In a few cases heart rate fell below 40 beats/min, but this only occurred in individuals which died within the next

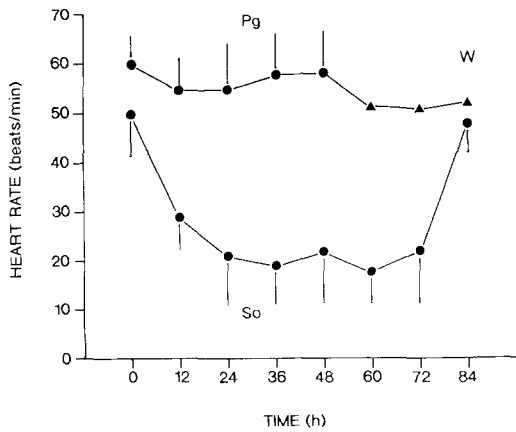


Fig. 1. Heart rate ($\bar{x} \pm 1$ SD) of *Patella granularis* (*Pg*) ($n=8-13$, except for triangles where $n=1$) and *Siphonaria oculus* (*So*) ($n=12$), during continuous exposure in air ($25 \pm 0.5^\circ \text{C}$, $80 \pm 5\%$ R.H.), and following 12 h reimmersion in water (*W*)

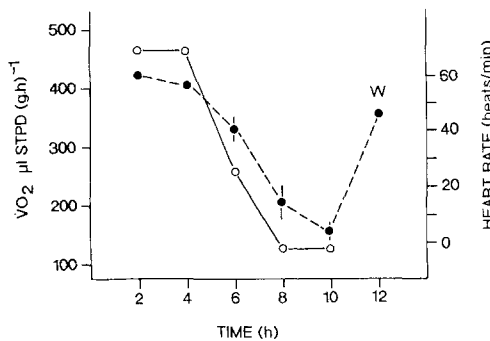


Fig. 2. Simultaneous measurements of heart rate (closed circles) and oxygen consumption (VO_2 at 25°C ; open circles) for an individual *S. oculus*, measured after intervals of exposure to a dry airstream (25°C), and following 2 h reimmersion in water (*W*). Heart rate is given as $\bar{x} \pm 1$ SD

12 h. Traces for *P. granularis* after long-term aerial exposure were characterized by beat to beat variability in amplitude and cardiac arrest (up to 1 min), characteristics indicative of stress. Periods of cardiac arrest and heart rates of dying limpets were not included in the analysis of the data. These results suggest that *P. granularis* depends on the maintenance of a relatively high metabolic rate. Lowered oxygen consumption rates following long-term aerial exposure (Marshall and McQuaid in prep.) must be a direct result of impairment of respiratory organ functioning, due to evaporative water loss.

Mean heart rate of *S. oculus* exposed to air declined rapidly (within 12 h) to 58% of the original rate, and then stabilized around 40% after 24 h. Heart rates of some individuals fell to below 10 beats/min (20% of original mean). No mortality was observed, and f_h returned to a level comparable to that recorded originally in air after 4 h of reimmersion. The relationship between aerial heart rate and oxygen consumption was confirmed by making simultaneous measurements (at 25°C) for four limpets exposed to a stream of silica-gel dried air. The oxygen

consumption was measured with a Gilson Differential Respirometer (Gilson Medical Electronics). The respirometer flasks were modified to allow for limpet size and impedance connecting leads. Dry tissue weight-specific oxygen consumption ($\dot{\text{V}}\text{O}_2$) was standardised to STPD (Fig. 2).

In addition to the lowering of f_h and $\dot{\text{V}}\text{O}_2$, *S. oculus* exhibited behavioural responses (withdrawal of the mantle skirt, and closure of the pneumostome) during prolonged aerial exposure. Reversal of these behavioural responses and an increase of 50% in the lowered f_h resulted from physical disturbance or exposure to 100% humidity. We interpret these behavioural and physiological responses as representing a metabolic steady state well below "standard" metabolic rate. Environmental anaerobiosis by this limpet seems unlikely, as there is no evidence of the utilization of anaerobic pathways in intertidal gastropods during aerial exposure when oxygen availability is not reduced. Indeed, the absence of anaerobiosis in air-exposed gastropods has been demonstrated biochemically (Wieser 1980; Kooijman et al. 1982; Brinkhoff et al. 1983), and by direct calorimetry (Pamatmat 1978; Hammen 1980).

Species living in the upper intertidal zone are faced with physiological stress due to temperature variation and water loss. Inactivity during emersion reduces desiccation, but also limits the available time for feeding. Consequently, food shortages are often experienced, and energy conserving mechanisms are important (Branch et al. 1988). Energy of the uppermost South African patellid, *P. granularis*, is conserved by their low aerial metabolic rate and relative temperature independence (low Q_{10}), compared with the other *Patella* species (Branch and Newell 1978). Temperature relationships of *S. oculus* during normal metabolism are in many respects similar to those of *P. granularis*. However, *S. oculus* tolerates a higher level of desiccation and extends its distribution considerably higher up the shore than *P. granularis*. Temperature-independent metabolic rate depression during prolonged emersion will allow enhanced conservation of energy reserves by *S. oculus*.

Depression of aerobic metabolism by *S. oculus* in air can reach as low as 18% of the normal rate (Marshall and McQuaid in prep.) and is comparable to that of terrestrial and freshwater pulmonate snails deprived of food or water. These species depress their aerobic rate during estivation to 10–30% of that of resting, non-estivating snails (von Brand et al. 1957; Barnhart and McMahon 1987). This characteristic is important for the survival of pulmonate snails on land, particularly in dry regions, and for the ability of freshwater pulmonates to colonise temporary aquatic environments.

Although such physiological adjustments often have an ecological basis, the similarity of facultative aerobic depression in *S. oculus* to that seen in many families of freshwater and terrestrial pulmonates (Machin 1975; McMahon 1983; Riddle 1983), suggests that it is a phylogenetic character. *Siphonaria* is the oldest extant pulmonate genus, dating to the Devonian period (Morton 1955) and has mainly primitive features (Solem 1985). *Siphonaria* has therefore presumably evolved in the ma-

rine environment rather than re-adapted from a terrestrial or freshwater environment. Metabolic rate depression by this marine species may therefore indicate pre-adaptation for a terrestrial existence within primitive marine pulmonates.

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