Effects of Hypoxia on Oxygen Consumption by Two Species of Freshwater Mussel (Unionacea : Hyriidae) from the River Murray

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Abstract

The mussel *Alathyria jacksoni* typically occurs in the main rivers of the Murray–Darling Basin and not in slow-flowing or standing waters. Conversely, *Velesunio ambiguus* is typical of billabongs and creeks and rarely occurs in big rivers except in the vicinity of impoundments. The exclusion of *V. ambiguus* from the main rivers probably reflects its weak anchorage, whereas the exclusion of *A. jacksoni* from billabongs may reflect its inability to withstand low levels of oxygen (hypoxia). At normal oxygen levels the mean rates of oxygen consumption for *A. jacksoni* and *V. ambiguus* are $21 \cdot 5$ (s.d. $= 6 \cdot 43$, $n = 17$) and $13 \cdot 5$ (s.d. $= 5 \cdot 85$, $n = 10$) μmol $g^{-0 \cdot 75}$ (dry tissue) h^{-1}, respectively (a body-mass exponent of $0 \cdot 75$ was included in calculations of the mass-specific oxygen consumption rate). When exposed to declining oxygen, *A. jacksoni* shows little or no regulatory ability, whereas *V. ambiguus* maintains a steady rate of oxygen consumption down to 65 torr. Under extreme hypoxia, *A. jacksoni* loses muscular tone but *V. ambiguus* closes its values and remains inactive. On removal from water *A. jacksoni* incurs a significant oxygen debt after 10 days, but *V. ambiguus* shows no oxygen debt after 15 days. In general, animals adapted to lotic environments may need more oxygen, and may be more susceptible to hypoxia, than those adapted to lentic environments.

Introduction

The hyriid freshwater mussels *Velesunio ambiguus* (Philippi) and *Alathyria jacksoni* Iredale are common in south-eastern Australia (Walker 1981*a*, 1981*b*). *V. ambiguus* occurs throughout the Murray–Darling Basin and beyond, including part of the Lake Eyre drainage and coastal areas of New South Wales, Victoria and Queensland. In contrast, *A. jacksoni* is restricted to the Murray–Darling Basin, where it is widespread although absent from the upper Darling region and some Victorian tributaries to the Murray.

There is a clear distinction between the kinds of habitat favoured by each species (Walker 1981*b*). *V. ambiguus* is associated with impoundments, lakes, billabongs and minor streams, but is not found in large rivers except in regions influenced by dams or weirs. *A. jacksoni* occurs in the open channel of large rivers where there is a strong current; it is rare in slow-flowing waters and absent from still waters. At some places along the River Murray, particularly downstream of weirs in South Australia, the two species appear to cohabit. In this situation, however, *A. jacksoni* generally occurs in the deeper waters of the main channel whereas *V. ambiguus* is restricted mostly to sheltered pockets along the margins.

A. jacksoni is comparatively large and heavy, and is a powerful burrower able to anchor itself against a strong current. The absence of the smaller, lighter *V. ambiguus* from this environment may reflect its weaker anchorage (Walker 1983). On the other hand, there is no obvious morphological reason why *A. jacksoni* should not occur in slow-flowing and

lacustrine environments. The explanation for its restricted distribution, therefore, may be of a physiological nature. In particular, the acknowledged importance of oxygen for riverine invertebrates (e.g. Hynes 1970) suggests that the respiratory physiology of these two species is worthy of study.

There is limited published information about the oxygen consumption of freshwater bivalves (e.g. Berg and Jonasson 1965; Salánki and Lukacsovics 1967; Lomte and Nagabhushanam 1971; McCorkle *et al.* 1979; Paterson 1983). The only pertinent data for mussels from the River Murray are those of Hiscock (1953*a*, 1953*b*), who measured respiration in specimens from Tailem Bend, South Australia, as part of a study on chloride regulation. Hiscock referred to the mussels as '*Hyridella australis*', an early synonym for *V. ambiguus*, but he was not aware of the presence of the second species, *A. jacksoni*, and the significance of his results is uncertain. There appear to be no studies that examine the oxygen consumption of mussel species in relation to riverine and lacustrine habitats.

There are studies, however, that compare the rates of oxygen uptake of freshwater animals other than mussels from lentic and lotic environments, for example in isopods and insect larvae (Fox and Simmonds 1933), insect larvae (Walshe 1948), trout fry (Washbourn 1936), crayfish (Park 1945; Bovbjerg 1952) and gastropods (Berg 1952, 1961; Berg and Ockelmann 1959). These reports suggest that animals from swiftly flowing streams generally have higher rates of oxygen consumption than their pond-dwelling counterparts, and are more susceptible to low oxygen levels (hypoxia).

The present study examined the hypothesis that the riverine mussel *A. jacksoni* is excluded from slow-flowing and still-water environments by its inability to withstand hypoxia. This involved using techniques of closed-system respirometry to monitor the effects of decreasing oxygen levels and extreme hypoxia on the respiration of *A. jacksoni*. Comparative observations were made also on the lentic species, *V. ambiguus*.

Materials and Methods

Collection and Maintenance

Mussels were collected in May 1986, 100 m downstream from Lock 3 at Overland Corner, South Australia. Within each species, shells of similar size were selected, to minimize variation due to age and condition (*A. jacksoni* length 10–13 cm, *V. ambiguus* 6–9 cm). The two species were kept in separate aquaria (60 × 30 × 45 cm) filled with pond water over coarse sand and equipped with under-gravel filters and a continuous air supply. In aquaria containing *A. jacksoni*, extra air stones were included to maintain rapid circulation of water (cf. Walker 1981*b*). The oxygen levels in all aquaria were monitored and never fell below 120 torr. The aquaria were maintained at 20 ± 1°C with a photo-period of 12 : 12 h light : dark. Although determinations of oxygen consumption were made within 3 weeks of collection, no mortalities occurred among mussels kept in this way for up to 2 months.

Measurement of Oxygen Consumption

Oxygen consumption was determined using closed-system respirometry. Individual mussels were sealed in a known volume of water and the fall in concentration measured over a known time interval. The apparatus consisted of 1-L (*V. ambiguus*) or 2-L (*A. jacksoni*) clear perspex 'Decor' containers with air-tight lids. These made it possible to maintain low oxygen tensions for long periods; for example, in containers of water held under experimental conditions, a level of 35 torr could be maintained for at least 19 h.

Before each determination, a 5-cm layer of sand (previously washed and dried at 100°C) was added to the chamber; this was weighed (±0·5 g) and the chamber filled with filtered pond water and re-weighed to indicate the volume of water (±5 mL). Mussels were left undisturbed for 30–45 min before measurements commenced.

The system was calibrated with air-equilibrated pond water before readings were made at 15–30 min intervals over 3–5 h. The water was sampled with a 2-mL plastic syringe inserted through a three-way stopcock fitted into the side of the chamber. The chamber volume was maintained by introducing an equivalent amount of water with approximately the same oxygen tension as that in the chamber prior to withdrawing a sample (1·5–2·0 mL). The oxygen content of the sample was then measured immediately.

Oxygen tensions were det discontinued when mussels and expose the mantle marg 'Blank' determinations (sand and other incidental effects (mussel activity is least: Hisco the possible effects of circad

Tolerance to Hypoxia

For these measurements, assumed to be in hypoxia, ow were monitored by the oxyge gills rapidly removed, rinsed filtered pond water. Pond w body fluids of unionid musse from other unionids maintai (Wernstedt 1944). A 1·5-mL tension measured as before.

Analysis

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A value for P_c, the criti regulate its oxygen uptake ar was determined by piecewise (SYSTAT Inc., Illinois). Befc differences among the groups 10,112 d.f.; $P < 0·001$; for used to compute a piecewise

where *a*, β_0, β_1 and β_2 are The parameters were determi allowance for the multiple v further by examination of th

Results

Oxygen Consumption

At high oxygen levels $n = 17$) and 13·5 μmol g and *V. ambiguus* respectiv (wet weight) h^{-1}, but wet

Figure 1 shows the ef by *A. jacksoni*. Overall, ambient oxygen supply, in of an inflection point, but

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Oxygen tensions were determined using a Blood Micro Analyzer (BMS 3 Mk II). Readings were discontinued when mussels closed their valves or lost muscular tone (causing the valves to gape and expose the mantle margins). Dry tissue weights were determined after drying at 70°C for 48 h. 'Blank' determinations (sand and water but no mussel) were made to correct for microbial respiration and other incidental effects (<2 torr h^{-1}). Determinations were made at 19–21°C, under light (when mussel activity is least: Hiscock 1950; Shirtley and Findley 1978), and during daylight hours (to avoid the possible effects of circadian rhythms: Salánki and Lukacsovics 1967).

Tolerance to Hypoxia

For these measurements, mussels were removed from the water for 5, 7, 10 and 15 days. They are assumed to be in hypoxia, owing to the presence of water trapped in the mantle cavity, and the effects were monitored by the oxygen consumption of excised gill tissue. The mussels were cut open and the gills rapidly removed, rinsed in filtered pond water and placed in a 25-mL plastic syringe containing filtered pond water. Pond water was assumed to be an effective physiological saline, given that the body fluids of unionid mussels are extremely dilute (Pantin 1962) and given also that excised gill tissue from other unionids maintains a steady rate of oxygen consumption for at least 24 h in fresh water (Wernstedt 1944). A 1·5-mL water sample was displaced from the syringe every 15 min and the oxygen tension measured as before. After 1·0–1·5 h, the gill tissue was dried at 70°C for 24 h and weighed.

Analysis

The mass-specific rate of oxygen consumption M_{O_2} (μmol g^{-1} h^{-1}) was calculated from

$$M_{O_2} = \frac{(P_i - P_f)1\cdot82V}{M^bT}$$

where P_i is the initial oxygen tension (torr), P_f is the final oxygen tension, 1·82 is the capacitance for oxygen in fresh water at 20°C (μmol torr^{-1} L^{-1}; De Jours 1975), V is volume (L), M is mass (g dry wt), b is an exponent of body mass and T is time (h). The value of the exponent is normally obtained by plotting log oxygen consumption (metabolic rate) against log body mass, yielding a straight line with slope b. It was not possible to obtain empirical values of b in this study; instead, a standard value of 0·75 (cf. Gordon et al. 1977) was employed for each species. The reported data are in terms of dry tissue weight (no shell) unless otherwise specified.

A value for P_c, the critical ambient oxygen tension at which an animal is no longer able to regulate its oxygen uptake and becomes a conformer (Bayne 1967; Mangum and Van Winkle 1973), was determined by piecewise linear regression using the NONLIN module of SYSTAT version 4·0 (SYSTAT Inc., Illinois). Beforehand, an ANOVA was applied to confirm that there were significant differences among the groups of multiple values of the dependent variable (for A. jacksoni $F_s = 15\cdot514$; 10,112 d.f.; $P < 0\cdot001$; for V. ambiguus $F_s = 4\cdot841$; 11,112 d.f.; $P < 0\cdot001$). The data were then used to compute a piecewise least-squares fit to the model

$$M_{O_2} = \beta_0 + \beta_1 P_x + \beta_2(P_x - a)(P_x > a),$$

where a, β_0, β_1 and β_2 are model parameters and a, in particular, is the point of inflection (P_c). The parameters were determined by an iterative procedure involving quasi-Newton minimization, with allowance for the multiple values of the dependent variable. The validity of the model was tested further by examination of the residuals for homoscedasticity.

Results

Oxygen Consumption

At high oxygen levels (120–150 torr), mean respiration rates of 21·5 (s.d. = 6·43, $n = 17$) and 13·5 μmol g$^{-0\cdot75}$ h^{-1} (s.d. = 5·85, $n = 10$) were determined for A. jacksoni and V. ambiguus respectively. The figure for V. ambiguus corresponds to 0·607 μmol g^{-1} (wet weight) h^{-1}, but wet-weight data were not recorded for A. jacksoni.

Figure 1 shows the effect of increasing hypoxia on the rate of oxygen consumption by A. jacksoni. Overall, the rate of consumption responded directly to decreases in the ambient oxygen supply, indicating little or no regulatory ability. There is a weak suggestion of an inflection point, but this could not be confirmed using the piecewise regression model
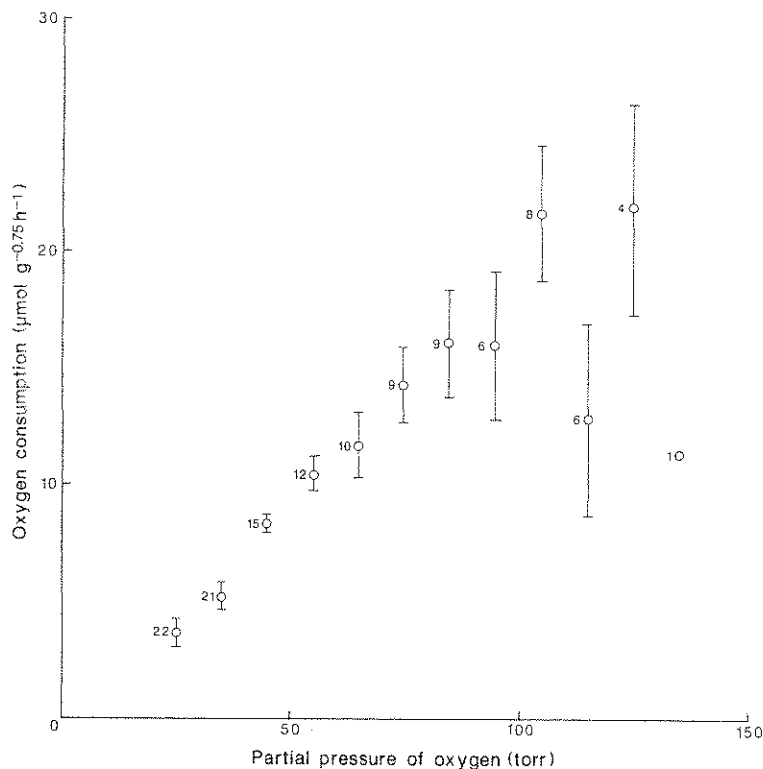
Fig. 1.   Rate of oxygen consumption ($\pm$ s.e. of mean) of *Alathyria jacksoni* exposed
to progressively decreasing levels of oxygen. Small numerals indicate sample sizes.

because the plot of residuals was fan-shaped, indicating heteroscedasticity. Although various
data transformations might have been used to identify a point of inflection, the associated
confidence limits are too wide to merit consideration.

In contrast, Fig. 2 shows that *V. ambiguus* maintained a steady rate of oxygen con-
sumption until a critical level was reached; beyond this point consumption declined with
the concentration in the water. The regression model parameters, with associated 95%
confidence limits, were $\beta_0 = -1 \cdot 007$ ($-3 \cdot 915$, $1 \cdot 901$), $\beta_1 = 0 \cdot 172$ ($0 \cdot 111$, $0 \cdot 233$),
$\beta_2 = -0 \cdot 176$ ($-0 \cdot 283$, $-0 \cdot 069$) and *a* (or P_c, the critical oxygen level) $= 65 \cdot 000$ torr
($64 \cdot 698$, $65 \cdot 302$). The *F*-ratio associated with the model was significant ($F_s = 116 \cdot 042$;
4,118 d.f.; $P < 0 \cdot 001$) and the residuals showed an acceptable (homoscedastic) distribution.

Comparison of Figs 1 and 2 suggests that there is a difference in the mean rates of
oxygen consumption, M_{O_2}, for the two species. This is confirmed by ANOVA ($F_s = 10 \cdot 401$;
1,25 d.f.; $P < 0 \cdot 05$).

Tolerance to Prolonged Hypoxia

The average rate of oxygen consumption for the gill tissue of *A. jacksoni* under normoxic
conditions was $1 \cdot 18$ μmol g$^{-0 \cdot 75}$ h^{-1} (s.d. $= 0 \cdot 37$, $n = 5$). After 10 days of hypoxia,
the rate of oxygen consumption in the gill tissue had increased to $2 \cdot 72$ μmol g$^{-0 \cdot 75}$ h^{-1}
(s.d. $= 0 \cdot 39$, $n = 5$). The difference is significant ($F_s = 24 \cdot 085$; 1,5 d.f.; $P < 0 \cdot 01$),
indicating an oxygen debt. For *V. ambiguus* the gill-tissue samples showed no significant
differences in M_{O_2} between normoxia and 10 or 15 days of hypoxia; this indicates that
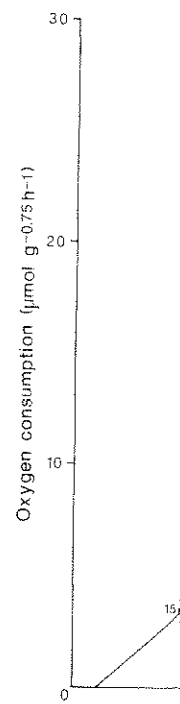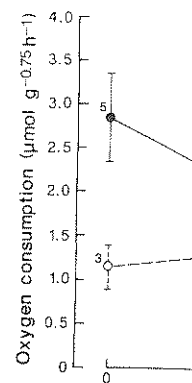there was no oxygen debt (Fig. 3).

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Behavioural Responses to

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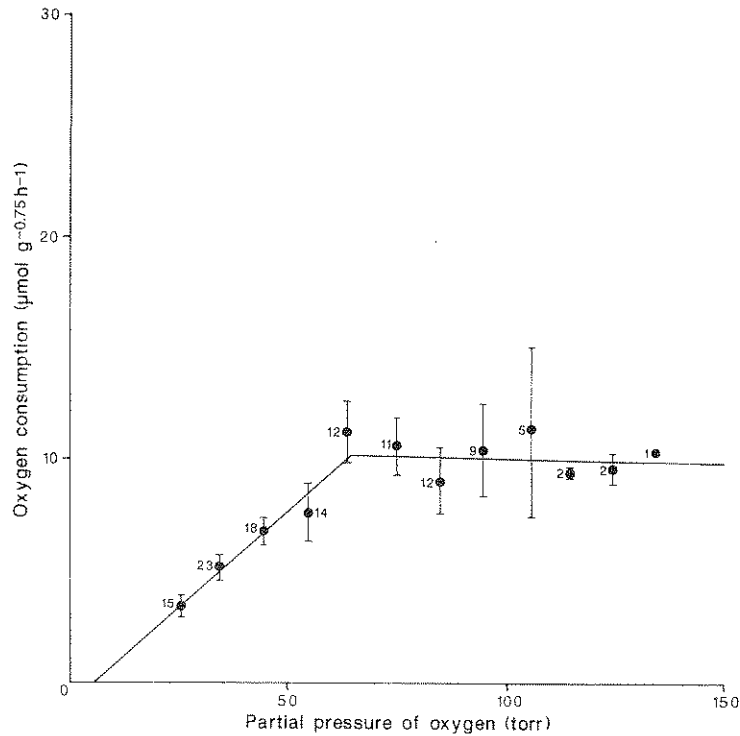Fig. 2. Rate of oxygen consumption ($\pm$ s.e. of mean) of *Velesunio ambiguus* exposed to progressively decreasing levels of oxygen. The lines of best fit were determined by piecewise linear regression (see text). Small numerals indicate sample sizes.

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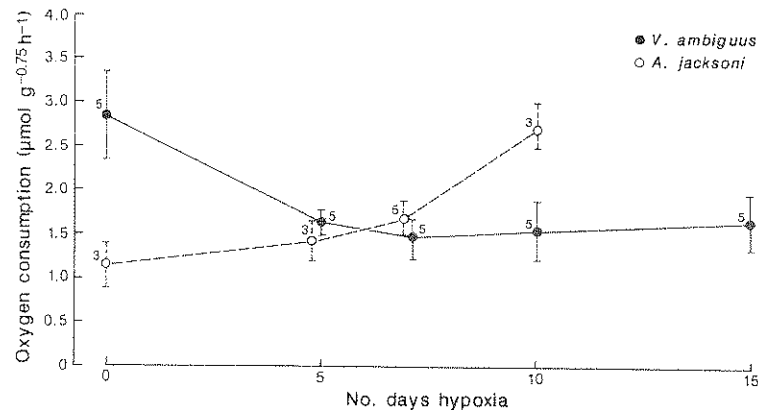
Fig. 3. Rates of oxygen consumption ($\pm$ s.e. mean) of excised gill tissue from *Alathyria jacksoni* and *Velesunio ambiguus* after removal from water for 5, 10 and 15 days. Small numerals indicate sample sizes.

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Behavioural Responses to Hypoxia

The two species behaved differently in response to hypoxia. Above 50–60 torr, *V. ambiguus* remained in a 'normal' state, with valves parted only enough to allow the siphons to protrude. From 50–20 torr the valve gape increased progressively and the siphons were

extended beyond the normal limit. At 25–15 torr the mussels retracted their siphons, closed their valves and did not re-open until returned to oxygenated water. Faced with increasing hypoxia, *A. jacksoni* also widened the gape of its valves and extended its siphons. Unlike *V. ambiguus*, however, *A. jacksoni* did not close its shell in response to severe hypoxia (25–15 torr); instead the valves would gape, with the mantle protruding and siphons expanded, indicating a loss of muscle tone.

Discussion

Closed-system respirometry has often been used in studies of respiration in marine bivalves (e.g. Bayne 1971; Vahl 1972; Booth and Mangum 1978; Widdows *et al.* 1979), although the method is open to criticism. One objection is that different oxygen levels are experienced only briefly by the animal as the ambient concentration declines (Famme 1980), whereas in the natural environment oxygen is likely to decline over longer periods, allowing the animals more time to acclimate. Another difficulty is the possible effect of increased CO_2 levels (hypercapnia). This was not measured here, but is unlikely to have been important because even a large decrease in the oxygen tension of the medium causes an increase in CO_2 tension of not more than a few torr (De Jours 1975, 1989). In addition, there is evidence that freshwater mussels can buffer accumulated carbon dioxide *via* the calcium present in their tissues and shells (Culbreth 1941). All these objections, *inter alia*, might be overcome using open-system respirometry, notwithstanding the technical difficulties involved. For the present, it must be acknowledged that the conditions experienced by an animal in a closed chamber are not like those in the natural environment. The present results therefore should be regarded with some caution.

The wide variation observed in the rates of oxygen consumption of *V. ambiguus* and *A. jacksoni* (Figs 1–2) is not markedly different from that reported for other bivalves. It may be partly the result of periods of valve closure (Childress and Mickel 1982); this is supported by studies indicating respiration rates five times higher in open (or active) periods than in periods of closure (Salánki and Lukacsovics 1967; Booth and Mangum 1978; McCorkle *et al.* 1979; Famme 1980). It is difficult, however, to ascertain the physiological state of mussel merely by examining the position of the valves. Both *A. jacksoni* and *V. ambiguus* may show no measurable oxygen uptake when the valves are open; this is true also for the marine bivalves *Mytilus edulis* and *Modiolus demissus* (Booth and Mangum 1978).

Another possible source of variation is intraspecific differences in the effects of environmental and physiological factors, including temperature, body size, condition and state of activity (Bayne 1967, 1971; Taylor and Brand 1975; Herreid 1980). In the present study, however, these differences were minimized by sampling at a site where the two species virtually coexist. The differences were also minimized by using mussels of similar size within each species and by completing observations soon after collection.

A. jacksoni and *V. ambiguus* show markedly different reactions to increasing hypoxia (150–20 torr). Following Bayne (1967) and Mangum and Van Winkle (1973), *V. ambiguus* may be regarded as an 'oxyregulator', able to maintain its respiration at normoxic levels until 65 torr (P_c), when respiration begins to decline with increasing hypoxia. It is possible that regulation is extended by increasing the rate of perfusion of the respiratory surfaces, as in the marine bivalve *Mytilus perna* (Bayne 1967). For *V. ambiguus* the ability to regulate oxygen uptake would be adaptive particularly in summer when oxygen levels in shallow billabongs and streams may fall. In contrast, *A. jacksoni* is an 'oxyconformer', unable to regulate its respiration at any level of ambient oxygen and therefore dependent upon a stable environmental supply. Although published data are few (e.g. Walker 1980), oxygen levels in the river-channel habitats of *A. jacksoni* appear to be consistently near saturation. In the River Murray below Lock 3, where mussels for this study were collected, monthly

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Differences between the two Murray species are evident also in their abilities to withstand prolonged hypoxia, when metabolic end-products accumulate in the body tissues incurring an 'oxygen debt' (Culbreth 1941; Akberali and Trueman 1985). The magnitude of the debt is measured by the increase in the rate of oxygen consumption on return to aerobic conditions (Gordon et al. 1977). In turn, the oxygen debt may be used to predict the mussel's anaerobic capacity; for example, a large debt would imply the accumulation of large quantities of metabolites, and the mussel would be less tolerant to periods of anaerobiosis than one which accumulates lower quantities of metabolites in the same time.

Excised gill tissue was used in preference to intact mussels to exclude variation caused by 'rest periods' (Salánki and Lukacsovics 1967). A further justification for this procedure is that excised gill tissue from unionid mussels is known to retain its activity and oxygen consumption for at least 24 h in ordinary freshwater (Wernstedt 1944). Other studies using a similar procedure include those of Badman and Chin (1973) and Waite and Neufield (1977).

The gill tissue of A. jacksoni developed a significant oxygen debt after 10 days' hypoxia, whereas that of V. ambiguus showed no debt after 15 days; this suggests that the latter species is better able to endure hypoxia. This complements Ch'ng-Tan's (1969) work, which showed V. ambiguus to be remarkably drought tolerant and able to withstand high levels of ammonia in the blood, extreme water loss and a two-fold increase in the ionic concentration of the body fluids. In addition, Walker (1981b) reported that the LD_{50} for V. ambiguus in extreme hypoxia at 18–20°C was 280 days (corresponding to $37 \cdot 3$ per cent weight loss), whereas that for A. jacksoni was 12 days ($19 \cdot 6$ per cent loss). Other published data suggest that V. ambiguus may not be exceptional. For example, Dance (1958) reported that an African freshwater bivalve (Aspatharia sp.), exposed for 5 months during a severe summer and carried for 12 months in the collector's jacket pocket, revived when placed in an aquarium at 22°C. The record, however, may rest with the central Australian Velesunio wilsonii (Lea); Ch'ng-Tan (1969) reported that five of six specimens revived when placed in water after five years in a cardboard box on a laboratory shelf.

The normoxic respiration rate determined for V. ambiguus [$0 \cdot 607$ μmol g^{-1} (wet weight) h^{-1}] is $1 \cdot 6$ times the rate calculated by Hiscock (1953b) for 'Hyridella australis' (syn. V. ambiguus) from the Murray [$0 \cdot 376$ μmol g^{-1} (wet weight) h^{-1}]. The difference might arise from different environmental or physiological conditions (Bayne 1967; Herreid 1980) or, as suggested earlier, from the unsuspected presence of A. jacksoni.

Prosser (1973) suggested that, to facilitate regulation, species adapted for hypoxic conditions should have comparatively low respiration rates even when oxygen levels are high. This is supported by the present data, as V. ambiguus showed a lower mean normoxic rate than A. jacksoni ($13 \cdot 5$ cf. $21 \cdot 5$ μmol g$^{-0.75}$ h^{-1}). Similar comparisons emerge from other studies (Fox and Simmonds 1933; Washbourn 1936; Walshe 1948; Macan 1961), suggesting that animals adapted to lotic waters generally require more oxygen than those adapted to lentic waters. A high metabolic rate and the consequent need for sustained high levels of oxygen suggest that lotic animals will be restricted to places where water movement ensures that there is sufficient oxygen. In comparison, lentic species may have to endure low levels of environmental oxygen, especially in summer, and the ability to maintain a normal metabolic rate then would be highly adaptive for life in billabongs or small streams.

The foregoing results support the idea that A. jacksoni is excluded from lentic environments by an inability to endure prolonged hypoxia. This hypothesis may be relevant for other investigations of the physiological and ecological differences between animals adapted to riverine and lacustrine environments. In the River Murray the contrasts between A. jacksoni and V. ambiguus are paralleled by differences between the River Murray crayfish, Euastacus armatus (von Martens), and the yabbie, Cherax destructor Clark. Like A. jacksoni, E. armatus is restricted to mainstream environments where there is a strong

current and (presumably) a consistently high level of oxygen; it does not occur in lentic floodplain environments. The yabbie *C. destructor*, like *V. ambiguus*, is typical of lentic waters and small streams and rarely occurs in big-river environments except in the vicinity of dams and weirs (cf. Lake and Sokal 1986). *E. armatus* is now near extinction in the regulated-flow environment of the lower Murray (Walker 1982), and there is evidence that populations of *A. jacksoni* have also declined (Walker 1981*b*). Unpublished studies of osmoregulation and respiration in the two crayfish species (Kaires 1979; Barley 1983) suggest that there may be interesting physiological parallels to be drawn with the mussels.

Acknowledgments

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