Implications of river damming: the influence of aquatic hypoxia on the diving physiology and behaviour of the endangered Mary River turtle

N. J. Clark[1], M. A. Gordos[2] & C. E. Franklin[1]

1 School of Integrative Biology, The University of Queensland, Brisbane, Qld, Australia
2 New South Wales Department of Primary Industries, Wollongbar Agricultural Institute, NSW, Australia

Abstract

River impoundments are characterized by low oxygen levels as a result of reduced water velocity and increased water depth. Bimodally respiring turtle species are likely to be highly sensitive to changes in aquatic PO_2 with decreases in oxygen levels impacting upon their diving ability. The acute and long-term effects of aquatic hypoxia on dive duration, oxygen consumption and blood respiratory properties were examined in hatchlings of the endangered Mary River turtle *Elusor macrurus*. It was hypothesized that acute exposure to aquatic hypoxia would cause a decrease in dive duration as a consequence of a decrease in reliance on aquatic respiration. With long-term exposure to hypoxia, we predicted that *Elu. macrurus* would have the capacity to compensate for the acute effect of hypoxia and that dive duration would increase due to an increase in aquatic respiration, haemoglobin concentration and oxygen affinity (P_{50}). When exposed to hypoxic conditions, aquatic respiration in *Elu. macrurus* was substantially reduced resulting in a 51% decrease in dive duration. Contrary to our predictions, *Elu. macrurus* hatchlings did not acclimate, and long-term exposure to hypoxic conditions caused *Elu. macrurus* to lose significantly more oxygen to the hypoxic water than the normoxic acclimated turtles. The exacerbation of long-term hypoxia on the respiratory physiology and diving ecology of *Elu. macrurus* raises concerns about the impacts of long-term environmental change as a result of habitat alteration on the survival of freshwater turtle populations.

Introduction

River damming is known to significantly change the ecological properties of rivers by converting narrow flowing systems into large stagnant reservoirs (Ward & Stanford, 1989; Bodie, 2001; Arthington, 2003). Environmental impacts associated with river damming include loss of pool-riffle sequences and reduced water flow, increased water depth and decreased aquatic oxygen levels (Ligon, Dietrich & Trush, 1995; Reese & Welsh, 1998). The impacts of these physio-chemical changes have largely been investigated in fish populations (Park *et al*., 2003; Antonio *et al*., 2007; Clarke, Telmer & Shrimpton, 2007; Fukushima *et al*., 2007) with very few studies considering the effects on freshwater turtles. In Australia, population monitoring results suggest the impacts of river damming on freshwater turtles are variable, with some species declining in numbers and others flourishing (Tucker, 1999; Limpus, Limpus & Hamann, 2002; Arthington, 2003). Identifying the cause of these declines has been identified as an important aspect of species conservation (Tucker, 1999). Conservation physiology is a relatively new field of scientific research which through the use of physiological tools, aims to provide a detailed mechanistic understanding of the causes of conservation problems (Wikelski & Cooke, 2006). Knowledge of the physiological relationships between an animal and the environment provides an understanding of the consequences of habitat alteration and can be used to predict the effects of future environmental change (Wikelski & Cooke, 2006). With increasingly more water infrastructure proposed for the future, understanding how freshwater turtles interact with a changing environment is essential for species conservation.

Freshwater turtles spend the majority of their time underwater, surfacing occasionally to respire aerially via their lungs. Some species of turtle also possess the ability to respire aquatically, acquiring oxygen from the water via diffusion through the skin or active ventilation of the buccopharynx and/or cloacal bursae (Girgis, 1961; Belkin, 1968; Stone, Dobie & Henry, 1992*a*; King & Heatwole, 1994). By supplementing their punctuated aerial oxygen supply with aquatic respiration, these bimodally respiring turtles are able to extend their dive duration and reduce surfacing frequency (Bagatto & Henry, 1999; Prassack,

Bagatto & Henry, 2001; Gordos & Franklin, 2002; Mathie & Franklin, 2006).

Aquatic respiration and diving behaviour in bimodally respiring animals is, however, dependent upon environmental conditions such as aquatic oxygen levels (Stone, Dobie & Henry, 1992b; Prassack et al., 2001; Priest & Franklin, 2002; Mathie & Franklin, 2006). At high levels of aquatic PO_2, diffusion of oxygen across the aquatic respiratory organs is enhanced and reliance on aquatic respiration increases. As ambient PO_2 decreases, the PO_2 diffusion gradient (water:blood) is reduced and energetic costs associated with aquatic respiration increase, decreasing the effectiveness of aquatic respiration (Stone et al., 1992b; Gordos, Franklin & Limpus, 2003; Jackson, 2007).

The relationship between aquatic PO_2 and the diving physiology and behaviour of bimodal breathers suggests that river damming may have a serious impact on turtle physiological ecology. However, with long-term exposure to hypoxia, some animals initiate a range of physiological responses that compensate for the acute effects of aquatic hypoxia (Prosser, 1991; Wilson & Franklin, 2002b; Seebacher, 2005; Angilletta et al., 2006). For example, after long-term exposure to aquatic hypoxia, some fish species are able to increase their aquatic oxygen uptake efficiency by increasing the haemoglobin concentration and oxygen affinity of their blood (Manwell, 1960; Wood & Johansen, 1972; Lomholt & Johansen, 1979; Soivio, Nikinmaa & Westmas, 1980; Jensen & Weber, 1982; Wells et al., 1989; Val, Silva & Almeida-Val, 1998). The beneficial acclimation hypothesis suggests that in a particular environment, an individual that has had the chance to acclimate to those conditions will have a higher performance/fitness than an individual that has not undergone an acclimatory response to those conditions (Prosser, 1991; Leroi, Bennett & Lenski, 1994; Wilson & Franklin, 2002b; Seebacher, 2005).

The aim of this study was to examine the influence of acute and long-term exposure to aquatic hypoxia on the diving physiology and behaviour of the bimodally respiring turtle Elusor macrurus. It was hypothesized that compared with normoxic conditions, acute exposure to aquatic hypoxia would cause a decrease in turtle dive duration due to a decrease in aquatic respiration. After long-term exposure to aquatic hypoxia, the dive duration of the turtles was expected to increase under hypoxic conditions due to an increased reliance on aquatic respiration and increase in blood respiratory properties (haemoglobin, haematocrit and oxygen affinity). The effects of aquatic hypoxia on turtle diving physiology and behaviour were examined in hatchling turtles. Hatchling turtles have a higher reliance on aquatic respiration than adults, and hence may be more susceptible to changes in environmental oxygen levels.

Materials and methods

Turtle collection and husbandry

Elusor macrurus eggs were collected from nesting sites along the Mary River and transported to The University of Queensland. The eggs were incubated in river bank sand in a Styrofoam box and temperature was allowed to fluctuate naturally. Upon hatching the turtles were placed into a shallow holding tank containing normoxic water for 1 week after which the turtles were transferred into normoxic ($n = 10$) or hypoxic ($n = 10$) acclimation treatments. Acclimation tanks (140 L) were identical, consisting of basking platforms, shelters and aerators. Turtles were exposed to a photoperiod of 12L:12D and kept at 23 °C. The normoxic acclimation treatment was bubbled with air ($PO_2 = 150–155$ mmHg) while the hypoxic acclimation treatment was bubbled with nitrogen to achieve aquatic hypoxia ($PO_2 < 30$ mmHg). Fifty per cent of the water surface in the tanks was covered by polystyrene to minimize gas exchange across the air–water interface. The hatchlings were acclimated for a minimum of 5 months at which time diving behaviour, aquatic respiration and blood oxygen affinity of both acclimation treatment groups were examined at the two aquatic oxygen levels, 30 and 155 mmHg.

Oxygen consumption

The aerial and aquatic oxygen consumption of the normoxic (12.46 ± 0.28 g) and hypoxic (12.11 ± 0.22 g) acclimated turtles was measured using closed-box respirometry. Experiments were conducted at both 155 mmHg (normoxic) and 30 mmHg (hypoxic) for each of the acclimation groups. The measurements were recorded at 23 °C and a red light was used to simulate darkness for the purpose of reducing turtle activity within the chamber. Before the beginning of experiments the turtles were weighed and wiped down with a 70% ethanol solution to remove oxygen-consuming bacteria. Turtles were then placed into the 900 mL respirometers and given 18 h to adjust to the chamber and recover from handling stress before measurements began. During this period, the water in the respirometer was bubbled with either air or nitrogen to achieve an aquatic PO_2 of 155 ± 10 and 30 ± 10 mmHg, respectively. Mineral oil was also added to the surface of the water during this period to prevent diffusion of gas across phases. At the beginning of the experimental trial, the air stones were switched off and the respirometers were then sealed and initial samples of water (5 mL) and air (20 mL) were taken from the sampling ports via a syringe to establish baseline levels of O_2. After an experimental period of 2 h, the final aquatic and aerial gas samples were taken and analysed for oxygen content (see Clark, Gordos & Franklin, 2008 for a complete description of the methods). To account for the allometric scaling of metabolic rate both aerial VO_2 and aquatic VO_2 were scaled to 0.75 and standardized to an average sized turtle (12 g). Percent respiration was estimated by expressing aquatic VO_2 as a proportion of total VO_2.

Diving behaviour

The diving behaviour of the normoxic and hypoxic acclimated turtles was examined at two test PO_2 levels (155 ± 10 and 30 ± 10 mmHg) in a large glass aquarium $150 \times 60 \times$

65 cm ($l \times w \times d$). Air was bubbled into the tank via air-stones for the 155 mmHg treatment while nitrogen was bubbled into the tanks for the 30 mmHg treatment. The aquarium contained a pebble substrate and benthic shelters, with water temperature maintained at 23 °C. The photoperiod was set at 12L:12D, with red lights used during the dark period to allow recording. Four individual turtles from one acclimation treatment were placed into the aquarium and given 24 h to become accustomed to the new environment. Diving behaviour was then recorded for 24 h using a networked video camera connected to a remote PC with Milestone Surveillance software. Turtles were allowed a minimum of 1 week rest before being tested at the second PO_2 level. The exposure of both acclimation groups to the test oxygen levels was randomized. Video files were analysed for resting dive durations which were defined as dives where the turtle sat still on the bottom of the tank for a period of >1 min. Mean and maximum dive durations were calculated for each turtle using a custom-written program (M. Gordos, unpubl. data).

Blood respiratory properties

To determine the blood respiratory properties of the normoxic and hypoxic acclimated turtles a 70–90 μL blood sample was collected from the cervical sinus of the turtles using a 25 G needle and 1 mL syringe (Rogers & Booth, 2004). The needle tip and plunger of the syringe were dusted with sodium heparin to prevent coagulation. The blood sample was then transferred into a 0.5 mL Eppendorf (North Ryde, Australia) tube and samples collected for analysis of haemoglobin concentration (Hb), haematocrit (Hct) and the determination of P_{50}, which was defined as the PO_2 at which 50% of the haemoglobin was saturated (see Clark et al., 2008 for a complete description of the methods).

Statistical analysis

The effects of acute and long-term exposure to aquatic hypoxia on diving behaviour and oxygen consumption were analysed using a two-way repeated measures analysis of variance (ANOVA). Where normality or equal variance failed, results were transformed before analysis. Percentage aquatic respiration was transformed using an inverse hyperbolic tangent transformation due to the negative percentages in this variable. Significant differences were further analysed using the Student–Newman–Keuls *post hoc* test. The influence of oxygen acclimation on Hb, Hct and P_{50} were analysed using a one-way ANOVA. All results are presented as mean ± standard error unless otherwise stated, with statistical significant differences considered at the level $P<0.05$.

Results

Oxygen consumption

Acute and long-term exposure to aquatic hypoxia had a significant effect on the respiratory physiology of the *Elu. macrurus* hatchlings. The total metabolic rate of the hatchl-
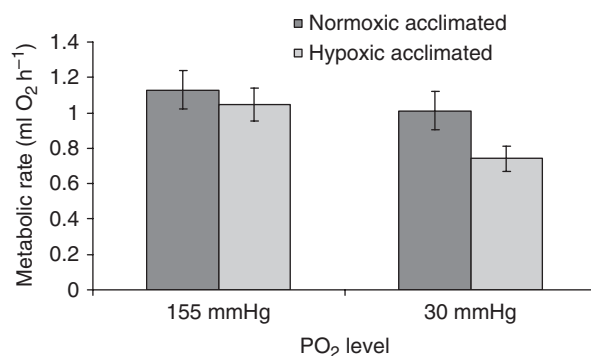

Figure 1 Influence of aquatic PO_2 on metabolic rate (mL O_2 h^{-1}) in normoxic and hypoxic acclimated hatchlings. Values represent mean ± SEM.
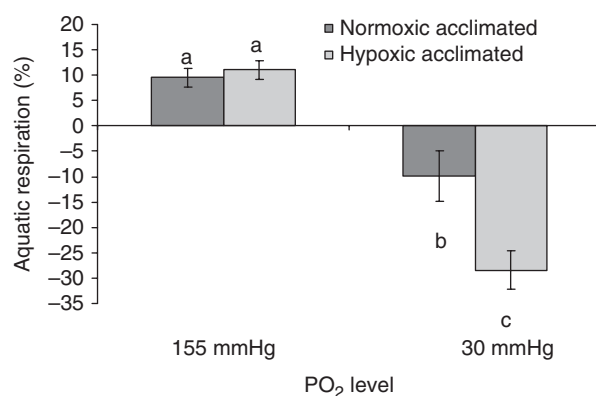

Figure 2 Influence of aquatic PO_2 on aquatic respiration (%) in normoxic and hypoxic acclimated hatchlings. Values represent mean ± SEM. Letter differences indicate significant differences.

ings was not influenced by either aquatic oxygen level ($F_{[1,36]} = 3.1$, $P>0.05$) or acclimation group ($F_{[1,36]} = 3.5$, $P>0.05$) (Fig. 1); however, a difference was recorded when the total oxygen consumption was partitioned according to respiratory medium. When the normoxic acclimated *Elu. macrurus* hatchlings were exposed to an aquatic PO_2 of 155 mmHg, aquatic respiration supported $9.5 \pm 1.81\%$ of the total metabolic rate (Fig. 2). Aquatic respiration was significantly reduced when the turtles were exposed to an aquatic PO_2 of 30 mmHg with the normoxic acclimated turtles losing $-9.8 \pm 4.99\%$ of their total oxygen supply to the water ($P<0.001$). Long-term exposure to aquatic hypoxia did not influence aquatic respiration at 155 mmHg ($11 \pm 1.86\%$, $P>0.05$), however there was a significant acclimation effect at 30 mmHg with the hypoxic acclimated turtles losing a higher percentage of aquatic oxygen ($-28.4 \pm 3.89\%$) to the water than the normoxic acclimated turtles ($P<0.001$) (Fig. 2).

Diving behaviour

Acute exposure to aquatic hypoxia had a significant effect on the diving behaviour of *Elu. macrurus* hatchlings (mean dive duration − $F_{[1,37]} = 10.21$, $P<0.01$; maximum dive
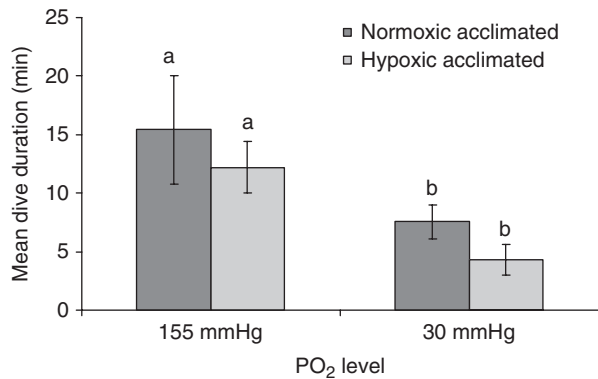
Figure 3 Influence of aquatic PO_2 on mean dive duration in normoxic and hypoxic acclimated hatchlings. Values represent mean $\pm$ SEM. Letter differences indicate significant differences.

Figure 4 Influence of aquatic PO_2 on maximum dive duration in normoxic and hypoxic acclimated hatchlings. Values represent mean $\pm$ SEM. Letter differences indicate significant differences.
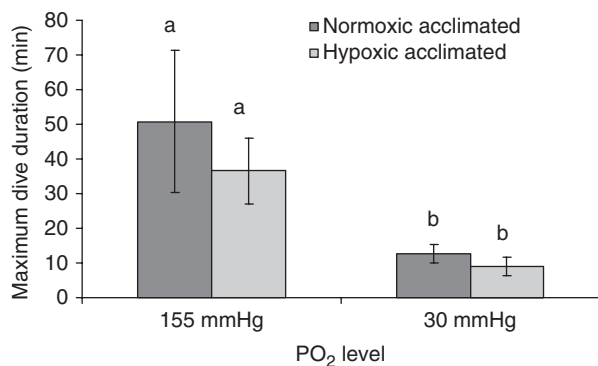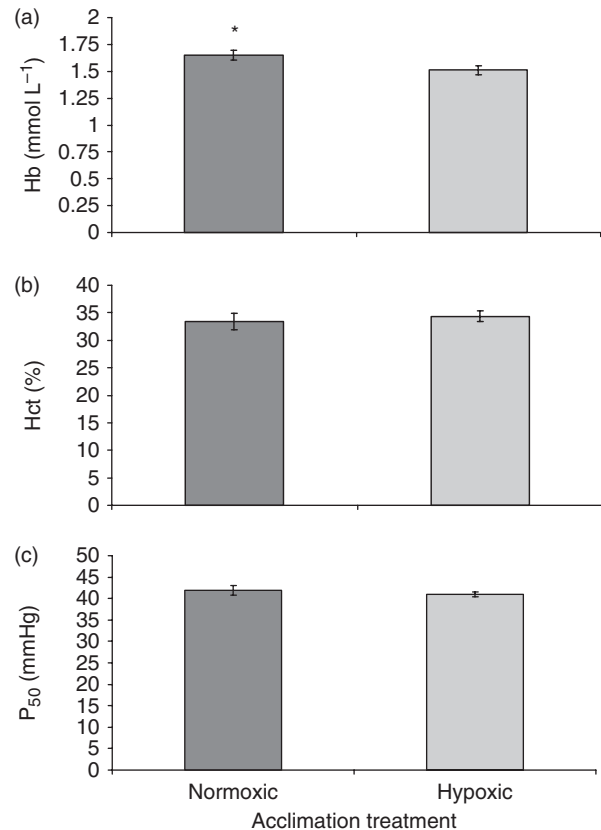

Figure 5 Influence of oxygen acclimation on (a) Hb, (b) Hct and (c) P_{50}, in *Elusor macrurus* hatchlings. Values represent mean $\pm$ SEM. Asterisks indicates significant difference.

duration – $F_{[1,36]} = 10.65$, $P < 0.01$). At an aquatic PO_2 of 30 mmHg, the mean dive duration of the normoxic acclimated turtles (7.54 ± 1.4 min) was 51% shorter than the dive durations recorded at 155 mmHg (15.43 ± 4.7 min, $P < 0.01$) (Fig. 3). Maximum dive duration was also significantly reduced at 30 mmHg with the normoxic ($P < 0.05$) acclimated turtles recording a dive duration of only 12.8 ± 2.7 min compared with 50.7 ± 20.5 min at 155 mmHg (Fig. 4). Long-term exposure to aquatic hypoxia did not significantly affect the diving behaviour of the *Elu. macrurus* hatchlings (mean dive duration – $F_{[1,37]} = 0.681$, $P > 0.05$; maximum dive duration – $F_{[1,36]} = 0.471$, $P > 0.05$).

Mean and maximum dive durations of the hypoxic acclimated turtles did not differ from the normoxic acclimated turtles at either 155 mmHg (mean dive duration = 12.20 ± 2.2 min; maximum dive duration = 36.6 ± 9.5 min) or 30 mmHg (mean dive duration = 4.30 ± 1.3 min; maximum dive duration = 9.0 ± 2.7 min) (Figs 3 and 4).

Blood respiratory properties

Hypoxic acclimated turtles had significantly lower Hb concentrations (1.51 ± 0.04 mmol L^{-1}) than the normoxic acclimated hatchlings (1.65 ± 0.05 mmol L^{-1}) ($F_{[1,19]} = 5.07$,

$P < 0.05$) (Fig. 5a). Hct levels were not influenced by aquatic hypoxia with no difference between the normoxic ($33.4 \pm 1.5\%$) and hypoxic ($34.3 \pm 0.99\%$) acclimated turtles ($F_{[1,18]} = 0.281$, $P > 0.05$) (Fig. 5b). P_{50} values of the normoxic and hypoxic acclimated turtles were 41.9 ± 1.08 and 41.0 ± 0.63 mmHg, respectively, and were not significantly different ($F_{[1,19]} = 0.530$, $P > 0.05$) (Fig. 5c).

Discussion

Knowledge of the relationships between animals and their environment is essential for understanding the conservational implications of long-term environmental change (Wikelski & Cooke, 2006). This study has demonstrated that aquatic respiration in *Elu. macrurus* hatchlings is significantly affected by acute exposure to aquatic hypoxia and that these affects are exacerbated after long-term exposure. In the natural environment, aquatic oxygen levels can vary acutely on a temporal and spatial scale or long-term as a result of human influence such as river damming (Walker, 1985; Wu, 2002; Gordos *et al.*, 2003).

Acute effects of aquatic hypoxia

Factors such as water depth, water velocity and aquatic vegetation can all influence how aquatic oxygen levels vary

on a spatial and temporal scale. For bimodally respiring turtles, variations in aquatic PO_2 can directly influence species ecology as a result of respiratory partitioning. The theory of optimal breathing (Kramer, 1988), states that reliance on aerial and aquatic respiration in bimodally respiring animals is dependent upon the costs associated with each form of respiration under specific conditions. Aquatic respiration is generally more energetically expensive than aerial respiration as water is 800 times denser, 60 times more viscous and has a lower oxygen capacitance than air (Dejours, 1994). Aerial respiration does, however, bear the energetic cost of travelling to the water surfaces and the reduced time available for other activities such as foraging (Dejours, 1994). Aquatic oxygen levels can influence the costs associated with both aerial and aquatic respiration and can therefore influence respiratory partitioning (Kramer, 1988). At 155 mmHg, aquatic respiration in the *Elu. macrurus* hatchlings supported 9.5% of the turtle's total oxygen consumption. This percentage is much lower than that reported in previous studies of *Elu. macrurus* where aquatic respiration supported ∼25% of the total oxygen consumption (Clark *et al.*, 2008). At 30 mmHg, respiratory partitioning shifted and aquatic respiration decreased significantly to the point where the turtles were actually losing oxygen to the surrounding water. To compensate for this loss of oxygen, per cent aerial respiration increased to above 100% so that overall metabolic rate remained constant. A similar result was found for the bimodally respiring fish, *Megalops cyprinoides*, where at 45 mmHg the fish were 100% reliant upon aerial respiration (Seymour *et al.*, 2007).

The change in respiratory partitioning in response to acute exposure to aquatic hypoxia had a direct effect on the turtle's dive duration. Dive duration in bimodally respiring turtles is positively correlated with reliance on aquatic respiration (Belkin, 1968; Bagatto *et al.*, 1997; Prassack *et al.*, 2001). For example, hatchling *Rheodytes leukops* have a significantly higher reliance on aquatic respiration (63%) than *Elseya albagula* (29%) and as a result, mean dive duration in this species is over 24 times longer than that of *Els. albagula* (Clark *et al.*, 2008). The change in respiratory partitioning that occurred during acute exposure to aquatic hypoxia resulted in the turtle's dive being supported entirely by aerial respiration and this decreased mean dive duration in aquatic hypoxia by 51%. The effect of acute exposure to aquatic hypoxia on dive duration was found to be dependent upon reliance on aquatic respiration in adult soft-shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*) and mud turtles (*Kinosternon subrubrum*) (Stone *et al.*, 1992b). Dive duration was independent of aquatic PO_2 in stinkpot and mud turtles, which have a relative low reliance on aquatic respiration (26 and 14% respectively), but positively correlated with aquatic oxygen level in the soft-shelled turtle, in which reliance on aquatic respiration is higher (38%) (Stone *et al.*, 1992a,b). The large decrease in dive duration that occurred in the *Elu. macrurus* hatchlings during acute exposure to aquatic hypoxia suggests that despite the low values recorded for aquatic respiration in

normoxia, the turtles were actually highly reliant upon this form of respiration during the normoxic diving behaviour trials. The cost of aerial respiration is likely to have been higher in the diving behaviour tank compared with the respirometry chamber due to a nearly seven-fold increase in water depth. The increased depth may have resulted in an increased reliance on aquatic respiration for the turtle, as has been demonstrated in the honey gourami (*Colisa chuna*) (Bevan & Kramer, 1986).

Long-term effects of aquatic hypoxia

Long-term exposure to aquatic hypoxia is known to elicit a range of physiological responses in fish species that allow them to compensate for the acute effect of hypoxia and establish a more efficient uptake of aquatic oxygen under hypoxic conditions (Prosser, 1991; Wilson & Franklin, 2002b; Seebacher, 2005). This can be demonstrated in the Antarctic fish *Pagothenia borchgrevinki* that after long-term exposure to hypoxic conditions, increased oxygen carrying capacity by 40% as a result of a 66% increases in Hb and a 34% decrease in P_{50} (Wells *et al.*, 1989). P_{50} and Hct in the *Elu. macrurus* hatchlings did not differ between the two acclimation groups indicating that this species did not acclimate these parameters to aquatic hypoxia. Hb concentrations were slightly lower in the hypoxic acclimated turtles and although this was a statistically significant difference, it is likely that this is not functionally significant.

The high P_{50} values recorded in this study demonstrate that at 30 mmHg the ability of the blood to bind aquatic oxygen was severely reduced and the respirometry results show that at this level of PO_2 the hatchlings were actually losing oxygen to the aquatic environment. Long-term exposure to aquatic hypoxia exacerbated this effect with the hypoxic acclimated turtles losing significantly more oxygen to the environment in hypoxic conditions than the normoxic acclimated hatchlings. This result may indicate that a beneficial acclimatory response had been initiated in the hatchlings in response to low oxygen levels but the level of hypoxia tested may have been too severe for these changes to function beneficially (Huey *et al.*, 1999; Loeschcke & Hoffmann, 2002; Wilson & Franklin, 2002a,b; Woods & Harrison, 2002). For example, an increase in reliance on aquatic respiration in the hypoxic acclimated turtles as a result of changes in cloacal bursae morphology or ventilation rate would benefit the hatchlings at mild levels of hypoxia but at severe levels would result in higher losses of oxygen from the turtle to the environment. Increases in gill surface area as a result of increases in gill filament length, the number of gill filaments and the size of secondary lamellae, is a common response of fish species to long-term exposure to aquatic hypoxia (Chapman & Hulen, 2001; Schaack & Chapman, 2003; Sollid *et al.*, 2003). It is not known whether the cloacal bursae of bimodally respiring turtles can display this kind of morphological plasticity.

Despite the increased loss of oxygen in the hypoxic acclimated turtles, dive duration did not differ between the two acclimation groups. The higher loss of oxygen in the

hypoxic acclimated hatchlings should have resulted in an increase in surfacing for aerial respiration and hence decrease in dive duration in hypoxic conditions. Diving vertebrates do not, however, always dive to their aerobic limit and it is possible that in the hypoxic conditions the normoxic acclimated turtles did not dive to their full aerobic capacity resulting in a reduced dive duration (Thompson *et al.*, 1991; Chappell *et al.*, 1993; Thompson & Fedak, 2001; Heithaus & Frid, 2003).

Conservation implications

Installation of large water impoundments are often associated with marked decreases in aquatic oxygen levels within the reservoir and in some cases throughout the immediate downstream reaches (Walker, 1985; Reese & Welsh, 1998; Bodie, 2001; Snoussi *et al.*, 2007). Such physio-chemical changes are likely to impact negatively upon bimodally respiring turtle species due to their respiratory physiology and diving ecology. Past studies on the impacts of river damming on freshwater turtle populations have revealed a decrease in the abundance of species with a high reliance on aquatic respiration (*R. leukops and Els. albagula*) while species with a lower reliance on aquatic respiration are flourishing (*Emydura signata*) (Tucker *et al.*, 2001; Limpus *et al.*, 2002; Arthington, 2003). These results suggest that species with a high reliance on aquatic respiration may be more susceptible to changes in environmental conditions than species with a low reliance. This study has demonstrated that the diving behaviour and physiology of *Elu. macrurus* hatchlings is significantly affected by acute exposure to aquatic hypoxia and that these affects are exacerbated after long-term exposure. Diving behaviour in vertebrates is known to be closely linked with activities such as foraging and predator avoidance (Kramer, 1988; Thompson & Fedak, 2001; Acevedo-Gutierrez, Croll & Tershy, 2002; Frid, Heithaus & Dill, 2007; Sparling *et al.*, 2007). Any changes in diving behaviour that occur in response to aquatic hypoxia may therefore influence these factors and potentially impact species survival. For example, a decrease in dive duration in aquatic hypoxia may cause a decrease in hatchling growth rate as a result of reduced time available for foraging. An increase in surfacing frequency also has the potential to influence survival by increasing the time that the hatchlings are exposed to predators within the water column and at the water surface. Findings from this study demonstrate the interaction between changes in environmental conditions (PO_2) and the physiological ecology of bimodally respiring turtles. The long-term consequences of these interactions need to be considered when addressing the impacts of river damming on freshwater turtle populations.

Acknowledgements

References

Acevedo-Gutierrez, A., Croll, D.A. & Tershy, B.R. 2002. High feeding costs limit dive time in the largest whales. *J. Exp. Biol.* **205**, 1747–1753.

Angilletta, M.J., Bennett, A.F., Guderley, H., Navas, C.A., Seebacher, F. & Wilson, R.S. 2006. Coadaptation: a unifying principle in evolutionary thermal biology. *Physiol. Biochem. Zool.* **79**, 282–294.

Antonio, R.R., Agostinho, A.A., Pelicice, F.M., Bailly, D., Okada, E.K. & Dias, J.H.P. 2007. Blockage of migration routes by dam construction: can migratory fish find alternative routes? *Neotrop. Ichthyol.* **5**, 177–184.

Arthington, A.H. 2003 *Burnet basin WAMP – current environmental condition and impacts of existing water resource development – appendix H*. Queensland Department of Natural Resources and Mines.

Bagatto, B., Guyer, C., Hauge, B. & Henry, R.P. 1997. Bimodal respiration in two species of central American turtles. *Copeia* **1997**, 834–839.

Bagatto, B. & Henry, R.P. 1999. Exercise and forced submergence in the pond slider (*Trachemys scripta*) and softshell turtle (*Apalone ferox*): influence on bimodal gas exchange, diving behaviour and blood acid-base status. *J. Exp. Biol.* **202**, 267–278.

Belkin, D.A. 1968. Aquatic respiration and underwater survival of two freshwater turtle species. *Respir. Physiol.* **4**, 1–14.

Bevan, D.J. & Kramer, D.L. 1986. The effect of swimming depth on respiratory behavior of the honey gourami, *Colisa chuna* (Pisces, Belontiidae). *Can. J. Zool.* **64**, 1893–1896.

Bodie, J.R. 2001. Stream and riparian management for freshwater turtles. *J. Environ. Mgmt.* **62**, 443–455.

Chapman, L.J. & Hulen, K.G. 2001. Implications of hypoxia for the brain size and gill morphometry of mormyrid fishes. *J. Zool. (Lond.)* **254**, 461–472.

Chappell, M.A., Shoemaker, V.H., James, D.N., Bucher, T.L. & Maloney, S.K. 1993. Diving behavior during foraging in breeding adelie penguins. *Ecology* **74**, 1204–1215.

Clark, N.J., Gordos, M.A. & Franklin, C.E. 2008. Diving behaviour, aquatic respiration, and blood respiratory properties: a comparison of hatchling and juvenile Australian turtles. *J. Zool. (Lond.)* **275**, 399–406.

Clarke, A.D., Telmer, K.H. & Shrimpton, J.M. 2007. Habitat use and movement patterns for a fluvial species, the Arctic grayling, in a watershed impacted by a large reservoir: evidence from otolith microchemistry. *J. Appl. Ecol.* **44**, 1156–1165.

Dejours, P. 1994. Environmental factors as determinants in bimodal breathing – an introductory overview. *Am. Zool.* **34**, 178–183.

Frid, A., Heithaus, M.R. & Dill, L.M. 2007. Dangerous dive cycles and the proverbial ostrich. *Oikos* **116**, 893–902.

Fukushima, M., Kameyama, S., Kaneko, M., Nakao, K. & Steel, E.A. 2007. Modelling the effects of dams on freshwater fish distributions in Hokkaido, Japan. *Freshwater Biol.* **52**, 1511–1524.

Girgis, S. 1961. Aquatic respiration in common Nile turtle, *Trionyx triunguis* (Forskal). *Comp. Biochem. Phys.* **3**, 206–217.

Gordos, M. & Franklin, C.E. 2002. Diving behaviour of two Australian bimodally respiring turtles, *Rheodytes leukops* and *Emydura macquarii*, in a natural setting. *J. Zool. (Lond.)* **258**, 335–342.

Gordos, M.A., Franklin, C.E. & Limpus, C.J. 2003. Seasonal changes in the diving performance of the bimodally respiring freshwater turtle *Rheodytes leukops* in a natural setting. *Can. J. Zool.* **81**, 617–625.

Heithaus, M.R. & Frid, A. 2003. Optimal diving under the risk of predation. *J. Theor. Biol.* **223**, 79–92.

Huey, R.B., Berrigan, D., Gilchrist, G.W. & Herron, J.C. 1999. Testing the adaptive significance of acclimation: a strong inference approach. *Am. Zool.* **29**, 323–336.

Jackson, D.C. 2007. Temperature and hypoxia in ectothermic tetrapods. *J. Therm. Biol.* **32**, 125–133.

Jensen, F.B. & Weber, R.E. 1982. Respiratory properties of tench blood and haemoglobin adaptation to hypoxic–hypercapnic water. *Mol. Phys.* **2**, 235–250.

King, P. & Heatwole, H. 1994. Non-pulmonary respiratory surfaces of the chelid turtle *Elseya latisternum*. *Herpetologica* **50**, 262–265.

Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89–94.

Leroi, A.M., Bennett, A.F. & Lenski, R.E. 1994. Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. *Proc. Natl. Acad. Sci. USA* **91**, 1917–1921.

Ligon, F.K., Dietrich, W.E. & Trush, W.J. 1995. Downstream ecological effects of dams. *Bioscience* **45**, 183–192.

Limpus, C.J., Limpus, D.J. & Hamann, M. 2002. Freshwater turtle populations in the area to be flooded by the Walla Weir, Burnett River, Queensland: baseline study. *Mem. Queensl. Mus.* **48**, 155–168.

Loeschcke, V. & Hoffmann, A.A. 2002. The detrimental acclimation hypothesis. *Trends Ecol. Evol.* **17**, 407–408.

Lomholt, J.P. & Johansen, K. 1979. Hypoxia acclimation in the carp – how it affects O_2 uptake, ventilation and O_2 extraction from the water. *Physiol. Zool.* **52**, 38–49.

Manwell, C. 1960. Comparative physiology – blood pigments. *Annu. Rev. Physiol.* **22**, 191–244.

Mathie, N.J. & Franklin, C.E. 2006. The influence of body size on the diving behaviour and physiology of the bimodally respiring turtle *Elseya albagula*. *J. Comp. Physiol. B* **176**, 739–747.

Park, Y., Chand, J., Lek, S., Cao, W. & Brosse, S. 2003. Conservation strategies for endemic fish species threatened by the three Gorges dam. *Conserv. Biol.* **17**, 1748–1758.

Prassack, S.L., Bagatto, B. & Henry, R.P. 2001. Effects of temperature and aquatic PO_2 on the physiology and behaviour of *Apalone ferox* and *Chrysemys picta*. *J. Exp. Biol.* **204**, 2185–2195.

Priest, T.E. & Franklin, C.E. 2002. Effect of water temperature and oxygen levels on the diving behavior of two freshwater turtles: *Rheodytes leukops* and *Emydura macquarii*. *J. Herpetol.* **36**, 555–561.

Prosser, C.L. 1991. *Environmental and metabolic animal physiology: comparative animal physiology*. 4th edn. Liss: Wiley.

Reese, D.A. & Welsh, H.H. 1998. Comparative demography of *Clemmys marmorata* populations in the Trinity River of California in the context of dam-induced alterations. *J. Herpetol.* **32**, 505–515.

Rogers, K.D. & Booth, D.T. 2004. A method of sampling blood from Australian freshwater turtles. *Wildl. Res.* **31**, 93–95.

Schaack, S. & Chapman, L.J. 2003. Interdemic variation in the African cyprinid *Barbus neumayeri*: correlations among hypoxia, morphology, and feeding performance. *Can. J. Zool.* **81**, 430–440.

Seebacher, F. 2005. A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? *J. Comp. Physiol. B* **175**, 453–461.

Seymour, R.S., Farrell, A.P., Christian, K., Clark, T.D., Bennett, M.B., Wells, R.M.G. & Baldwin, J. 2007. Continuous measurement of oxygen tensions in the air-breathing organ of Pacific tarpon (*Megalops cyprinoides*) in relation to aquatic hypoxia and exercise. *J. Comp. Physiol. B* **177**, 579–587.

Snoussi, M., Kitheka, J., Shaghude, T., Kane, A., Arthurton, R., Tissier, M.L. & Virji, H. 2007. Downstream and coastal impacts of damming and water abstraction in Africa. *Environ. Mgmt.* **39**, 587–600.

Soivio, A., Nikinmaa, M. & Westmas, K. 1980. The blood oxygen binding properties of hypoxic *Salmo gairdneri*. *J. Comp. Physiol. B* **136**, 83–87.

Sollid, J., De Angelis, P., Gundersen, K. & Nilsson, G.E. 2003. Hypoxia induces adaptive and reversible gross morphological changes in crucian carp gills. *J. Exp. Biol.* **206**, 3667–3673.

Sparling, C.E., Georges, J., Gallon, S.L., Fedak, M. & Thompson, D. 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Anim. Behav.* **74**, 207–218.

Stone, P.A., Dobie, J.L. & Henry, R.P. 1992*a*. Cutaneous surface-area and bimodal respiration in soft-shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*), and mud turtles (*Kinosternon subrubrum*). *Physiol. Zool.* **65**, 311–330.

Stone, P.A., Dobie, J.L. & Henry, R.P. 1992*b*. The effect of aquatic O_2 levels on diving and ventilatory behavior in soft-

shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*), and mud turtles (*Kinosternon subrubrum*). *Physiol. Zool.* **65**, 331–345.

Thompson, D. & Fedak, M.A. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim. Behav.* **61**, 287–296.

Thompson, D., Hammond, P.S., Nicholas, K.S. & Fedak, M.A. 1991. Movements, diving and foraging behaviour of grey seals *Halichoerus grypus*. *J. Zool. (Lond.)* **224**, 223–232.

Tucker, A.D. 1999 *Cumulative effects of dams and weirs on freshwater turtle populations: Fitzroy, Kolan, Burnett and Mary River catchments*. Queensland Parks and Wildlife Service, Queensland Department of Natural Resources.

Tucker, A.D., Limpus, C.J., Priest, T.E., Cay, J., Glen, C. & Guarino, E. 2001. Home ranges of Fitzroy River turtles (*Rheodytes leukops*) overlap riffle zones: potential concerns related to river regulation. *Biol. Conserv.* **102**, 171–181.

Val, A.L., Silva, M.N.P. & Almeida-Val, V.M.F. 1998. Hypoxia adaptation in fish of the Amazon: a never-ending task. *S. Afr. J. Zool.* **33**, 107–114.

Walker, K.F. 1985. A review of the ecological effects of river regulation in Australia. *Hydrobiologia* **125**, 111–129.

Ward, J.V. & Stanford, J.A. 1989. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology. *Can. Spec. Publ. Fish. Aquat. Sci.* **106**, 56–64.

Wells, R.M.G., Grigg, G.C., Beard, L.A. & Summers, G. 1989. Hypoxic responses in a fish from a stable environment: blood oxygen transport in the Antarctic fish *Pagothenia borchgrevinki*. *J. Exp. Biol.* **141**, 97–111.

Wikelski, M. & Cooke, S.J. 2006. Conservation physiology. *Trends Ecol. Evol.* **21**, 38–46.

Wilson, R.S. & Franklin, C.E. 2002*a*. The detrimental acclimation hypothesis – response. *Trends Ecol. Evol.* **17**, 408–408.

Wilson, R.S. & Franklin, C.E. 2002*b*. Testing the beneficial acclimation hypothesis. *Trends Ecol. Evol.* **17**, 66–70.

Wood, S.C. & Johansen, K. 1972. Adaptations to hypoxia by increasing HbO_2 affinity and decreasing red cell ATP concentration. *Nature* **237**, 278–279.

Woods, H.A. & Harrison, J.F. 2002. Interpreting rejections of the beneficial acclimation hypothesis: when is physiological plasticity adaptive? *Evolution* **56**, 1863–1866.

Wu, R.S.S. 2002. Hypoxia: from molecular responses to ecosystem responses. *Mar. Pollut. Bull.* **45**, 35–45.