



Hypoxia tolerance and oxygen regulation in Atlantic salmon, *Salmo salar* from a Tasmanian population

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ABSTRACT

For aquatic ectotherms, increasing water temperatures cause an exponential increase in metabolic rate and decreasing oxygen solubility. Fish species that regulate their metabolic rate to low dissolved oxygen concentrations are understood to be hypoxia tolerant whereas salmonid fish are considered to be classic metabolic conformers and their metabolic rate is dependent on the environmental oxygen concentration. This study examined Atlantic salmon, *Salmo salar*, undergoing a progressive hypoxia at optimal temperatures and at temperatures nearing the upper thermal tolerance limit for the species to determine if metabolic regulation occurred. Oxygen consumption was measured on individual Atlantic salmon (150.7 ± 40.8 g) in 66-L static respirometers; oxygen measurements were taken every 5 min until the fish lost equilibrium. Metabolic regulation was observed at all temperatures and occurred in 67, 50 and 50% of the fish at 14, 18 and 22 °C, respectively. The plateau metabolic rate (VO_{2PL}) was 293.4 ± 24.5 mg·kg·h⁻¹ at 22 °C which was significantly higher than in the 14 and 18 °C treatments (191.1 ± 24.5 and 203.9 ± 12.6 mg·kg·h⁻¹, respectively). This difference was also reflected in the critical oxygen threshold (P_{crit}) where the value for the 22 °C treatment (4.59 ± 0.32 mg·L⁻¹) was significantly higher than those of the 14 and 18 °C treatments (3.46 ± 0.14 and 3.39 ± 0.26 mg·L⁻¹ respectively). These results indicate that some fish from the Tasmanian population of Atlantic salmon have the ability to regulate metabolic rate to low oxygen concentrations and therefore show a relatively high degree of hypoxia tolerance.

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1. Introduction

Temperature is the most important abiotic factor influencing metabolic rate in ectotherms (Brett and Groves, 1979). As temperature increases towards the thermal tolerance limit, metabolic rate increases exponentially with corresponding decreases in growth and growth efficiency (Jobling, 1994; Katersky and Carter, 2007). In addition to increased metabolic rate, fish must also contend with the decreasing oxygen solubility associated with increasing water temperatures. Hypoxia is most often associated with high summer temperatures and is exacerbated by feeding due to the increase in oxygen demands from post-prandial metabolism (Jobling, 1994). Understanding the thermal physiology of an aquatic species is fundamental for both aquaculture and fisheries research as to how animals will cope under new conditions. Atlantic salmon has a wide thermal tolerance range of around 1 to 26 °C (Elliott and Elliott, 2010; Wallace, 1993) and as one of the most important commercial species

worldwide, makes an excellent model fish for examining the effects of increased temperatures on metabolic rate. As global climate change occurs water temperatures are increasing to the extent that in many regions Atlantic salmon are increasingly likely to be exposed to temperatures nearing the upper tolerance limit in both fresh and sea water (Pankhurst and King, 2010). This is especially the case for Atlantic salmon in Tasmania, SE Australia where the rate of increase in water temperature is predicted to exceed the global average (Hobday, et al., 2007; Ridgway, 2007).

Fish species generally respond to decreasing oxygen concentrations in one of two ways. They are either oxygen conformers, whereby metabolic rate decreases with the decreasing environmental oxygen concentration, or oxygen regulators whereby the fish maintains a constant metabolic rate over a wide range of environmental oxygen concentrations until a critical oxygen threshold (P_{crit}) is reached (Farrell and Richards, 2009; Ultsch, et al., 1981). Once the P_{crit} has been reached the oxygen regulators become oxygen conformers and metabolic rate becomes dependent upon the environmental oxygen concentration. Highly active species, like salmonid fishes, are generally considered to be oxygen conformers influenced by the need for high levels of oxygen to meet their high routine metabolic demands (Gardner and King, 1922; Hughes, 1973; Marvin and Heath, 1968). Whereas, species which are

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more sedentary, like carp and eels are generally more hypoxia tolerant (Farrell, 1991; Gamperl and Farrell, 2004).

To our knowledge, despite numerous investigations into the respiration of salmonid fish (e.g. Brett, 1964; Farrell, 2002, 2007; Leef, et al., 2007; Powell, et al., 2000; Regan, et al., 2010; Sadler, et al., 2000; Steinhilber, et al., 2008) only one published study has shown that Atlantic salmon are able to regulate their metabolism to oxygen concentration of $\sim 4 \text{ mg}\cdot\text{L}^{-1}$ (Stevens, et al., 1998). Stevens et al. (1998) study was conducted on groups of fish and only examined the group metabolic rate, therefore it was not possible to determine whether all fish tested were regulators or if some fish were conformers. In recent years, preliminary experiments conducted in Tasmania (Smith and Renshaw, unpublished data) supported the observations of Stevens et al. (1998). Against this background, the aims of this study were to confirm whether Atlantic salmon, from the Tasmanian population were able to regulate their metabolic rate at both an optimal temperature and at elevated temperatures which approach the thermal tolerance limits of the species. If this population has the ability to regulate their metabolic rate, it would have important implications for the management of Atlantic salmon aquaculture.

2. Materials and methods

2.1. Experimental fish

All experimental fish were sourced from the Salmon Enterprises of Tasmania Pty. Ltd. (SALTAS, Wayatinah, Tasmania, Australia) 2009 production cohort. This population of Atlantic salmon originated from the Phillip River, Nova Scotia, Canada (Reilly, et al., 1999) and following successive importations of ova to the Australian mainland in the mid 1960s and to Tasmania in the mid 1980s (Reilly, et al., 1999), SALTAS has managed the genetic resources of the stock on behalf of the Tasmanian salmon farming industry (Elliott and Kube, 2009). Fish utilised in the present experiments were held in a 2000-L outdoor flow through tank separate to the general population and were fed daily. Fish were held in fresh water at ambient temperature. Individual fish were removed from this tank just prior to being placed in the respirometer for a minimum 12 h acclimation period, fish were not fed during this period. Fish used in high temperature experiments were transferred to a recirculation system which was held at a constant temperature for 3–4 weeks prior to the experiments being conducted. A minimum of eight fish were measured at each of the experimental temperatures 14 ($n=9$), 18 ($n=8$) and 22 °C ($n=10$).

2.2. Respirometry experiments

Individual Atlantic salmon ($150.7 \pm 40.8 \text{ g}$, $n=27$) were placed into 66-L static respirometer chambers. There were four individual chambers in total and each chamber was fitted with a HACH IntelliCAL Luminescent dissolved oxygen probe (HACH Company, Loveland, Colorado, USA) which was calibrated with air-saturated water at each test temperature. Once fish were placed in the chamber, a plexi-glass lid was sealed and tested to ensure a water-tight fit. Once sealed, the water flow was adjusted to $6\text{-L}\cdot\text{min}^{-1}$ and the fish acclimated overnight (for a minimum of 12 h). The following morning, any remaining air bubbles were removed from all chambers (experimental and control) and the water flow stopped. During the experiment, the fish exhibited very little activity and predominantly rested on their fins on the bottom of the chamber. Oxygen measurements were automatically recorded every five minutes until the fish lost its equilibrium. At this time the water flow was reinstated and the fish was left to recover for 20 min. Once the fish had recovered, it was removed from the respirometer chamber and euthanized by anaesthetic overdose (Aqui-S $50 \text{ mg}\cdot\text{L}^{-1}$) and transection of the spinal

cord before to being weighed. During each run, one chamber was left empty to serve as a control and the oxygen consumption of the control chamber was subtracted from the oxygen consumption of the test chamber and then metabolic rate were calculated as:

$$\text{VO}_2 = ((\text{Co}_{2\text{A}} - \text{Co}_{2\text{B}}) \cdot \text{T}^{-1}) \cdot \text{V}/\text{W} \quad (1)$$

where VO_2 is the oxygen consumption rate ($\text{mg}\cdot\text{kg}\cdot\text{h}^{-1}$), $\text{Co}_{2\text{A}}$ is the oxygen concentration ($\text{mg}\cdot\text{L}^{-1}$) at the start of the measurement period, $\text{Co}_{2\text{B}}$ is the oxygen concentration ($\text{mg}\cdot\text{L}^{-1}$) at the end of the measurement period, T is the time between the measurements, V is the volume of the respirometer chamber and W is the whole fish weight (kg) (Cech Jr., 1990). VO_2 was calculated from all fish that were classified as regulators from normoxic levels to the critical oxygen threshold (P_{crit}).

2.3. Statistical analysis

For all individual fish, a piece-wise regression was conducted on the raw data dissolved oxygen (DO) measurements (every five minutes) to determine whether the fish was a regulator or a conformer and the P_{crit} . A fish was determined to be an oxygen regulator if a number of criteria were met: 1) the piece-wise regression was significant overall ($p < 0.05$); 2) a P_{crit} could be identified; 3) the rate of oxygen consumption below the P_{crit} decreased linearly; 4) there was no significant relationship between oxygen concentration and the rate of oxygen consumption above the P_{crit} , therefore there was a plateau in the oxygen consumption rate; 5) the plateau lasted for a minimum of three hours. A conformer exhibited a linear decrease in metabolic rate with decreasing DO. ANOVA was used to determine if differences occurred between the mean metabolic rate and P_{crit} at different temperatures. Regression analysis was used to determine the relationship between the metabolic rate over the plateau region and the P_{crit} . All differences were considered significant at $p \leq 0.05$.

3. Results

At all temperatures both regulators and conformers were observed. Overall, 56% of fish tested ($n=15$) met the 5 criteria for classification as oxygen regulators whilst 26% of the population tested ($n=7$) were oxygen conformers. The remainder of the fish did not meet enough of the criteria to be classified as oxygen regulators, neither did they show a pattern consistent with that of an oxygen conformer. Regulators consisted of 67, 50 and 50% of the populations at 14, 18 and 22 °C, respectively. Conformers tended to increase in

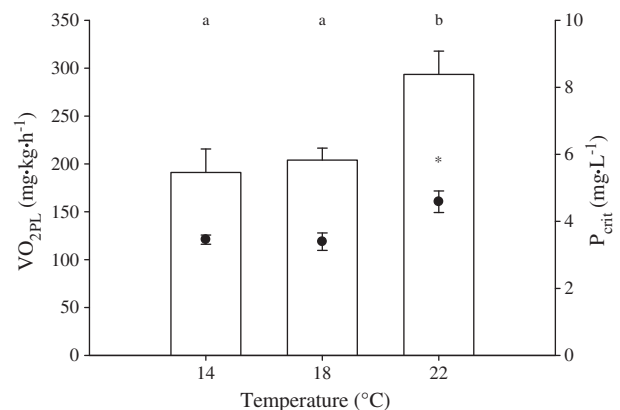


Fig. 1. The effect of temperature on the plateau metabolic rate ($\text{VO}_{2\text{PL}}$, $\text{mg}\cdot\text{kg}\cdot\text{h}^{-1}$, bars) and the critical oxygen threshold (P_{crit} , $\text{mg}\cdot\text{L}^{-1}$), for Atlantic salmon, *Salmo salar*. Letters indicate a significant ($p < 0.05$) difference between the $\text{VO}_{2\text{PL}}$ and temperatures and the * indicates a significant difference in the P_{crit} between temperatures.

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