

Effects of body mass and water temperature on routine metabolism of American paddlefish *Polyodon spathula*

J. T. PATTERSON*[†], S. D. MIMS* AND R. A. WRIGHT[‡]

*Division of Aquaculture, Kentucky State University, Frankfort, KY 40601, U.S.A. and

[‡]Department of Fisheries & Allied Aquacultures, Auburn University, Auburn, AL 36849, U.S.A.

(Received 3 May 2012, Accepted 15 January 2013)

This study quantified the effects of temperature and fish mass on routine metabolism of the American paddlefish *Polyodon spathula*. Thermal sensitivity, as measured by Q_{10} value, was low in *P. spathula*. Mean Q_{10} was 1.78 while poikilotherms are generally expected to have Q_{10} values in the 2.00–2.50 range. Mass-specific metabolism did not decrease with increased fish size to the extent that this phenomenon is observed in teleosts, as evidenced by a mass exponent (β) value of 0.92 for *P. spathula* compared with 0.79 in a review of teleost species. Other Acipenseriformes have exhibited relatively high β values for mass-specific respiration. Overall *P. spathula* metabolism appears to be more dependent on body mass and less dependent on temperature than for many other fishes. An equation utilizing temperature and fish mass to estimate gross respiration for *P. spathula* was derived and this equation was applied to respiratory data from other Acipenseriformes to assess inter-species variation. *Polyodon spathula* respiration rates across water temperature and fish mass appear most similar to those of Atlantic sturgeon *Acipenser naccarii* and white sturgeon *Acipenser transmontanus*.

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Key words: Acipenseriformes; bioenergetics modelling; ram ventilation; respirometry; thermal sensitivity.

INTRODUCTION

Regardless of species or life-stage, two factors that strongly influence respiration in fishes and indeed biological rates in all organisms are temperature and body mass (Eccles, 1985; Gillooly *et al.*, 2002). Hence, measurements of the effects of temperature and body mass on respiration are necessary to generate statistical and simulation models of metabolism for a given species (Caulton, 1978; Wieser & Forstner, 1986; Hölker, 2003; Siikavuopio *et al.*, 2008; Pirozzi & Booth, 2009).

This study quantified the effects of body size and water temperature on routine metabolism in American paddlefish *Polyodon spathula* (Walbaum 1792) (Polyodontidae) to provide functional relationships necessary to build tools that could help improve management of the species. *Polyodon spathula* are obligate ram ventilators,

[†]Author to whom correspondence should be addressed at present address: LSU Agricultural Center, Aquaculture Research Station, Louisiana State University, Baton Rouge, LA 70820, U.S.A. Tel.: +1 225 7652848; email: jtpatterson@agcenter.lsu.edu

so in this study, as in other studies of ram ventilators, routine metabolism is regarded as occurring at the swimming velocity which must be maintained in order for the animal to respire (Dowd *et al.*, 2006; Fitzgibbon *et al.*, 2008). First, knowledge gained on the respiratory metabolism of *P. spathula* will build understanding of a phylogenetically ancient chondrosteian species whose only close relative, the Chinese paddlefish *Psephurus gladius* (Martens 1862) (Polyodontidae), is critically endangered if not extinct (Onders *et al.*, 2008; Zhang *et al.*, 2009). Second, determination of routine metabolism in *P. spathula* over a range of temperatures experienced and masses attained in natural systems will be critical to the development of bioenergetics models for this species. Such models would allow exploration of the effects of environmental factors and food availability on growth and consumption by *P. spathula* (Hanson *et al.*, 1997; Hartman & Hayward, 2007). Bioenergetics models are useful tools in determining the consumptive demand of a fish population on prey resources. Specifically, measurement of metabolic requirements and development of bioenergetics models may help determine the impacts of stocking *P. spathula* on receiving systems. *Polyodon spathula* have been stocked in reservoirs in the U.S.A. for over 40 years (Graham, 1986). In recent years, interest has expanded to stocking *P. spathula* in water supply lakes by a process known as reservoir ranching (Onders *et al.*, 2001). In reservoir ranching, juvenile *P. spathula* are stocked into relatively closed impoundments where they feed primarily on zooplankton and other invertebrates throughout their life until females are harvested for their black roe at age 8–14 years (Mims & Shelton, 2005). Interest in culturing *P. spathula* for caviar in the U.S.A. has increased as a result of banned importation of beluga *Huso huso* (L. 1758) (Acipenseridae) caviar (Peterman & Petrie-Hanson, 2006). Zooplankton consumption estimates for *P. spathula*, which could be generated using a bioenergetics approach, could be coupled with primary production data for receiving waters to help fisheries managers determine practical *P. spathula* stocking rates that would not adversely affect populations of resident fishes.

Despite the long-term stocking of *P. spathula* into lacustrine environments for conservation or caviar production and the ancient phylogeny of the species, few studies have examined the respiratory physiology of *P. spathula*. The studies that exist worked primarily with juveniles (Burggren & Bemis, 1992; Sanderson *et al.*, 1994). This study used a wide range of *P. spathula* masses encompassing juveniles to mature adults to examine the effects of temperature and body mass on routine metabolism in *P. spathula* across an environmentally relevant range for both variable parameters.

MATERIALS AND METHODS

FISH SOURCE AND CARE

Polyodon spathula used in this study ranged from 0.05 to 20.50 kg and were grown in reservoirs in the Commonwealth of Kentucky. These fish were progeny of wild-caught fish from the Lower Mississippi River drainage. After gillnetting from reservoirs, fish were maintained in ponds at Kentucky State University until transfer to large in-ground tanks for temperature acclimation. The fish were acclimated 1° C day⁻¹ and then held in flow-through tanks of aerated dechlorinated municipal water for at least 3 days at the designated experimental temperature. During the holding period, fish were subjected to the natural photoperiod (38° N)

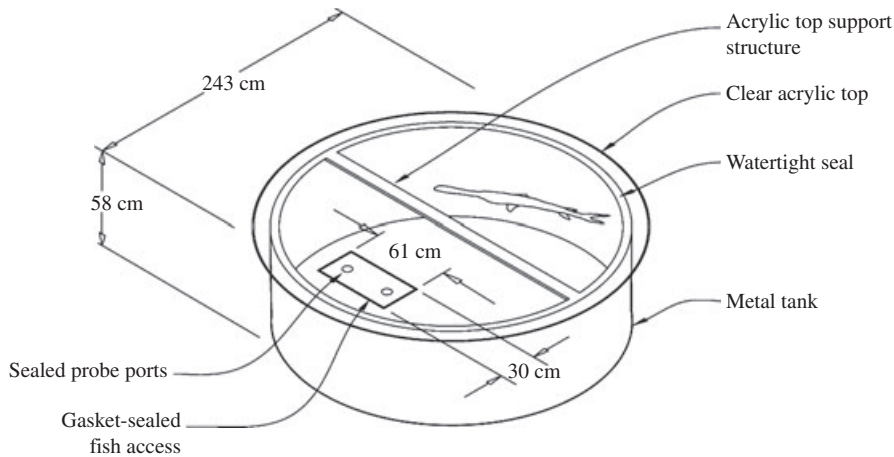


FIG. 1. Technical drawing of the large static respirometer used in trials on large- and medium-size classes of *Polyodon spathula*.

available in a greenhouse and were not fed. Experimental animals were divided into three size groups (mass range, mean \pm S.E. mass, n): small (0.05–1.34 kg, 0.39 ± 0.05 kg, 28), medium (1.86–5.30 kg, 3.01 ± 0.16 kg, 26) and large (7.85–20.50 kg, 11.73 ± 0.52 kg, 27).

RESPIROMETERS

Two circular static respirometers were designed and constructed to accommodate the size range and behaviour of *P. spathula* following the recommendations of Steffensen (1989). Fish mass relative to water volume allowed sufficient oxygen consumption that trials lasted <4 h and respirometer volume was adequate for free range of swimming motion. Constant swimming behaviour of the fish due to the necessity of ram ventilation thoroughly mixed the water in the chambers, preventing gas stratification within the device. The respirometer used for the small-size group had a diameter of 108 cm, a height of 54 cm and a volume of 511 l. Medium- and large-size groups were tested in a respirometer with a diameter of 223 cm, a height of 58 cm and a volume of 2271 l (Fig. 1). The chamber was filled with dechlorinated tap water and aerated with atmospheric air using a large airstone until *c.* 80% of oxygen saturation was reached. The respirometer was placed into a larger enclosure that served as a flow-through water bath to maintain a stable temperature within the chamber. The entire top surface of both respirometers was constructed of clear Plexiglas[®] to allow detection and elimination of air bubbles within the chamber. The lid had a gasket-sealed door for fish access and insertion of temperature and oxygen probes. After the placement of temperature and oxygen probes, the respirometer was sealed at the insertion points with a rubber stopper to form a completely closed system preventing any exchange with air external to the respirometer.

EXPERIMENTAL PROTOCOL

Experiments were conducted from December 2007 to September 2008. Each of the three temperature groups was tested during a matched seasonal period to avoid any confounding effects from annual metabolic cycles (10[°] C December to March, 20[°] C May to June and 30[°] C July to September). Replicate trials at nominal temperatures of 10, 20 and 30[°] C had mean \pm S.E. temperature values of 10.5 ± 0.2 , 21.8 ± 0.3 and 29.5 ± 0.1 [°] C. Temperature was recorded and maintained within ± 0.5 [°] C for each trial, and the mean was recorded as a single value for that trial. Oxygen concentration was monitored when the respirometer was sealed and

experimental data collection began after a period of acclimation when oxygen consumption rate stabilized, generally 45–75 min. Oxygen consumption was measured by taking a reading every 10 s over a period of at least 1.5 h but not more than 4 h using an oxygen meter with a microcathode electrode fitted with a low permeability membrane (Strathkelvin 782 with 1302 electrode ± 0.01 mg l⁻¹; www.strathkelvin.com). This study was designed to test *P. spathula* respiration under normoxic conditions, trials were therefore terminated if dissolved oxygen levels inside the respirometer were below 3.75 mg l⁻¹. At least eight fish were tested at each temperature and size group ($n = 81$). Tanks were thoroughly cleaned between each trial to reduce the abundance of microbes. To check for microbial respiration, the experimental procedure was conducted without fish at all the three temperatures, in duplicate for each size of respirometer as well as before and after trials.

Metabolic rate (mg O₂ h⁻¹) and mass-specific (mg O₂ h⁻¹ kg⁻¹) respiration rates were calculated using software provided with the oxygen meter. Q_{10} values describing the effect of temperature on respiration rate were calculated using the equation: $Q_{10} = (R_2 R_1^{-1})^{10(T_2 - T_1)^{-1}}$, where R_1 is the rate at the lower temperature T_1 and R_2 is the rate at the higher temperature T_2 (Eccles, 1985; Mayfield & Cech, 2004). Q_{10} is a unitless temperature coefficient frequently used to describe the rate of increase in a biological system due to a 10° C increase in temperature. In this experiment, where T_1 and T_2 were *c.* 10° C apart, the exponent in the equation generally approximated 1 and the resulting Q_{10} was essentially a ratio of respiration rates at higher and lower temperatures. Measurement of Q_{10} provided a basis for comparison across different biological systems. Experimental data were used to describe the effects of fish mass on respiration rate using the power function

$$Y_t = \alpha M^\beta \quad (1)$$

where Y_t describes the oxygen consumption (mg O₂ h⁻¹) for a fish weighing M (kg) at temperature t (° C). The effects of mass (β) and temperature (α) were calculated to produce a predictive model for *P. spathula* respiration using those two variables.

STATISTICAL ANALYSIS

Mean routine respiration rates (mg O₂ kg⁻¹ h⁻¹) from each temperature and mass group treatment were calculated. The effect of body mass, temperature and the interaction of these factors were determined by two-way ANOVA. Differences among respiration rates of the sub-set of animals within either mass or temperature groupings were determined by one-way ANOVA and the Ryan–Einot–Gabriel–Welch (REGWQ) *post hoc* test. Slopes and intercepts of linear regressions describing the relationship of mass to respiration rate were compared across the three temperatures using ANCOVA. ANOVA and ANCOVA analyses were performed using SAS/STAT version 8.2 (SAS Institute Inc.; www.sas.com). Regression analyses were used to generate parameters for a predictive model of *P. spathula* oxygen consumption. Generation of this predictive model for oxygen consumption as a function of temperature and fish mass followed the methods of Caulton (1978). All tests were conducted at a significance level of $\alpha = 0.05$.

RESULTS

Body masses were significantly different across size classes at a given temperature and not significantly different across temperatures at a given size class with the exception of the medium-size class at 10° C which was significantly larger than the groups tested at higher temperatures (ANOVA, $F_{2,23} = 9.67$, $P < 0.001$). This difference had no effect on subsequent modelling of respiration because each trial

TABLE I. Mean \pm S.E. routine respiration rate ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) and mass of *Polyodon spathula* grouped by body mass and water temperature. Superscript lower-case letters indicate significance ($P < 0.05$) across experimental temperatures for the respiration rates of each size class (rows); *, a significantly different value for respiration rate between size classes at each temperature (columns) (Ryan–Einot–Gabriel–Welch *post hoc*; $P < 0.05$)

Size class	Experimental temperature ($^{\circ}$ C)		
	10	20	30
Small			
Rate	91.88 \pm 6.06 ^c	157.49 \pm 22.54 ^b	287.78 \pm 27.34 ^{a*}
Mass (kg)	0.28 \pm 0.03	0.50 \pm 0.13	0.42 \pm 0.06
<i>n</i>	10	9	9
Medium			
Rate	80.08 \pm 8.94 ^c	137.23 \pm 8.88 ^b	173.5 \pm 13.37 ^a
Mass (kg)	3.80 \pm 0.34	2.88 \pm 0.14	2.44 \pm 0.15
<i>n</i>	8	9	9
Large			
Rate	59.23 \pm 4.97 ^{c*}	111.80 \pm 6.10 ^b	202.52 \pm 9.03 ^a
Mass (kg)	11.33 \pm 0.56	11.34 \pm 0.95	12.65 \pm 1.06
<i>n</i>	8	9	10

represented a separate data point in these analyses. Size classes and temperature groups showed significant differences in routine respiration rates (Table I). Temperature always significantly increased respiration rate while respiration rate across size classes at a given temperature was significantly lower for large fish at 10° C and higher for small fish at 30° C. An unexpected significant interaction (ANOVA, $F_{4,77} = 4.04$, $P < 0.01$) between the effects of size class and temperature on routine oxygen consumption existed. This interaction was probably due to the respiration rates of the medium-size class at 30° C, which were reduced relative to expected values across temperature for the other two size classes. Microbial oxygen consumption measured in blank respirometers of both sizes at all three temperatures never accounted for $>2.7\%$ of observed oxygen consumption when fish were present, hence no correction factor was necessary. In addition, respiration rates in individual trials remained constant over time, indicating that any toxic metabolite production did not reach a threshold sufficient to affect metabolism. No reduction in respiration rate was observed before the $3.75 \text{ mg} \cdot \text{l}^{-1}$ low oxygen threshold as *P. spathula* are oxyregulators until near the fatal degree of hypoxia (Burggren & Bemis, 1992). The temperature increase from 10 to 20° C significantly increased routine oxygen consumption in small ($Q_{10} = 1.76$), medium ($Q_{10} = 1.54$) and large ($Q_{10} = 1.71$) fish. Similarly, the increase from 20 to 30° C significantly increased respiration in small ($Q_{10} = 1.89$), medium ($Q_{10} = 1.40$) and large ($Q_{10} = 2.43$) fish.

Owing to a curvilinear relationship between fish mass and routine respiration, a double \log_{10} transformation was used to describe the data (Fig. 2). For the purpose of modelling, the effect of mass on respiration from the three temperature treatments were calculated as separate regressions (Table II). Slopes from the three linear regressions describing the relationship between mass and respiration rate at different temperatures were not significantly different (ANOVA, $F_{2,77} = 0.45$,

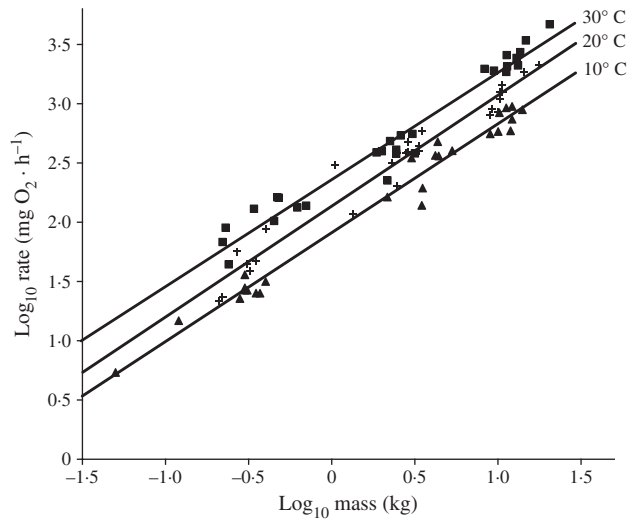


FIG. 2. Relationships of \log_{10} metabolic rate to \log_{10} body mass at different temperatures for *Polyodon spathula* during static respirometry trials at 10° C (■), 20° C (+) and 30° C (▲) (see Table II).

$P > 0.05$), and the mean of these values (0.918) was used to describe β in equation (1). Elevation (α) significantly increased with temperature (ANOVA, $F_{2,77} = 102.0$, $P < 0.001$). Plotting α against the temperature resulted in a graph which is described by the power function

$$\alpha = 7.66 t^{0.979}. \quad (2)$$

Substituting α in equation (1) with its equivalent as determined in equation (2), the temperature–mass respiratory model for *P. spathula* can be completed as

$$Y = 7.66 t^{0.979} M^{0.918} \quad (3)$$

where Y describes gross oxygen consumption ($\text{mg O}_2 \text{ h}^{-1}$) at a given temperature (° C) t and mass (kg) M . This theoretical oxygen uptake value can subsequently

TABLE II. Relation between oxygen uptake and mass at three temperatures for *Polyodon spathula*. β and r^2 were determined using the data in Fig. 2

Temperature (° C)	Regression equation		n
	$Y = \text{oxygen uptake}$ (mg h^{-1}); $x = \text{mass (kg)}$	r^2	
10	$Y = 80.41x^{0.918}$	0.98	26
20	$Y = 133.12x^{0.935}$	0.96	27
30	$Y = 236.65x^{0.902}$	0.96	28

n , number of fish tested at each temperature; size range of fish = 0.05–20.50 kg.

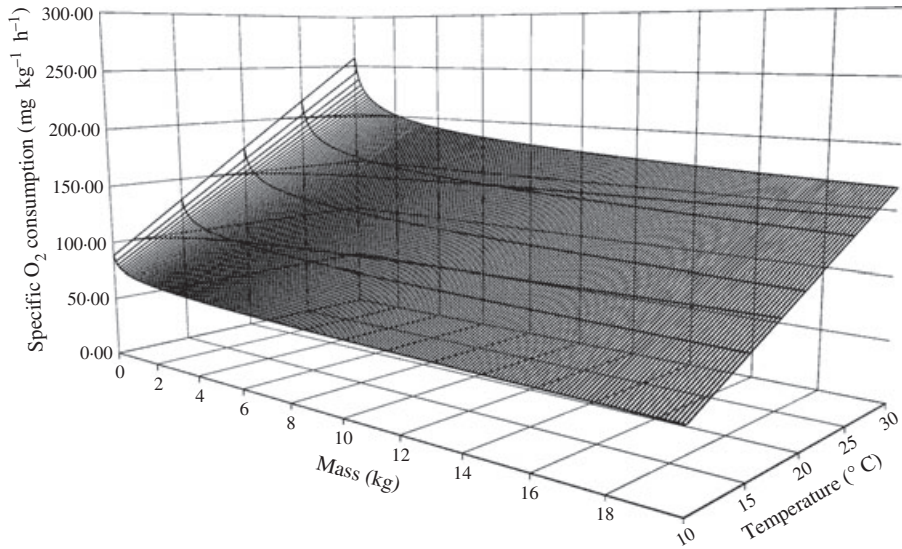


FIG. 3. Response surface of specific oxygen consumption (y) of *Polyodon spathula* in relation to water temperature (t) and fish mass (M). Data generated using the equation $Y = 7.66t^{0.979}M^{0.918}$.

be divided by M to provide a theoretical mass-specific routine metabolic rate. A response surface of data generated using the respiration equation (Fig. 3) provides a graphical representation of the modelled interactions between mass, temperature and routine oxygen consumption in *P. spathula*. Figure 3 shows the increased respiratory temperature sensitivity in smaller relative to larger fish.

DISCUSSION

To place results for *P. spathula* in context with other species of Acipenseriformes, available data on routine metabolism from this order are reported with predicted values calculated using equation (3) (Table III). Predicted metabolism values obtained for *P. spathula* fit well with experimentally observed values across all masses at 10 and 20 °C. At 30 °C, however, the predictive model for *P. spathula* deviates by *c.* 15–20% from observed respiration rates as calculated by $[(\text{theoretical rate} - \text{observed rate}) \div \text{observed rate}] \times 100$. Two factors may have contributed to this reduced fidelity as the model approaches its upper temperature bounds. First, observations suggest that temperatures of 30 °C or higher are physiologically stressful for *P. spathula*. No mortalities were observed during or after the acclimation period but the additional stress of transfer to the respirometer at 30 °C occasionally resulted in mortality, whereas no negative impacts of transfer were observed at the lower temperatures. Second, magnitude of the s.e. for mean respiration rates was highest for each mass group at 30 °C (Table I). These factors probably contributed to the reduced fidelity of the temperature–mass model at 30 °C. The masses of some fishes listed in Table III fall below the 0.05–20.50 kg range upon which the predictive respiration model in this study is based. It is not advisable to extrapolate such models beyond

TABLE III. Mean routine metabolism ($\text{mg O}_2 \text{ h}^{-1} \text{ g fish}^{-1}$) of Acipenseriformes compared with predicted routine metabolism ($\text{mg O}_2 \text{ h}^{-1} \text{ g fish}^{-1}$) calculated using equation (3), the temperature–mass model for *Polyodon spathula*. Table based on Mayfield & Cech (2004)

Species	Mass (g)	Temperature ($^{\circ}\text{C}$)	Routine metabolism	Predicted metabolism	Difference	Reference
Siberian sturgeon	1800	15	0.06	0.10	0.04	Nonnotte <i>et al.</i> (1993)
<i>Acipenser baerii</i>						
White sturgeon	63	20	0.18	0.18	0.00	Crocker & Cech (1997)
<i>Acipenser transmontanus</i>	950	15	0.08	0.11	0.03	Burggren & Randall (1978)
	2000	18	0.10	0.12	0.02	Ruer <i>et al.</i> (1987)
Green sturgeon	22.3	11, 19, 24	0.10, 0.13, 0.27	0.11, 0.19, 0.23	0.01, 0.06, 0.04	Mayfield & Cech (2004)
<i>Acipenser medirostris</i>	851	11, 19, 24	0.16, 0.20, 0.27	0.08, 0.14, 0.17	-0.08, -0.06, -0.10	Mayfield & Cech (2004)
Atlantic sturgeon	26	26	0.28	0.25	-0.03	Secor & Gunderson (1998)
<i>Acipenser oxyrinchus</i>	31	19	0.21	0.18	-0.03	Secor & Gunderson (1998)
Adriatic sturgeon	198	23	0.11	0.19	0.08	McKenzie <i>et al.</i> (1997)
<i>Acipenser naccarii</i>						
Paddlefish	390	10, 20, 30	0.09, 0.16, 0.29	0.08, 0.16, 0.23	-0.01, 0.00, -0.06	This study
<i>Polyodon spathula</i>	3010	10, 20, 30	0.08, 0.14, 0.17	0.07, 0.13, 0.20	-0.01, -0.01, 0.03	This study
	11730	10, 20, 30	0.06, 0.11, 0.20	0.06, 0.12, 0.17	0.00, 0.01, -0.03	This study

their experimental range (Chipps & Wahl, 2008) but these cases were included in Table III because the difference in mass was only a factor of 2 from this study. A publication which measured respiration in *P. spathula* (Burggren & Bemis, 1992), however, was not included in Table III because fish masses (2–10 g) were at least a factor of 5 lower than the smallest fish used in the model from this study.

Fish in this study were functioning in a state of routine aerobic metabolism because external stimuli were reduced to the greatest extent possible and animals swam with only enough velocity to respire. Specific dynamic action, a postprandial increase in metabolism which reflects costs of processing and assimilating food, was minimized by withholding feed for at least 3 days prior to all trials (Secor, 2009; Fu *et al.*, 2011). The two sizes (511 and 2271 l) of static respirometers provided the appropriate environment to monitor oxygen consumption over a suitably brief time period. Cech (1990) emphasized the importance of keeping trial length as short as possible in order to minimize microbial oxygen activity and associated oxygen consumption. Gooding *et al.* (1981) noted the importance of using the correct size of static respirometers when they investigated respiration in skipjack tuna *Katsuwonus pelamis* (L. 1758) (Scombridae). A 16 000 l respirometer required nearly 24 h to conduct a single trial on *K. pelamis* of masses reaching 3.8 kg. A smaller tank of 2400 l was found more appropriate for conducting static respirometry on fish of this mass. In this study, the ratio of water volume to fish mass inside the respirometer was low enough to allow accurate determination of the relationship between mass and respiration in trials of 4 h duration or less.

Gross rates of oxygen consumption increased as mass increased. The mass-specific consumption rate, however, followed an inverse relationship to mass. These findings are similar to those of previous researchers (Neumann *et al.*, 1981; Eccles, 1985; Brick & Cech, 2002). Clarke & Johnston (1999) examined 138 studies relating oxygen consumption to body mass and temperature in 69 teleost species and found that the value of the mass exponent β in equation (1) was 0.79 ± 0.11 . The β value of 0.918 reported in this study for *P. spathula* indicates less decline in specific respiration with increased mass than is typically observed in teleosts. Another Acipenseriformes, the green sturgeon *Acipenser medirostris* Ayres 1854 (Acipenseridae) was found to have an even higher β of 1.07. A $\beta > 1$ indicates that mass-specific respiration actually increased with fish mass in *A. medirostris* (Table III). In *A. medirostris*, the slopes of the relationship between \log_{10} -transformed body mass and respiration rates at temperatures of 11, 19 and 24 °C were 1.10, 1.11 and 0.99 (Mayfield & Cech, 2004). These slopes are higher than those calculated for *P. spathula* (Table II), further highlighting the increased influence of body mass on respiration in *A. medirostris*.

The size range of *P. spathula* in this study corresponded to what would be present in a reservoir ranching system. This work represents the first documented respirometry experiment on *P. spathula* ranging in mass from <0.10 to >20.00 kg. The results provide insight on the routine respiration of a large pelagic ram ventilator. While testing a species across as much of its size range as possible is advisable, the large mass range used in this study may have led to decreased precision of the predictive model for respiration. Although body sizes were tested in a continuous range, increased sample size of the largest and smallest animals at the extremes of the spectrum may have improved the fidelity of the model throughout its range.

Water temperature is the most important abiotic factor affecting the metabolism of fishes. A 10° C increase will affect the metabolism and subsequent oxygen consumption of a fish by 50–300% depending on species (Smith, 1991). Q_{10} values are widely used in metabolic studies as a standard for quantifying changes in respiration rate with temperature, with higher values indicating higher temperature sensitivity. The mean Q_{10} value for *P. spathula* (1.78 ± 0.15) is lower than the 2.0–2.5 range expected for fishes and other poikilothermic animals (Cech *et al.*, 1985). This means that *P. spathula* metabolism exhibited less thermal sensitivity than most species. Studies have reported increasing Q_{10} values with increasing mass (Eccles, 1985; Moser & Hettler, 1989; Hölker, 2003). This study produced no observable trends in Q_{10} among mass classes. Mean Q_{10} values across the three mass classes, however, indicate that *P. spathula* generally have greater thermal sensitivity in the 20–30° C range (1.91 ± 0.29) than in the 10–20° C range (1.67 ± 0.06). *Acipenser medirostris* have also been observed to produce increased Q_{10} values in a higher temperature range, with the effect being much more pronounced than in *P. spathula*. Measuring routine metabolism, Mayfield & Cech (2004) observed a Q_{10} value of 1.50 when temperatures increased from 11 to 19° C but a much greater Q_{10} of 4.12 when temperatures increased from 19 to 24° C.

Species-specific inherent activity rate is potentially a strong modifier of the effect of temperature and body mass on routine respiration rate (Clarke & Johnston, 1999). Burggren & Bemis (1992) observed that small juvenile *P. spathula* normally maintain 70–80% of maximum sustainable velocity; these observations indicate that this high rate declines as the fish grows. Despite the necessity of constant swimming, the inherent metabolic activity of large juvenile and adult *P. spathula* should not be characterized as high. By contrast, 0.6–3.8 kg *K. pelamis* at 23–24° C respired at a mean rate of 520 mg O₂ kg⁻¹ h⁻¹ when allowed to swim at preferred speed in a static respirometer (Gooding *et al.*, 1981). In bluefin tuna *Thunnus maccoyi* (Castelnau 1872) (Scombridae) of larger body mass (19.6 kg), routine metabolic rate averaged 460 mg O₂ kg⁻¹ h⁻¹ at 19° C (Fitzgibbon *et al.*, 2008). Data from this study indicate that *P. spathula* of similar body mass in water of similar temperature respire at a rate roughly three times less than that observed in *T. maccoyi*. In the sandbar shark *Carcharhinus plumbeus* (Nardo 1827) (Carcharhinidae), whose inherent activity rate more closely resembles *P. spathula* than the tunas, routine metabolic rate was in the range 202–127 mg O₂ kg⁻¹ h⁻¹ for body masses between 1.03 and 7.17 kg at 25° C (Dowd *et al.*, 2006). As expected, these rates correspond more to the range of those measured in *P. spathula*.

In summary, *P. spathula* metabolism as measured in this study is more dependent on body mass and less dependent on temperature than many fish species. Routine respiration rates measured for *P. spathula* provide both the temperature and mass-specific function necessary for the typical functions used in bioenergetics models that would determine the estimates for consumption and growth potential in both field and controlled aquaculture settings (Hanson *et al.*, 1997). To further develop a bioenergetics model, other important parameters including specific dynamic action, coefficients of egestion and excretion and mass and temperature dependence of consumption rate need to be quantified.

Thanks to R. J. Onders for assistance in constructing respirometers and capturing experimental animals. Assistance for conducting trials was provided by D. Jones, P. Auberry, W. Ziegler and A. Redden. The technical drawing (Fig. 1) is by R. T. Mann.

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