



The effect of body size and temperature on respiration of *Galaxias maculatus* (Pisces: Galaxiidae)

Journal:	<i>New Zealand Journal of Marine and Freshwater Research</i>
Manuscript ID	NZJM-2016-0012.R2
Manuscript Type:	Research Paper
Date Submitted by the Author:	24-Aug-2016
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1 **The effect of body size and temperature on respiration of *Galaxias***
2 ***maculatus* (Pisces: Galaxiidae)**

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10 Running head: Specific respiration rate of *G. maculatus*

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13 **Abstract**

14 Body mass and temperature are primary determinants of metabolic rate in ectothermic
15 animals. Oxygen consumption of post-larval *Galaxias maculatus* was measured in
16 respirometry trials under different temperatures (5-21°C) and varying body masses (0.1-
17 >1.5g) spanning a relevant range of thermal conditions and sizes. Specific respiration
18 rates (R in $\text{gO}_2 \text{ g}^{-1}\text{d}^{-1}$) declined as a power function of body mass and increased
19 exponentially with temperature and was expressed as: $R=0.0007 * W^{-0.31} * e^{0.13 * T}$. The
20 ability of this model to predict specific respiration rate was evaluated by comparing
21 observed values with those predicted by the model. Our findings suggest that respiration
22 rate of *G. maculatus* is the result of multiple interactive processes (intrinsic and
23 extrinsic factors), that modulate each other in “meta-mechanistic” ways; this would help
24 to explain the species’ ability to undergo the complex ontogenetic habitat shifts
25 observed in the lakes of the Andean Patagonic range.

26

27 **Key words:** temperature; body mass; respiration; bioenergetics modelling; *Galaxias*
28 *maculatus*; Patagonia

29

30 **Introduction**

31 Bioenergetic models offer an effective framework for examining processes that regulate
32 trophic interactions and growth of fish populations, allowing both quantitative and
33 predictive analysis of factors influencing the structure and dynamics of predator and
34 prey populations (Brandt & Hartman 1993; Ney 1993). In Argentinian Patagonia,
35 bioenergetic models have been used to analyse ecological impacts of exotic salmonids
36 in lakes (Vigliano et al. 2009; Juncos et al. 2011; 2013; 2015). Fully parameterized
37 bioenergetic models for native Patagonian fishes do not currently exist, but would be
38 extremely useful tools to address many of the emerging issues facing these species and
39 their communities such as response to climate change, estimation of carrying capacity,
40 and bioenergetic consequences of alternative life history strategies.

41 *Galaxias maculatus* (Jenyns 1842) is a species with a wide circumpolar
42 distribution, exhibiting diadromous and landlocked life history patterns (Cussac et al.
43 2004). The species plays an important role in trophic coupling across freshwater-
44 estuarine-marine, pelagic-benthic, and lotic systems in temperate regions of the southern
45 hemisphere (Cussac et al. 2004; McDowall et al. 1994). In South America, this species
46 express both life history strategies, constituting an important component of native
47 aquatic communities (Pascual et al. 2002; Cussac et al. 2004). Landlocked populations
48 of *G. maculatus* in Argentinian Patagonia show ontogenetic movements as well as diel
49 horizontal and vertical movements within lakes (Cussac et al. 1992; Rechencq et al.
50 2011; 2014, Milano et al. 2013). Ontogenetic habitat shifts occur as individuals achieve
51 a threshold size of approximately 28 mm total length, metamorphosing and shifting
52 from pelagic to littoral habitats (Barriga et al. 2002), and gradually shifting from a
53 planktonic-littoral to a littoral-benthic diet (Cervellini et al. 1993). In addition, diel
54 movements to avoid predators and improve feeding (Milano et al. 2013) expose fish to

55 varying water temperatures. Both types of movements are considered key processes in
56 habitat coupling of Patagonian Andean lakes (Milano et al. 2013), where this species
57 plays an important role in linking lower and upper trophic levels (Modenutti et al. 1993;
58 Macchi et al. 1999). Larval galaxiids are the primary link between plankton and
59 piscivorous fishes, and the post-larval ontogenetic habitat shift links the pelagic and
60 benthic habitats (Reissig et al. 2015; Vigliano et al. 2009; Juncos et al. 2011; 2013;
61 2015). Consequently, for many Andean lakes in Patagonia, *G. maculatus* serve as a
62 keystone prey species responsible for maintaining food web stability in the face of
63 salmonids introductions (Juncos et al. 2013).

64 Due to the importance of *G. maculatus* in Patagonia, developing a bioenergetic
65 modelling approach would enhance understanding for how changing thermal conditions
66 and body sizes affect feeding, growth, distribution, and habitat use by *G. maculatus* and
67 thus influence their ontogenetic shifts in energy-matter transfers between trophic levels
68 and habitats. Given the important effects of body mass (Randall et al. 2002) and
69 environmental temperature on metabolic rate (Jobling 1995) and potential interactions
70 between these factors, a unified approach that accounts for the combined effects of both
71 factors is needed to understand how ontogeny and environmental variability affect
72 growth and trophic interactions of this key species. Therefore the objective for this
73 paper was to parameterize a respiration function corresponding to the Wisconsin-type
74 bioenergetics modelling framework (Kitchell et al. 1977; Hanson et al. 1997), by
75 estimating mass-specific rates of respiration (R) of *G. maculatus* as functions of body
76 mass and water temperature.

77

78 **Material and methods**

79 *Galaxias maculatus* were collected using baited traps from Moreno Lake (41° 80' 50"
80 S, 71° 83' 20" W; near San Carlos de Bariloche, Nahuel Huapi National Park, Río
81 Negro Province, Argentina). Post-larval fish were collected at different times of the year
82 at different sizes (37-79 mm, 0.12-2.88 g; Table 1) as needed for the experiments,
83 avoiding individuals in reproductive status. Collected fish were transported immediately
84 to the laboratory in aerated freshwater tanks. In the laboratory, fish were gradually
85 acclimatized to experimental temperatures by 1 °C per day for up to one week,
86 depending on the difference between the temperature at capture (9.5-17.9°C) and the
87 target experimental temperatures (5-21°C; Table 1), after which fish were maintained at
88 a constant target temperature and photoperiod (13L: 11D) until used in the trials.. Fish
89 were fed maintenance rations of live food (i.e. mosquito larvae; cladocerans; copepods).

90 For respirometry trials, we used an acrylic closed chamber (diameter = 9 cm,
91 length = 18 cm, volume = 1.1L) in a controlled temperature incubator. These
92 respirometers have been used successfully for this species in previous studies (Milano et
93 al. 2010, 2013). Each trial was conducted with an individual *G. maculatus* deprived of
94 food for 24 hours prior to the test; each fish was used only once. The chamber was
95 completely filled with water from the same source and under identical temperature
96 conditions as used in the acclimation aquarium. Oxygen concentrations and
97 temperatures were recorded continuously during the experiments at -s intervals using a
98 digital oxygen meter (YSI Model 5000) connected to the respirometry chamber. Data
99 were transferred to a computer via HyperTerminal (RS232 serial port). The oxygen
100 measuring probe (Pro-BOD Probe) mixed the water with a stirring paddle. No water
101 was exchanged during the experiment. To reduce the effect of handling stress from
102 these trials, we measured oxygen concentration for 25 hours, eliminating the first hour
103 of data from the analysis (Milano et al. 2013). Dissolved oxygen concentrations were

104 not allowed to drop below 5mg/L during the trials. The respiration trials were conducted
105 as a factorial combination of five temperatures: 5, 9, 13, 17 and 21 °C and body masses
106 (range: 0.12-2.88 g) binned into size classes of 0.1 g, 0.5 g, 1.0 g and >1.5 g (Table 1).

107 Specific rates of respiration (R) were estimated from the slope of dissolved
108 oxygen versus time multiplied by the volume of water in the chamber and divided by
109 the body mass of the fish, expressed as $\text{g (O}_2\text{) g (fish)}^{-1} \text{ d}^{-1}$. Using the naming
110 convention for parameters in the Wisconsin Bioenergetics Model (Hanson et al. 1997),
111 the effect of body mass on R at a given water temperature was described by the
112 allometric function: $R=RA W^{RB}$, while the effect of body mass and temperature on R
113 was modelled using the basic form of the respiration function $R=RA W^{RB} e^{(RQ T)}$
114 (equation 1 in Hanson et al. 1997; Stewart et al. 1983). Where R is the specific rate of
115 respiration ($\text{gO}_2 \text{ g}^{-1} \text{ d}^{-1}$), RA is the intercept of the allometric mass function ($\text{gO}_2 \text{ g}^{-1} \text{ d}^{-1}$),
116 W is body mass (g), RB is the slope of the allometric mass function, RQ is the
117 exponential coefficient for the temperature dependence function, and T is water
118 temperature (C°).

119 Simple linear regressions were used to estimate RA and RB coefficients for each
120 temperature separately using the log-transformed data of R and W . In order to account
121 for the effect of T a multiple linear regression analysis was used to estimate the
122 corresponding RA , RB and RQ coefficients. An analysis of covariance (ANCOVA) was
123 used to test homogeneity of the slope of the linear relationship among R and T (with W
124 as a covariate). This equation was tested through the absence of significant interaction
125 between T and W , after checking that the assumptions of linearity and independence
126 between the W and T were met.

127 The model was further evaluated by comparing the observed experimental values
128 with predicted values by the model. Following Mayer & Buttler (1993) we evaluated

129 the model through: the mean absolute percent error ($E\% = 100 [\sum |y_o - y_p| / |y_o|] / n$, where y_o
 130 represented observed values, y_p predicted values and n the number of pairs); the
 131 modelling efficiency ($EF = 1 - \frac{\sum (y_o - y_p)^2}{\sum (y_o - y_m)^2}$, where y_o and y_p were the same as
 132 described previously, and y_m was the mean of observed values); the coefficient (r^2) of
 133 the linear regression between observed and predicted values; and through testing of the
 134 deviation of the slope (b) from 1 by the F-test (Harrison 1990) and of the intercept (a) of
 135 the regression line from 0 by the t-test.

136

137 **Results**

138 The specific respiration rate of *G. maculatus* declined with body mass at most
 139 temperatures, but this allometric relationship weakened at the highest temperature
 140 (Table 2; Fig. 1). For a particular T , the exponent RB (in the equation $R = RA W^{RB}$) was -
 141 0.32; -0.32; -0.34 and -0.25 at 5; 9; 13 and 17°C respectively (Table 2). However, both
 142 the value and fit of RB declined rapidly at 21°C (RB = -0.10), and no statistically
 143 significant relationship with W was observed at 21 °C (Table 2). Given this lack of
 144 linearity, we excluded the 21 °C data from the analysis. There were no significant
 145 differences among the RB values at different T (i.e. 5-17°C), as demonstrated by the
 146 lack of significant interaction between T and W (ANCOVA, $F_{3,46} = 0.175$; $P = 0.913$).
 147 This shows that the relationship of specific respiration rate of *G. maculatus* with W is
 148 uniform among 5 and 17 °C. The specific respiration rate increased significantly as a
 149 function of temperature and decreased as a function of body mass (Fig. 2). Estimation
 150 of the RA, RB, and RQ through multiple linear regression yielded the following specific
 151 respiration rate equation ($R^2 = 0.87$; $n = 54$; $P < 0.0001$; Fig. 3):

152

$$R = 0.0007 * W^{-0.31} * e^{0.13 * T}$$

153 The ability of the model to predict specific respiration rate was evaluated by
154 comparing the observed experimental values with those predicted by the model (among
155 5 and 17°C). The comparison between observed and predicted specific respiration rate
156 under experimental conditions resulted in the mean absolute percentage errors of (E%)
157 = 18.01%, a modelling efficiency (E_F) = 0.85 and a $R^2 = 0.86$ (Fig 4). The intercept $a =$
158 0.0004 (± 0.0002) of the linear regression did not differ significantly from 0 (t-test;
159 $P=0.061$), and slope $b = 0.95$ (± 0.052) did not differ significantly from 1 (F-test; $P >$
160 0.05).

161

162 Discussion

163 This is the first study in which the specific respiration rate of *G. maculatus* has been
164 tested under the combined effects of body mass and temperature, across a relevant size
165 range of juveniles and adults (0.1 to >1.5g), and a broad temperature range (5–21°C).
166 The specific respiration rate of *G. maculatus* followed the expected declining power
167 function with body mass and exponential increase with temperature. The model fit the
168 experimental data well for all but the warmest temperature (21°C). Although the model
169 performed well when evaluated for model efficiency, slope and intercept (Harrison
170 1990; Mayer & Buttler 1993), a true corroboration of the model against independent
171 data has not been conducted due to uncertainties associated with limitations or
172 comparability of other independent data sets.

173 The specific respiration rates of *G. maculatus* obtained in this study ranged from
174 0.0017 to 0.0087 $\text{gO}_2 \text{g}^{-1} \text{d}^{-1}$ and were in agreement with values produced over more
175 limited ranges of temperatures or body masses (Encina-Montoya et al. 2011; Milano et
176 al. 2013; Urbina & Glover 2013). In previous studies, the respiration rate for *G.*
177 *maculatus* had been estimated for fixed temperatures and varying masses. Ríos (1979)

178 determined the allometric relationship between oxygen consumption and body size (on
179 the order on 0.1-2g) at 15 °C for lake and river populations of *G. maculatus* as R (mlO₂
180 h⁻¹) = 0.25 $W^{0.61}$ (lake) and $R = 0.269 W^{0.60}$ (river), finding no significant differences
181 between the slopes for both populations. More recently, Encina-Montoya et al. (2011)
182 reported $b = 0.612$ for *G. maculatus* at 12 °C (0.02-1.5g), whereas Urbina & Glover
183 (2013) reported $b = 0.82$ at 14°C (0.14-11.28g). Our estimate of RB was -0.31 when fit
184 simultaneously to body mass and temperature. After converting RB in this study from a
185 specific rate (g O₂ g⁻¹ d⁻¹) to an absolute rate by adding 1.0 produced a value of 0.69 (g
186 O₂ d⁻¹) in units comparable to the other studies. The allometric slope from our study,
187 while accounting for a broad range of temperatures and an ecologically relevant range
188 of body masses, was similar to two of the three studies (Rios 2919; Encina-Montoya et
189 al. 2011) conducted at single temperatures, but deviated more from the study that
190 included a much broader range of body masses, including extremely large individuals
191 (Urbina & Glover 2013). While this potential shift in the allometry of respiration
192 associated with larger sizes deserves further attention, most *G. maculatus* landlocked
193 populations are predominantly composed of sizes approximately 80 mm (2-3 g) or
194 smaller. Therefore, we believe our model can reasonably represent the generalized
195 respiration relationships for the ecologically significant fraction of post-larval *G.*
196 *maculatus*.

197 As a mobile consumer with distinct ontogenetic shifts in diet and habitat use, *G.*
198 *maculatus* provides crucial links among production pathways of littoral, benthic and
199 pelagic zones (Cussac et al. 1992, Barriga et al. 2002, Rechencq et al. 2011; 2014;
200 Milano et al. 2013). The ability to quantify their metabolic and trophic responses to
201 changing environmental conditions will advance our understanding of habitat coupling
202 processes in Patagonian oligotrophic lakes. Accurate parameterization of mass- and

203 temperature-dependent effects on metabolic rates as presented here can be combined
204 with mass - and temperature-dependent functions for maximum consumption and waste
205 losses functions to construct a full bioenergetics model for the species. Such a model
206 will facilitate a clearer understanding of the role of *G. maculatus* as both a mobile
207 consumer and prey in varying habitats and seasonally fluctuating temperatures. This
208 capability will be critically important for addressing local and regional management
209 issues related both to short and long term human impacts such as urban development
210 and global warming.

211

212 **Acknowledgments**

213 We want to thank M. Beveraggi for allowing access to the lake through her property.
214 This work was partially supported by Universidad Nacional del Comahue (CRUB-
215 UNC-B0016), Agencia Nacional de Promoción Científica y Tecnológica (ANPCYT-
216 PICT 2010-1455), and Consejo Nacional de Investigaciones Científicas y Técnicas
217 (CONICET). Any use of trade, firm, or product names is for descriptive purposes only
218 and does not imply endorsement by the U.S. Government.

219

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304

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305 Figures captions

306 Figure 1. Relationships between the log-specific respiration rate and log-body mass (W
307 g) of *Galaxias maculatus* at different temperatures (T °C). Plotted lines represent best-fit
308 regressions for each temperature.

309 Figure 2. Relationship between the specific respiration rate and temperature (T C°) of
310 *Galaxias maculatus* at different body masses (W g). Plotted lines represent best-fit
311 regressions for each body mass.

312 Figure 3. Specific respiration rates under the combined effects of body mass and
313 temperature of *Galaxias maculatus*. $R = 0.0009 W^{-0.26} e^{0.11T}$ model for fitted curves at
314 varying temperatures. Plotted lines represent best-fit regressions for each temperature.

315 Figure 4. Observed vs. predicted specific respiration rate of *Galaxias maculatus*. Solid
316 line indicates linear regression between observed and predicted values and dotted line
317 indicates 1:1 relationship.

318

319 Table captions

320 Table I. Body mass (g, mean \pm S.E.); specific metabolic rate ($\text{gO}_2 \text{g}^{-1} \text{d}^{-1}$, mean \pm S.E.)

321 and fish number of *Galaxias maculatus* at different test temperatures and body masses.

322 Table II. Predictive models of specific respiration rate (R , $\text{gO}_2 \text{g}^{-1} \text{d}^{-1}$) of *Galaxias*

323 *maculatus* using fish body mass (W , g) and water temperature (T , $^{\circ}\text{C}$) as explicative

324 variables (Coefficient estimation \pm S. E. Standard error).

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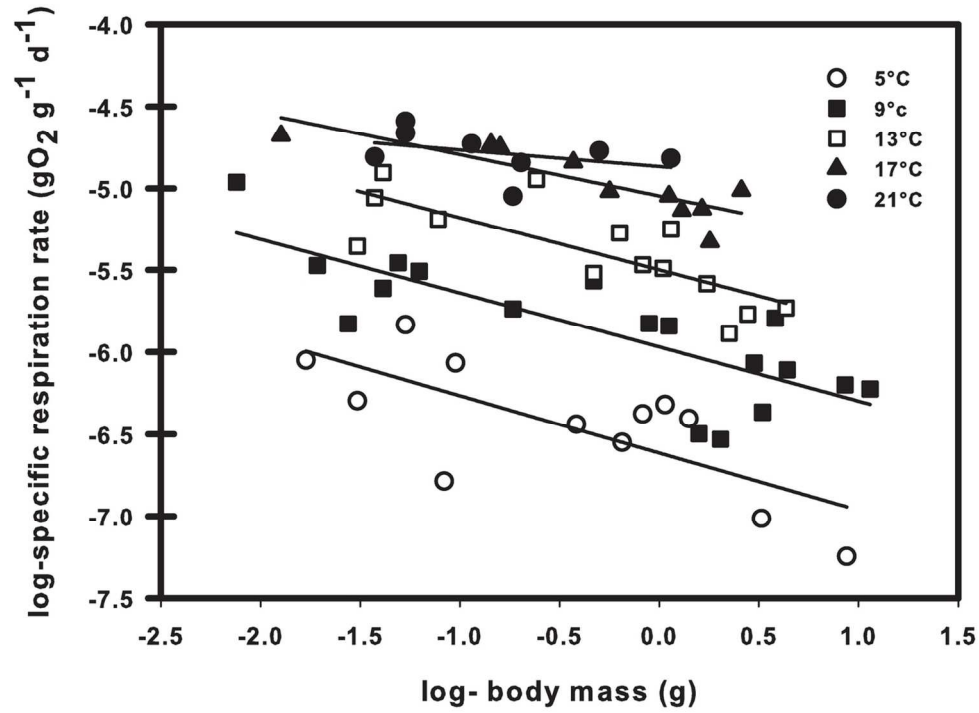


Figure 1. Relationships between the log-specific respiration rate and log-body mass (W g) of *Galaxias maculatus* at different temperatures (T °C). Plotted lines represent best-fit regressions for each temperature.

Figure 1.EPS
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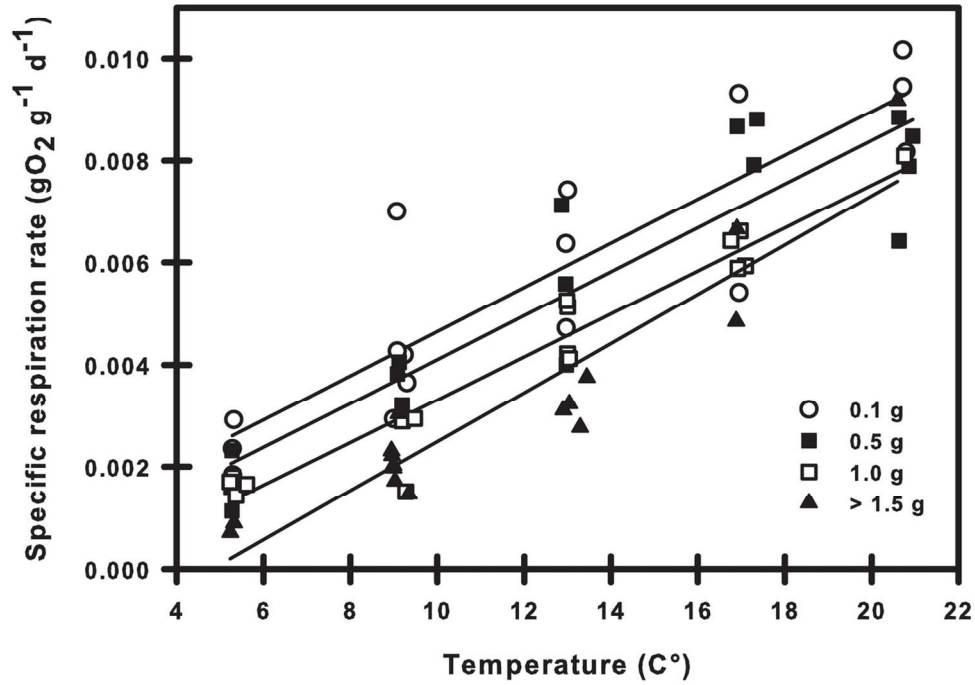


Figure 2. Relationship between the specific respiration rate and temperature (T C°) of *Galaxias maculatus* at different body masses (W g). Plotted lines represent best-fit regressions for each body mass.

Figure 2.EPS
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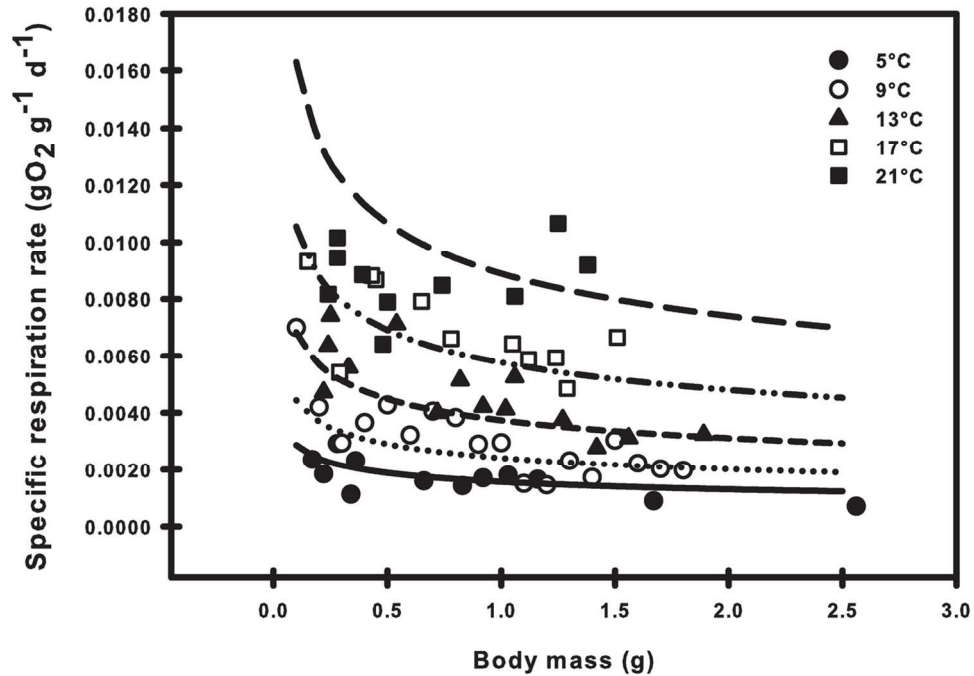


Figure 3. Specific respiration rates under the combined effects of body mass and temperature of *Galaxias maculatus*. $R = 0.0009 W^{-0.26} e^{0.11T}$ model for fitted curves at varying temperatures. Plotted lines represent best-fit regressions for each temperature.

Figure 3.EPS
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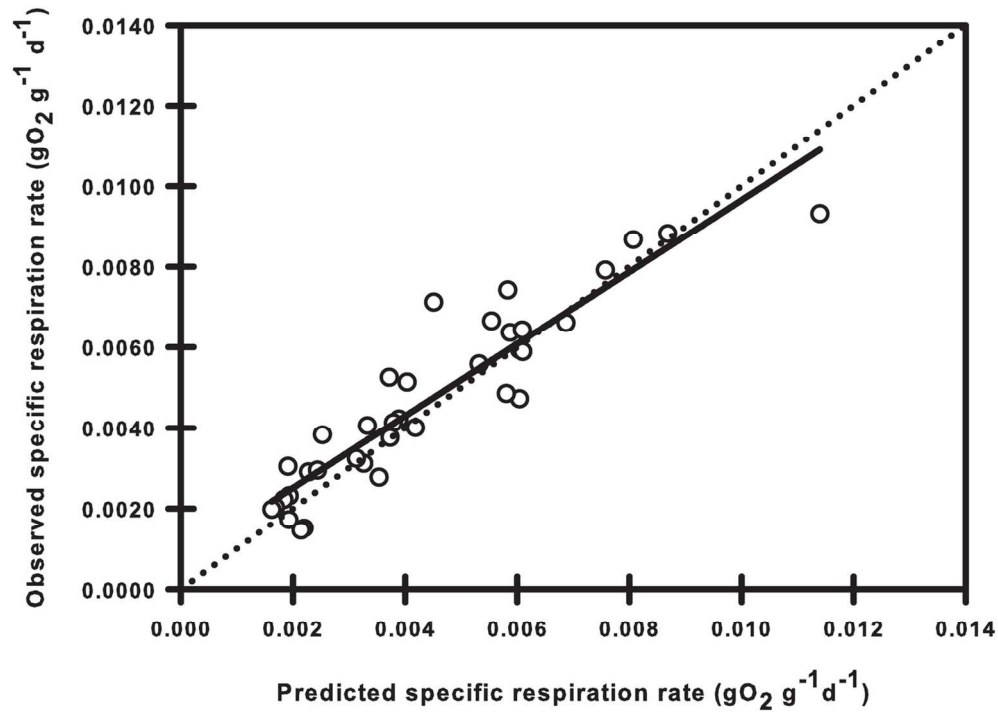


Figure 4. Observed vs. predicted specific respiration rate of *Galaxias maculatus*. Solid line indicates linear regression between observed and predicted values and dotted line indicates 1:1 relationship.

Figure 4.EPS
123x95mm (300 x 300 DPI)

Table I. Body mass (g, mean \pm S.E.); specific metabolic rate ($\text{gO}_2 \text{g}^{-1} \text{d}^{-1}$, mean \pm S.E.) and fish number of *Galaxias maculatus* at different test temperatures and body masses.

<i>W</i> (g)	0.1	0.5	1.0	>1.5	Total mean by <i>T</i>
<i>T</i> (C°)					
5	0.22 \pm 0.06 0.0024 \pm 0.0005 n=3	0.45 \pm 0.18 0.0017 \pm 0.0005 n=3	0.99 \pm 0.14 0.0016 \pm 0.0001 n=4	2.12 \pm 0.63 0.0008 \pm 0.0001 n=2	0.0017 \pm 0.0006 n=12
9	0.21 \pm 0.06 0.0044 \pm 0.0015 n=5	0.5 \pm 0.21 0.0037 \pm 0.0004 n=3	1.07 \pm 0.14 0.0025 \pm 0.0008 n=3	1.97 \pm 0.55 0.0021 \pm 0.0005 n=7	0.0031 \pm 0.0013 n=18
13	0.24 \pm 0.02 0.0066 \pm 0.0014 n=3	0.53 \pm 0.19 0.0056 \pm 0.0016 n=3	0.96 \pm 0.11 0.0047 \pm 0.0006 n=4	1.54 \pm 0.26 0.0032 \pm 0.0004 n=4	0.0048 \pm 0.0015 n=14
17	0.22 \pm 0.99 0.0077 \pm 0.0028 n=2	0.51 \pm 0.12 0.0085 \pm 0.0005 n=3	1.05 \pm 0.19 0.0062 \pm 0.0004 n=4	1.40 \pm 0.16 0.0058 \pm 0.0013 n=2	0.0070 \pm 0.0015 n=11
21	0.27 \pm 0.02 0.0093 \pm 0.0010 n=3	0.53 \pm 0.15 0.0080 \pm 0.0011 n=4	1.06 \pm 0.16 0.0081 \pm 0.0011 n=2	1.32 \pm 0.09 0.0099 \pm 0.0010 n=2	0.0087 \pm 0.0012 n=11
Total mean by <i>W</i>	0.0056 \pm 0.0027 n=16	0.0056 \pm 0.0027 n=16	0.0041 \pm 0.0022 n=17	0.0036 \pm 0.0028 n=17	

Model	Temperature	RA± S.E.	RB± S.E.	RQ± S.E.	R ²	P
$R=RA W^{RB}$	5	0.001±0.09	-0.34±0.10		0.53	0.007
$R=RA W^{RB}$	9	0.003±0.06	-0.32±0.06		0.65	<0.0001
$R=RA W^{RB}$	13	0.004±0.06	-0.32±0.07		0.60	0.001
$R=RA W^{RB}$	17	0.006±0.04	-0.25±0.06		0.71	0.002
$R=RA W^{RB}$	21	0.007±0.06	-0.10±0.10		0.14	0.352
$R=RA W^{RB} e^{RQ T}$	5-17	0.0007±0.09	-0.31±0.04	0.13±0.01	0.84	<0.0001

For Peer Review Only