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1 **Allometric relationship between body mass and aerobic metabolism**

2 **inzebrafish *Daniorerio***

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24 The relationship between body mass and metabolic rate was investigated through the
25 assessment of active and standard metabolic rate at different life stages in zebrafish *Danio rerio*
26 (5 day-old larvae, 2 month-old juveniles and 6 month-old adults). Scaling exponents and
27 constants were assessed for standard ($R_S=0.273M^{0.965}$ in $\text{mgO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) and active metabolic
28 rate ($R_A=0.799M^{0.926}$ in $\text{mgO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$). These data provide the basis for further experiments
29 regarding the effects of environmental factors on aerobic metabolism throughout the life cycle
30 of this species.

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32 Key words: allometric scaling exponent, aerobic metabolism, zebrafish

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48 Active metabolic rate (R_A) is the maximal aerobic metabolic rate of an organism in a highly
49 active state and standard metabolic rate (R_S) is the minimal metabolic rate necessary for
50 supporting maintenance activities (e.g. ventilation) measured in resting, starved and non-
51 maturing individual (Fry, 1947; Brett, 1964). Aerobic metabolic scope (R_{AS}) is the difference
52 between R_A and R_S and represents the capacity of an organism to provide oxygen to sustain
53 energy demanding activities (Fry, 1947). R_{AS} can be influenced by a set of environmental
54 parameters such as temperature, oxygen and salinity (Shurmann & Steffensen, 1997;
55 Lefrançois & Claireaux, 2003; Johansen & Jones, 2011). It has therefore been used in many
56 studies to assess the influence of environmental factors on metabolic performance and energy-
57 demanding activities in various fish species (Fry, 1971; Priede, 1985; Claireaux & Lefrançois,
58 2007). It has been demonstrated, in many species however, that intrinsic parameters such as
59 ontogeny and body size can also influence metabolism independently of any effects of
60 environmental conditions (Clark & Johnston, 1999; Bokma, 2004; Killen, 2007, 2010; Moran
61 & Wells, 2007)

62 Zebrafish *Danio rerio* (Hamilton 1822) is a small teleost species whose biological
63 characteristics make it suitable for experimental studies (e.g. small size, easy breeding, high
64 fecundity; Miklosi & Andrew, 2006; Lawrence, 2007). Its short life cycle and rapid
65 development also facilitate investigations regarding the effects of environmental factors on
66 different lifestages. In the last two decades, some studies have been published regarding the
67 metabolic performance of the *D. rerio* exposed to various environmental constraints (Plaut &
68 Gordon, 1994; Plaut, 2000; Marit & Weber, 2011, 2012). Despite the increasing interest in
69 *D. rerio*, only the studies of Barrionuevo & Burggren (1999) and Burggren (2005) investigated
70 how body mass influenced metabolism, although they did not establish the regression
71 describing this relationship. The aim of the present study was therefore to investigate the
72 allometric relationship between body mass and metabolic rate in *D. rerio*, and derive the

73 species-specific scaling exponent. This was achieved by measuring R_A and R_S at three different
74 life stages.

75

76 Ten broodstock couples (wild-type Tuebingen strain, *TU*) were reared together in a 10 l tank.
77 Spawnings were obtained from these couples each week over two months. In order to avoid
78 any bias due to familial characteristics, at least 5 spawns were mixed. Then, 100 larvae were
79 randomly selected and reared to be tested at three different life stages: (i) larvae, 5 days post
80 fertilization, (ii) 60 dpf juveniles and (iii) 5 months old adults. From 2 weeks onwards, fish
81 were kept in groups of 10 individuals in 3 l aquaria with system water prepared as a mix of
82 reverse-osmosis treated and tap water (both being filtered through sediment and activated
83 charcoal filters) to obtain a water with constant conductivity of 300 μ S. Fish were reared at a
84 constant temperature of 28 °C under artificial light with a constant photoperiod of 14h:10h
85 (L:D) and were fed with dry food (Inicio plus, Biomar, France, <http://www.biomar.com>) and
86 brine shrimp (Océan Nutrition Europe BVBA, Belgium, <http://www.oceannutrition.eu>) in the
87 morning and afternoon, respectively. Fish were fasted 24 h prior to the experiments.

88 To assess their metabolic rate, fish were placed into circular size-adapted respirometers. For
89 larvae, the set-up consisted of 4 independent glass micro respirometer chambers (diameter d =
90 1.12 cm, volume V = 0.985 $\cdot 10^{-3}$ l; Loligo systems, Denmark). For the two other life stages, 8
91 larger respirometers were run simultaneously (d = 3.75 cm, V =0.061 l and 7.50 cm, 0.179 l for
92 juveniles and adults respectively). Respirometers were submerged into buffer tanks (depth \times
93 length \times height: 10 \times 20 \times 31 cm for larvae, 10 \times 75 \times 75 cm for juveniles and adults) and filled
94 with temperature-controlled, oxygenated system water as above. Flush pumps controlled the
95 water supply in each respirometer. Each flush pump was controlled by a timer, allowing
96 intermittent flow respirometry (Steffensen, 1989) where phases of oxygen renewal alternated
97 with phases of oxygen consumption measurements with a period of 15:15 min for larvae and

98 30:30 min for both juveniles and adults. In addition, the set-up was completed by a multi-
99 channel peristaltic pump was used to mix the water within each respirometer. Each
100 respirometer was equipped with a fiber optic sensor (PreSens) connected to a multichannel
101 oxygen measuring system (OXY 4 mini, PreSens) to record dissolved oxygen levels. Optic
102 fibers were calibrated at 0% and 100% of air saturation at a temperature of 28°C. A factor of
103 conversion based on oxygen solubility into water was used to convert oxygen data from
104 percentage saturation to $\text{mgO}_2\cdot\text{l}^{-1}$ (i.e. 100% was equivalent to $7.94\text{mgO}_2\cdot\text{l}^{-1}$ for a 28°C
105 temperature and a 0 salinity). Oxygen saturation was recorded every five seconds with the
106 program Oxyview (PreSens).

107 Larvae were tested in groups of 10 individuals per chamber. Juveniles and adults were tested
108 individually; each fish was only tested once. Each experimental trial comprised two
109 consecutive steps. First, to assess R_A , fish metabolism was increased through chasing
110 (Schurmann & Steffensen, 1997; Lefrançois & Claireaux, 2003; Jourdan-Pineau *et al.*, 2010;
111 Cannas *et al.*, 2013, Clark *et al.*, 2012). Each group of larvae or individual fish was
112 transferred from the rearing aquaria to a 6-7 ml Petri dish or one liter tank respectively, where
113 they were chased with a stick. When exhausted (i.e. did not respond to stimulation), they were
114 transferred in respirometers to measure oxygen consumption over 20 min. After this first
115 measurement of oxygen consumption, a second one was performed to confirm the accuracy of
116 the R_A assessment. To do that fish were chased again inside the respirometer and their oxygen
117 consumption measured for a new period of 20 min. To estimate R_S , fish were left undisturbed in
118 the respirometer for 48h, during which oxygen consumption was regularly and automatically
119 measured. After the 48h period of measurements, the fish were removed from the
120 respirometers and anesthetized with benzocaine at a concentration of $50\text{mg}\cdot\text{l}^{-1}$. The wet body
121 mass of each individual was determined, as well as the standard length L_S of juveniles and
122 adults: (a) larvae, 5 dpf ($n=11$ groups of 10 larvae; mean \pm S.E., mass, $M=0.245\cdot 10^{-3}\pm 0.036\cdot 10^{-3}$

123 ³g), (b) 60 dpf juveniles ($n=14$, $M=0.097 \pm 0.035$ g, $L_S=18.5 \pm 2.2$ mm) and (c) 5 months
124 adults ($n=22$, $M=0.326 \pm 0.103$ g, $L_S=26.9 \pm 1.9$ mm).

125

126 A blank measurement without fish was performed before and after each trial, to quantify
127 background respiration. Linear change is assumed in background oxygen consumption over the
128 48h-experimental trial and subtracted the calculated background from the corresponding total
129 oxygen consumption measured.

130 The non specific aerobic metabolic rate (or oxygen consumption MO_2 in $mgO_2.h^{-1}$) was
131 calculated according to the following formula:

132

$$133 \quad MO_2 = \Delta[O_2] \cdot V \cdot \Delta t^{-1} \quad \text{equation (1)}$$

134

135 where $\Delta[O_2]$ (in $mgO_2.l^{-1}$) is the variation in oxygen concentration during the measurement
136 period Δt (in h) and V (in l) is the volume of the respirometer. MO_2 correspond to the
137 R_A , the maximal MO_2 obtained after the fish being chased, or to the R_S , which is the
138 MO_2 assessed according to the method described by Steffensen et al. (1994). Briefly, to assess
139 R_S , the frequency distribution of the MO_2 values was plotted recorded during the last 24 hours
140 of each trial. This generally produced a bimodal distribution where the higher and the lower
141 mode were considered to reflect routine metabolic rate, i.e. energy required by the animal for
142 normal activity, and R_S , respectively. R_A and R_S were assessed for each individual.

143 The non specific aerobic metabolic rate of organisms typically increases with body mass
144 according to the allometric equation:

145

$$146 \quad R = aM^b \quad \text{equation (2)}$$

147

148 where R is the metabolic rate (R_S or R_A in $\text{mgO}_2\cdot\text{h}^{-1}$), a is the species-specific scaling constant
149 (or proportionality constant), M is the body mass (in g), and b is the scaling exponent. This
150 equation is a power function, where the value of b provides information on how the variable
151 of interest changes with body size.

152 Equation (2) can be linearized with a log transformation:

153

$$154 \quad \log Y = \log a + b \log M \quad \text{equation (3)}$$

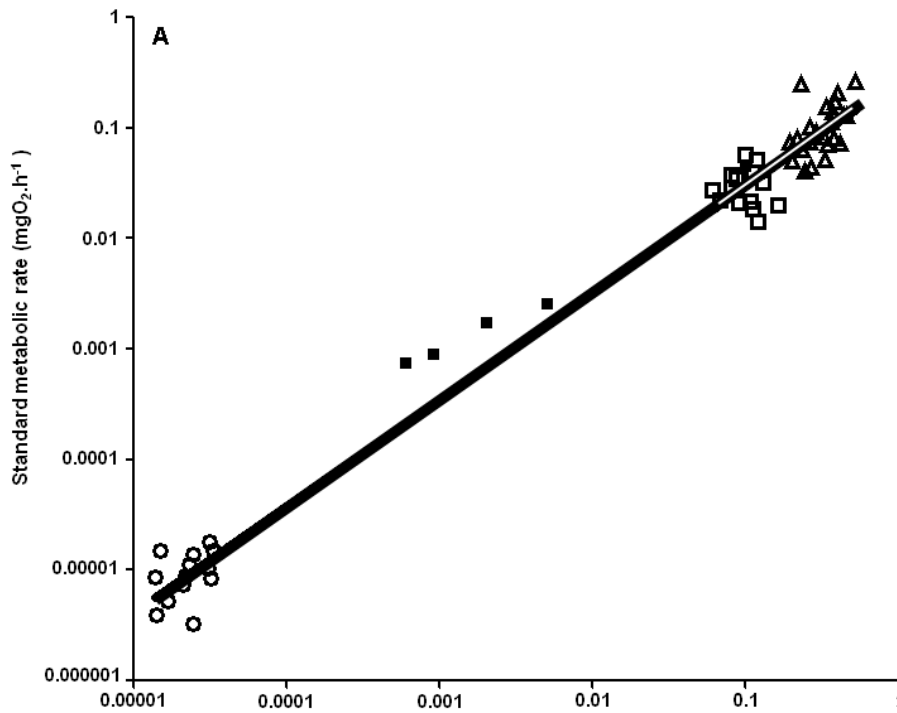
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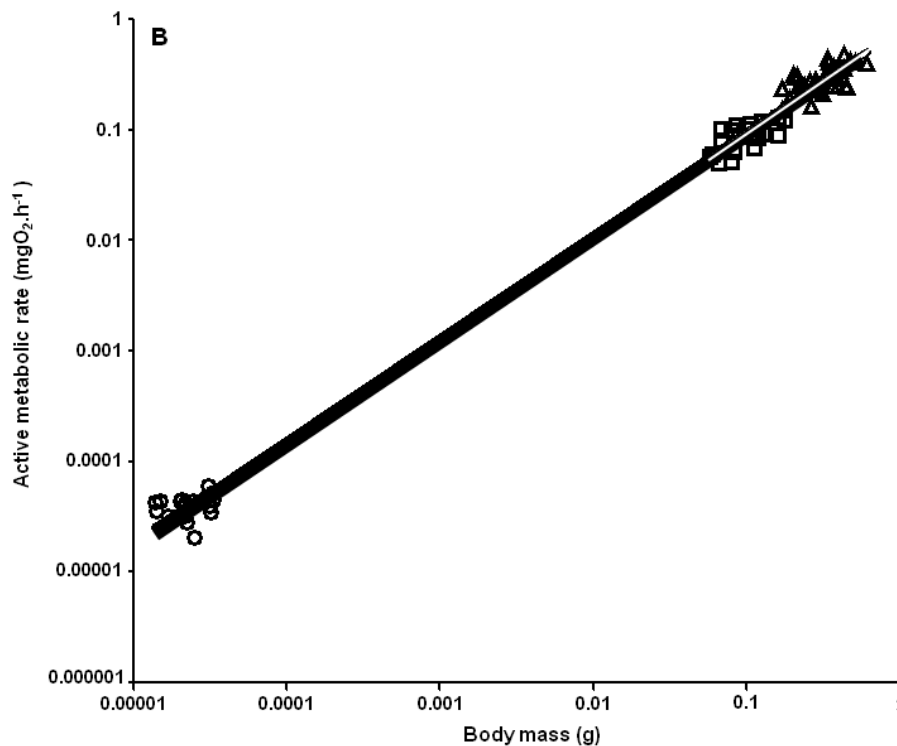
156 The logarithm base 10 of each metabolic variable (R_S or R_A) was therefore plotted against the
157 logarithm base 10 of body mass. Fitting a linear regression allowed provided the scaling
158 exponent b and the log of the scaling coefficient ($\log a$), i.e. the slope and the intercept,
159 respectively. Previous studies in fishes (Post & Lee, 1996; Killen, 2007; Moran & Wells,
160 2007) have argued the metabolic rate of larvae is likely to scale differently from juveniles and
161 adults because of their incomplete development. These groups were, therefore, analyzed
162 separately. A first linear regression was therefore derived for the three stages and a second
163 considering only juveniles and adults. The two scaling exponents b and scaling factors a
164 were then compared as described by Zar (1984) with a modification of the t-test. Results were
165 considered significant at $P < 0.05$.

166

167 For R_S , scaling factor a_{RS} and scaling exponent b_{RS} was 0.273 ± 0.038 (\pm S.E.) and
168 0.965 ± 0.015 , respectively when the three life stages were considered. These constants were
169 0.276 ± 0.084 and 0.969 ± 0.110 , respectively, when only juveniles and adults were taken into
170 consideration. These values did not differ significantly for either constant (Student's t-test,
171 $t_{1,82} = -0.00127$, $P > 0.05$; Student's t-test, $t_{1,81} = 0.00068$, $P > 0.05$, respectively). The same
172 pattern was observed for R_A . Scaling factors ($a_{RA(L+J+A)} = 0.799 \pm 0.024$ and

173 $a_{RA(J+A)}=0.809\pm0.051$) as well as scaling exponents ($b_{RA(L+J+A)}=0.926\pm0.009$ and
174 $b_{RA(J+A)}=0.931\pm0.068$) did not differ significantly whether larvae were considered or not
175 (Student's t-test, for a_{RA} : $t_{1.81}=0.01270$, $P>0.05$; for b_{RA} : $t_{1.81}=0.00596$, $P>0.05$). Data for
176 "resting metabolic rate" of *D. rerio* at 28°C, reported by Barrionuevo & Burggren (1999) and
177 Burggren (2005) and converted to $\text{mgO}_2\cdot\text{h}^{-1}$, were consistent with R_S values measured in the
178 current study (Fig. 1A). It appears that their data fit with standard metabolic rate regression.
179





181

182 FIG. 1. Relationships between aerobic metabolic rate and body mass for *D. rerio*. On each graph, the black line
 183 represents the scaling relationship across the three life stages: 5 day-old larvae (\circ , L), 2 month-old juveniles (\square ,
 184 J) and 6 month-old adults (Δ , A). The white line shows the scaling only for juveniles and adults (J+A). The
 185 scaling factor a and scaling exponent b were estimated through the allometric equation $R=aM^b$ (equation 2). For
 186 each of these constants, the value is expressed as the average (\pm standard error). For standard metabolic rate
 187 (graph A), considering all stages $R_{S(L+J+A)}$ is equal to $0.799 (\pm 0.038) M^{0.965 (\pm 0.085)}$ for $n=50$ ($P<0.0001$),
 188 considering juveniles and adults, $R_{A(J+A)}$ is equal to $0.809 (\pm 0.084) M^{0.969 (\pm 0.110)}$ for $n=37$ ($P<0.0001$). Regarding
 189 active metabolic rate (graph B): $R_{A(L+J+A)}$ $0.273(\pm 0.024)M^{0.926(\pm 0.010)}$ for $n=78$ ($P<0.0001$), $R_{A(J+A)}$
 190 $0.276(\pm 0.051)M^{0.931(\pm 0.068)}$ for $n=60$ ($P<0.0001$). In addition, the studies of Barrionuevo & Burggren (1999) and
 191 Burggren (2005) measured oxygen consumption in fish presenting a resting state at the temperature of 28 °C
 192 which permitted to complete our data set regarding the standard metabolic rate at the same temperature. After
 193 conversion into $\text{mgO}_2 \cdot \text{h}^{-1}$, these values were added on the graph (A, \blacksquare).

194

195

196 This is the first study examining the scaling of metabolic rate with body mass over the
 197 lifecycle of *D. rerio*. The results indicate that a single scaling exponent can be employed
 198 irrespective of life stages in this species. This is in agreement with the observations made by
 199 Killen *et al.* (2007) on three species of marine teleost (e.g. ocean
 200 pout *Macrozoarces americanus* Bloch & Schneider 1801; lumpfish *Cyclopterus lumpus*, sL. 1758;
 201 and shorthorn sculpin *Myoxocephalus scorpius*, L. 1758), while the contrary was shown by

202 Post & Lee (1996) for other species (e.g. the common carp *Cyprinus carpi*, L. 1758; rainbow
203 trout *Oncorhynchus mykiss*, Walbaum 1792; sea bream *Pagrus major*, Temminck & Schlegel
204 1843). White & Seymour (2011) studied mass-specific R_S of 31 fish species and reported that
205 several species have higher allometric exponents in early larval stages compared to their later
206 stages. Also, in their study of yellowtail kingfish *Seriola lalandi* (Valenciennes 1833), Moran
207 & Wells (2007) considered that the allometric exponent changed continually during
208 development. In fact, metabolism in larvae may be affected by processes specific to this early
209 ontogenic stage such as higher rates of protein turnover, development of energy consuming
210 tissue or organs, or the progressive transition from cutaneous gas exchange to branchial
211 respiration or changes in swimming ability (Post & Lee, 1996; Killen *et al.*, 2007; White &
212 Seymour, 2011; Gore & Burggren, 2012). Nonetheless, understanding of ontogenic changes in
213 aerobic scope in fishes throughout remains limited. In *D. rerio*, the general pattern observed
214 may be related to its short lifecycle, 5dpf larvae having already completed most of their
215 organogenesis (Kimmel *et al.*, 1995). It could be interesting to obtain data for 21dpf, when
216 larval metamorphosis occurs with maturation of several physiological functions and the
217 completion of the transfer of respiratory gas exchange from predominantly cutaneous to
218 predominantly branchial.

219 As expected, the scaling exponents b_{RA} and b_{RS} differed significantly from 1, confirming that
220 metabolic rate scaled allometrically with body mass in this species (Student's t-test,
221 $t_{1,47}=55.88$, $P<0.0001$ for b_{RA} ; $t_{1,47}=5.224$, $P<0.05$ for b_{RS}).

222 Although studies by Kleiber (1932) on mammals and Hemmingsen (1960) on unicells,
223 multicellular ectotherms and endotherms suggested that 0.75 was a universal scaling
224 exponent, recent investigations on fishes have revealed significant heterogeneity in scaling
225 exponents among species (Glazier, 2005, 2006, 2009c; White *et al.*, 2006; Downs *et al.*, 2008;
226 White, 2011). Among the teleosts, several studies have found that the scaling exponent of

227 metabolic rate differed from 0.75 (Post & Lee 1996; Clark & Johnston, 1999; Bokma, 2004;
228 Peck, 2004), which is in agreement with the present results. It is worth noticing that a lot of
229 scaling studies in teleosts are based on routine or “resting” metabolic rate, rather than R_S or
230 R_A . This is not directly comparable with the present results, but illustrates the interspecific
231 variation in allometric scaling exponents among fishes. For instance, Moran & Wells (2007)
232 found a scaling exponent of 0.90 for *S. lalandi*. Bokma (2004) examined intraspecific
233 allometry for the sea trout *Salmo trutta* in various life stages and found b_{RMR} to be 0.86.
234 Indeed, lifestyle, swimming mode and environmental characteristics of the habitat are all
235 known to modify metabolic rate, as well as the scaling exponent in fishes (Killen *et al.*, 2007,
236 2010). Previous studies have also found that b_{RA} was significantly different from b_{RS} (Brett &
237 Glass, 1973; Weiser, 1985; Weibe *et al.*, 2004; Killen *et al.*, 2007), and this was true in *D.*
238 *rerio* (Student’s t-test $t_{1,94}=4.475$, $P<0.05$), which is also suggested by several studies.
239 However, b_{RA} generally tends to be higher than b_{RS} (Weibe *et al.*, 2004; Killen *et al.*, 2007)
240 while the opposite was observed in *D. rerio*, where $b_{RA}<b_{RS}$. This may, at least in part, reflect
241 the fact that *D. rerio* is a domesticated species that has been reared in laboratory for many
242 generations, whereas the study by Killen *et al.* (2007) was on individuals captured in wild.
243 In conclusion, this study estimated the scaling exponent b across three life stages of *D. rerio*
244 (5 dpf to 6 month old fish). This provides a basis for further experiments regarding the effects
245 of environmental factors on aerobic metabolism in this species.

246

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