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1 Original article

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3 **Sex-related differences in oxygen consumption recovery after high-intensity**  
4 **rowing exercise during childhood and adolescence**

5

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31

32

33 **DECLARATIONS**

34 **Author contribution statement**

35 HM, CT and SR designed the research. JB, AD, HM, CT and SR collected the data and  
36 performed the research. JB, AD and SR analysed the data and supervised the research. JB and  
37 SR wrote the manuscript. JB, HM, AD, CT and SR provided critical revisions important for  
38 intellectual content of the finished manuscript, approved the final version of the manuscript, and  
39 agree to be accountable for all aspects of the work in ensuring that questions related to the  
40 accuracy or integrity of any part of the work are appropriately investigated and resolved. All  
41 persons designated as authors qualify for authorship, and all those who qualify for authorship are  
42 listed.

43  
44 **Ethics approval**

45 The present study was approved by an institutional ethics review board (Comité d'Éthique pour  
46 la Recherche en Sciences et Techniques des Activités Physiques et Sportives – CERSTAPS,  
47 n°2019-18-09-36) and conformed to the standards of use of human participants in research as  
48 outlined in the *Sixth Declaration of Helsinki*.

49  
50 **Consent to participate**

51 Written informed consent was obtained from all individual included in the study and from their  
52 parents or legal guardians.

53  
54 **Consent for publication**

55 Participants (and their parents or legal guardians) signed informed consent regarding publishing  
56 their data.

57

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66

67 **Conflict of interest**

68 The authors declare no competing interests. The results of the study are presented clearly,  
69 honestly and without fabrication, falsification or inappropriate data manipulation.

70

71 **ABSTRACT**

72 **Purpose:** The aim of this study was to determine sex-related differences in oxygen consumption  
73 recovery after high-intensity exercise during childhood and adolescence.

74 **Methods:** Forty-two boys and 35 girls (10–17 years) performed a 60-s all-out test on a rowing  
75 ergometer. Post-exercise oxygen consumption recovery was analysed from (i) the  $\dot{V}O_2$  recovery  
76 time constant obtained from a bi-exponential model ( $\tau_1\dot{V}O_2$ ), and (ii) excess post-exercise  
77 oxygen consumption calculated over a period of 8 minutes (EPOC<sub>8</sub>) and until  $\tau_1\dot{V}O_2$  was reached  
78 (EPOC $\tau_1$ ). Multiplicative allometric modelling was used to assess the concurrent effects of body  
79 mass (BM) or lean body mass (LBM), and age on EPOC<sub>8</sub> and EPOC $\tau_1$ .

80 **Results:** EPOC<sub>8</sub> increased significantly more in boys from the age of 14 years. However, the sex  
81 difference was no longer significant when EPOC<sub>8</sub> was analysed using an allometric model  
82 including BM + age or LBM + age. In addition, despite a greater increase in EPOC $\tau_1$  in boys  
83 from the age of 14 years,  $\tau_1\dot{V}O_2$  was not significantly different between sexes whatever age.

84 **Conclusion:** While age and LBM accounted for the sex-related differences of EPOC during  
85 childhood and adolescence, no significant effect of age and sex was observed on the  $\dot{V}O_2$   
86 recovery time constant after high-intensity exercise.

87

88 **KEY WORDS:** excess post-exercise oxygen consumption;  $\dot{V}O_2$  recovery time constant; girls;  
89 multiplicative allometric modelling; age.

90 **ABBREVIATIONS**

91	ANOVA	Analysis of variance
92	AOD	Accumulated oxygen deficit
93	BM	Body mass
94	EPOC	Excess post-exercise oxygen consumption
95	EPOC <sub>8</sub>	Excess post-exercise oxygen consumption calculated for 8 minutes after an
96		all-out 60-s rowing exercise
97	EPOC <sub>τ<sub>1</sub></sub>	Excess post-exercise oxygen consumption obtained until τ <sub>1</sub> $\dot{V}O_2$ was
98		reached
99	LBM	Lean body mass
100	PCr	Phosphocreatine
101	τ <sub>1</sub> $\dot{V}O_2$	$\dot{V}O_2$ recovery time constant
102	$\dot{V}O_2$	Oxygen uptake
103	$\dot{V}O_{2peak}$	Peak oxygen uptake

## 104 INTRODUCTION

105           During the recovery from exercise, numerous physiological processes take place, aimed  
106 at restoring homeostasis, functional capacity and/or performance. These processes are not linear  
107 and their kinetics are widely different (27). The kinetics of these processes have mostly been  
108 studied in adults, although some comparative paediatric data do exist (18). From a cardio-  
109 respiratory perspective, some studies have reported a faster recovery of oxygen consumption  
110 ( $\dot{V}O_2$ ) in prepubertal boys compared with men after high-intensity exercise (8, 15, 21, 40). For  
111 instance, using bi-exponential modelling, Zanconato et al. (40) reported a lower  $\dot{V}O_2$  recovery  
112 time constant ( $\tau_1 \dot{V}O_2$ ) in 7-11-year-old children compared with 26-42-year-old adults after a one-  
113 minute cycle exercise performed at 125% of maximal oxygen uptake. However, given the small  
114 number of studies of children and the lack of data from adolescents, this finding remains to be  
115 confirmed. In addition, no study has analysed  $\dot{V}O_2$  recovery kinetics in girls during high-  
116 intensity exercise and the concurrent effect of age and sex on  $\tau_1 \dot{V}O_2$  following high-intensity  
117 exercise during childhood and adolescence remains to be documented.

118           In the male population, several mechanisms have been proposed to explain the child-adult  
119 difference in the initial phase of  $\dot{V}O_2$  recovery kinetics. Suggestions include the smaller body  
120 size of prepubertal boys which reduces circulation time into the blood compartment (12).  
121 Moreover, due to their different body composition (*e.g.*, less lean body mass (LBM)) prepubertal  
122 children are likely to have lower nonoxidative metabolism at the onset of high-intensity exercise  
123 (6, 13), allowing a faster post-exercise  $\dot{V}O_2$  recovery. If these mechanisms hold true, one might  
124 suggest that  $\tau_1 \dot{V}O_2$  could be shorter in girls compared to boys from the age of 14 years. Indeed, it  
125 has recently been shown that non-oxidative energy production measured from accumulated  $O_2$   
126 deficit (AOD) increases more extensively in boys than girls from the age of 14 years (6), *i.e.*  
127 about the time of significant sex-related changes in LBM and fat mass (7, 36). However, this  
128 assumption remains to be proven.



129           Beyond the  $\dot{V}O_2$  recovery kinetics, post-exercise  $O_2$  consumption is also characterised by  
130 the amount of  $O_2$  to be refunded after high-intensity exercise, *i.e.* excess post-exercise oxygen  
131 consumption (EPOC). The amount of post-exercise  $O_2$  represents the additional amount of  $O_2$   
132 used by the body to re-establish metabolic homeostasis related to increased body temperature,  
133 hormone production, and energy substrate depletion during exercise (5, 19). EPOC could be  
134 associated with AOD and its determinants, *i.e.* exercise intensity and duration (5, 25), and  
135 individual body dimensions (35). Indeed, Tahara and colleagues (35) showed significant positive  
136 correlations between EPOC, body mass (BM) and LBM in 16- to 21-year-old male athletes. This  
137 result has also been reported by Campos et al. (9) in 28-year-old professional cyclists for whom  
138 EPOC was positively associated with total and lower limb lean mass. A higher muscle power  
139 production associated with greater lower limb lean mass could more favourably increase AOD,  
140 and thereby EPOC and  $\tau_1\dot{V}O_2$  (the two parameters being positively correlated in the study by  
141 Campos et al. (9)). To our knowledge, changes in EPOC during childhood and adolescence have  
142 not been studied. However, as for  $\tau_1\dot{V}O_2$ , EPOC may increase more extensively in boys than  
143 girls from the age of 14 years due to a greater gain in BM, particularly LBM and greater  
144 concomitant metabolic disturbances during high intensity exercise in boys at the time of puberty  
145 (6). In addition, while the concept of EPOC has been used in adults, it has been mostly expressed  
146 ratio-scaled with BM to compare populations of different body size and composition (*e.g.*, males  
147 vs females or sprinters vs long distance runners) (26, 31). However, ratio scaling with BM has  
148 been demonstrated to be inappropriate for comparing children and adolescents of both sexes (37,  
149 38), as ratio scaling with BM does not create BM-free physiological variables during childhood  
150 and adolescence (38). Numerous studies have demonstrated the fallacy of ratio scaling  
151 physiological variables and it has been compellingly argued that with cross-sectional data,  
152 allometric scaling based on log-linear regression with multiple covariates is the method of choice  
153 when investigating the development of physiological variables during growth (30, 37, 38).

154 Furthermore, as sex-related differences in EPOC between girls and boys from age 14 onwards  
155 could be influenced not only by changes in BM but also by concurrent changes in age, growth  
156 and maturation. Thus, concurrently controlling for both BM + age is preferred to just controlling  
157 for BM (2, 3, 37). However, as fat mass is metabolically inert (20), LBM as a surrogate of  
158 muscle mass is likely to be a more appropriate covariate of physiological variables during  
159 exercise than BM (2, 3). LBM varies with age and sex (7), therefore, allometric analyses  
160 including both LBM + age as covariates are likely to provide more insights into EPOC than  
161 when EPOC is allometrically scaled with BM + age. In addition, previous studies of both  
162 paediatric aerobic and anaerobic fitness have consistently demonstrated that with LBM + age  
163 controlled for, maturation is a non-significant covariate (2, 3).

164 Therefore, the aim of the present study was to examine sex-related differences in  $\dot{V}O_2$   
165 recovery kinetics (*i.e.*,  $\tau_1 \dot{V}O_2$ ) and EPOC after high-intensity exercise during childhood and  
166 adolescence. We hypothesised that (i) boys would have higher absolute EPOC values than girls  
167 from the age of 14 years, (ii) the sex difference would persist when EPOC is allometrically  
168 scaled with BM + age, (iii) the sex difference would not be significant when EPOC is  
169 allometrically scaled with LBM + age, and (iv) girls would have faster  $\dot{V}O_2$  recovery kinetics  
170 than boys from the age of 14 years (*i.e.*, lower  $\tau_1 \dot{V}O_2$ ).

171

## 172 **MATERIALS AND METHODS**

### 173 **Subjects**

174 Forty-two male and thirty-five female rowers aged from 10 to 17 years volunteered to  
175 participate in the present study. All participants trained on average “on water” two to three times  
176 per week with similar training volumes between girls and boys. Training sessions lasted from 60  
177 to 90 min and included various exercises aimed at improving rowing performance through  
178 movement technique, coordination in the boat between rowers, pacing strategies, etc. The

179 training programme was specifically designed to improve rowing mechanical efficiency rather  
180 than components of physical fitness, notably anaerobic capacity or muscle strength. None of the  
181 participants had a family history of cardiovascular disease or was under medication. The present  
182 study was approved by an institutional ethics review board (Comité d'Éthique pour la Recherche  
183 en Sciences et Techniques des Activités Physiques et Sportives – CERSTAPS, n°2019-18-09-36)  
184 and conformed to the standards of use of human participants in research as outlined in the *Sixth*  
185 *Declaration of Helsinki*. The participants were informed of the experimental procedures and  
186 gave their written assent before any testing was conducted. In addition, written informed consent  
187 was obtained from the parents or legal guardians of the participants.

188

## 189 **Experimental design**

190         Volunteers were tested in two experimental sessions separated by at least 48 hours.  
191 Participants were instructed not to undertake any strenuous activity during the 24 hours  
192 preceding each session. The first session was dedicated to gathering participants' physical  
193 characteristics (anthropometric measurements and body composition) and peak oxygen uptake  
194 ( $\dot{V}O_{2\text{peak}}$ ) assessment. During the second session, the volunteers performed a 60-s all-out test.  
195 The two exercise sessions were carried out on a rowing ergometer (Model D, Concept2,  
196 Morrisville, VT, USA). The participants were fully familiarised with the equipment. The  
197 computer of the ergometer continuously delivered the power output. The resistance factor was  
198 set by the investigators between 100 and 130 according to age, sex, and the expertise level of  
199 young rowers. The same resistance factor was kept for both tests. Verbal encouragement was  
200 systematically provided by the investigators during each exercise session.

201

202

203

## 204 **Experimental measurements**

### 205 *Session 1: anthropometric characteristics and body composition*

206           Body mass (BM in kg) was measured using a digital weight scale with a precision of  $\pm$   
207 0.01 kg (Seca 899, Seca, Germany). Standing height (in m) was assessed using a stadiometer  
208 with a precision of  $\pm$  1 mm (Seca 213, Seca, Germany). Skinfold thicknesses were measured at  
209 the triceps and subscapular sites using a Harpenden calliper (British Indicators Ltd, St Albans,  
210 UK) and the mean value from three reproducible measurements was calculated. The  
211 measurements were taken by the same experienced investigator on the right side of the body to  
212 reduce variability in the results for girls and boys. Body fat percentage and LBM (in kg) were  
213 determined using the equations developed by Slaughter et al. (34). These equations are specific  
214 to sex, ethnicity and age, and are recommended for assessing body fat and LBM in children and  
215 adolescents (8-18 years of age).

216

### 217 *Session 1: maximal oxygen uptake test*

218           Each participant performed a progressive test to exhaustion to determine  $\dot{V}O_{2\text{peak}}$  (in  
219  $\text{L}\cdot\text{min}^{-1}$ ). The initial power was set between 40 and 80 W during the first five minutes and the  
220 power was incremented by 10-30 W every 3 minutes according to age, sex and the expertise  
221 level of participants.

222           Oxygen uptake, carbon dioxide output and ventilation were continuously monitored using  
223 a breath-by-breath analyser (Quark CPET, Cosmed, Italy). The gas analysers were calibrated  
224 before each test using a gas mixture of known concentration (16.0%  $\text{O}_2$  and 5%  $\text{CO}_2$ ).  
225 Calibration of the flowmeter was performed with a 3-L air syringe. Heart rate was continuously  
226 recorded with a heart rate monitor (HRM-Dual, Garmin, Kansas, USA).  $\dot{V}O_{2\text{peak}}$  was considered  
227 to be reached during the last step when at least two of the following criteria were met: (i)  $\dot{V}O_2$   
228 levelling-off, (ii) maximal respiratory exchange ratio  $\geq 1.1$  and (iii) maximal heart rate  $\geq 95\%$  of

229 the age-predicted maximal heart rate ( $208.609 - 0.716 \cdot \text{age}$ ) (33). Forty-eight (62%) participants  
230 out of 77 showed a  $\dot{V}O_2$  plateau at completion of the maximal test. The criterion for a  $\dot{V}O_2$   
231 plateau was the  $\dot{V}O_2$  levelling-off despite an increase in minute ventilation at maximal effort  
232 (16).

233

#### 234 *Session 2: 60-s all-out test*

235 After a standardised 15-min warm-up at about 130-140  $\text{beats} \cdot \text{min}^{-1}$  and two short sprints  
236 (10-s) in the last 5 minutes, all participants performed a 60-s rowing all-out test followed by an  
237 8-min sitting recovery. Before starting the test, each participant was requested to ensure that their  
238 technique is as close as possible to what they would do on the water. The starting position was  
239 standardized so as the participants have the arms straight, the knees against the trunk, the  
240 shoulders in front of the hips and the shins vertical. The feet were strapped during the test. The  
241 60-s all-out test was performed 10-min after the end of the warm-up. They were asked to  
242 participants to provide their maximal effort at each stroke throughout the test. No feedback was  
243 given on split time, stroke rate or covered distance. The investigators strongly encouraged the  
244 volunteers during each test. Cardio-respiratory parameters were continuously measured using a  
245 breath-by-breath analyser (Quark CPET, Cosmed, Italy). Individual accumulated oxygen deficit  
246 (AOD in  $\text{L O}_2 \text{ Eq.}$ ) was determined as previously described (6, 13). In addition, the recovery  
247 kinetics of oxygen consumption were modelled and the excess post-exercise oxygen  
248 consumption (EPOC) calculated (see below for further details).

249

250

251

252

#### 253 **Measurements and calculations**

254 *Oxygen uptake recovery kinetic modelling*

255 The post-exercise  $\dot{V}O_2$  recovery kinetics were determined by considering the net changes  
256 of each value, *i.e.* minus baseline (net  $\dot{V}O_2$ , in  $L \cdot \text{min}^{-1}$ ), which was obtained during 3-min before  
257 the warm-up. The breath-by-breath  $\dot{V}O_2$  were interpolated second-by-second between 0 and 8  
258 minutes and the recovery kinetics were then modelled using a biexponential function (Origin  
259 2020b, Massachusetts, USA), as previously proposed after high-intensity exercise (40):

260

261 
$$\dot{V}O_2(t) = A \times e^{\frac{t}{\tau_1}} + B \times e^{\frac{t}{\tau_2}} + C \quad (\text{Eq. 1})$$

262

263 where  $\dot{V}O_2(t)$  is the oxygen uptake at the time  $t$ , A and B the amplitudes of the fast and slow  
264 components, respectively,  $\tau_1$  and  $\tau_2$  the corresponding time constants and C the  $\dot{V}O_2$  at rest. The  
265 determination coefficients ( $r^2$ ) ranged between 0.82 and 0.98 (mean  $\pm$  SD:  $0.93 \pm 0.03$ ; IC95%:  
266 0.92-0.94).

267

268 *Excess Post-exercise Oxygen Consumption (EPOC) calculation*

269 Excess post-exercise oxygen consumption was calculated by subtracting the integrated  
270 area under resting  $\dot{V}O_2$  from the integrated area under the  $\dot{V}O_2$  recovery curve over the first 8  
271 minutes of recovery (EPOC<sub>8</sub>) and until  $\tau_1$  was reached (EPOC <sub>$\tau_1$</sub> ). EPOC <sub>$\tau_1$</sub>  was calculated to  
272 quantify the rapid replenishment of phosphocreatine as well as reoxygenation of myoglobin (19).  
273 Those two parameters were expressed in absolute value (L), and with allometric exponents (*i.e.*,  
274  $\text{BM} + \text{age}$ ;  $\text{LBM} + \text{age}$ ) (see below for further details). The EPOC<sub>8</sub>/AOD ratio was also  
275 calculated to know whether the changes in AOD and EPOC<sub>8</sub> evolved in the same proportions  
276 during childhood and adolescence with respect to sex.

277 *Allometric modelling procedure*

278 As BM, LBM and age may have influenced EPOC during recovery, we further  
279 investigated the influence of these factors on EPOC<sub>8</sub> and EPOC<sub>τ<sub>1</sub></sub> through a multiplicative  
280 allometric model proposed by Nevill and Holder (29). This procedure considers the influence of  
281 the size descriptor (*i.e.*, BM or LBM) and age on EPOC variables (*i.e.*, EPOC<sub>8</sub> or EPOC<sub>τ<sub>1</sub></sub>) as  
282 follows:

283

$$284 \quad \text{EPOC variable} = \text{size descriptor}^b \cdot \exp(a + c \cdot \text{age}) \cdot \varepsilon \quad (\text{Eq. 2})$$

285

286 where  $a$  is the proportionality coefficient,  $b$  the scaling factor associated with the size descriptor  
287 (*i.e.*, BM or LBM),  $c$  the scaling factor associated with age, and  $\varepsilon$  the normally distributed error.

288 The statistical approach to allometry is to use a multiple logarithmic transformation, as  
289 previously done by Carvalho et al. (10), as follows:

290

$$291 \quad \log(\text{EPOC variable}) = b \cdot \log(\text{size descriptor}) + a + c \cdot \text{age} + \log \varepsilon \quad (\text{Eq. 3})$$

292

293 where  $a$  is the intercept,  $b$  and  $c$  are the slopes of the multiple linear regression. These slopes are  
294 calculated by ordinary multiple regression analysis (Rstudio, Massachusetts, USA) where  $b$  and  $c$   
295 are equal to the scaling factors.

296

### 297 **Statistical analysis**

298 Statistical procedures were performed using Statistica 8.0 software (Statsoft, Inc., USA).

299 Descriptive statistics were expressed as mean  $\pm$  standard deviation (SD) by age group (group 1:

300 10-11.9 yr, group 2: 12-13.9 yr, group 3: 14-15.9 yr, group 4: 16-17.9 yr) and sex, as proposed

301 by Doré et al. (14) and Bardin et al. (6). Data were screened for normality of distribution and

302 homogeneity of variances using a Shapiro-Wilk test and the Levene's test, respectively. Two-  
303 way ANOVA was used to examine the effects of sex and age group on the participants' physical  
304 and fitness characteristics, EPOC<sub>8</sub> and EPOC<sub>τ<sub>1</sub></sub> (in absolute values and scaled with allometric  
305 exponents), AOD, EPOC<sub>8</sub>/AOD ratio and τ<sub>1</sub>  $\dot{V}O_2$ . When ANOVA revealed a main or interaction  
306 significant effect, an HSD Tukey's *post-hoc* test was applied to test the discrimination between  
307 means. The effect size and statistical power have also been reported. The effect size was assessed  
308 using the partial eta-squared ( $\eta^2$ ) and ranked as follows: ~ 0.01 = small effect, ~ 0.06 = moderate  
309 effect,  $\geq 0.14$  = large effect (11). Linear regression models between age, BM, LBM, EPOC<sub>8</sub>,  
310 EPOC<sub>τ<sub>1</sub></sub> and AOD were fitted by the least-squares method by considering boys and girls  
311 separately, and the squared Bravais-Pearson determination coefficients ( $r^2$ ) of these linear  
312 regression models were calculated. The linear regressions between age, BM, LBM, EPOC<sub>8</sub> and  
313 EPOC<sub>τ<sub>1</sub></sub> were established to check the effects of age, BM and LBM on EPOC<sub>8</sub> and EPOC<sub>τ<sub>1</sub></sub> and  
314 then justify the use of BM + age or LBM + age as scaling factors through the multiplicative  
315 allometric models. The statistical significance level was set at 5% ( $p < 0.05$ ).

316

## 317 **RESULTS**

### 318 **Participants' physical and fitness characteristics**

319 Participants' characteristics are described by age group and sex in Table 1. Statistical  
320 analysis revealed significant sex  $\times$  age group interaction effects for height ( $F_{(3, 69)} = 5.69, p <$   
321  $0.001, \eta^2 = 0.20, \text{power} = 0.93$ ), BM ( $F_{(3, 69)} = 7.98, p < 0.001, \eta^2 = 0.26, \text{power} = 0.99$ ), body fat  
322 ( $F_{(3, 69)} = 3.40, p < 0.05, \eta^2 = 0.13, \text{power} = 0.74$ ), LBM ( $F_{(3, 69)} = 11.85, p < 0.001, \eta^2 = 0.34,$   
323  $\text{power} = 0.99$ ) and  $\dot{V}O_{2\text{peak}}$  in absolute values ( $F_{(3, 68)} = 11.00, p < 0.001, \eta^2 = 0.33, \text{power} =$   
324  $0.99$ ) but not for  $\dot{V}O_{2\text{peak}}$  allometrically scaled with LBM + age ( $F_{(3, 68)} = 0.64, p = 0.593, \eta^2 =$   
325  $0.03, \text{power} = 0.18$ ). No sex-related significant difference was observed for height, LBM and  
326  $\dot{V}O_{2\text{peak}}$  before the age of 14 years, and for BM before the age of 16 years. However, between



327 14.0 and 17.9 years, boys exhibited significantly higher values than girls for height, LBM and  
328  $\dot{V}O_{2peak}$  ( $p < 0.001$ ). Boys also showed significantly higher values than girls for BM ( $p < 0.01$ )  
329 between 16.0 and 17.9 years. Finally, girls had significantly higher values for body fat than boys  
330 whatever age group ( $p < 0.05$  at least).

331

332 - Please insert Table 1 near here -

333

### 334 **Determination coefficients and allometric exponents**

335 In boys, age was positively correlated with BM ( $r^2 = 0.67$ ,  $p < 0.001$ ) and LBM ( $r^2 =$   
336  $0.68$ ,  $p < 0.001$ ). In girls, age was positively correlated with LBM ( $r^2 = 0.11$ ,  $p < 0.05$ ) but not  
337 with BM ( $p = 0.143$ ).  $EPOC_8$  was positively associated with age (boys:  $r^2 = 0.75$ ,  $p < 0.001$ ;  
338 girls:  $r^2 = 0.37$ ,  $p < 0.001$ ), BM (boys:  $r^2 = 0.79$ ,  $p < 0.001$ ; girls:  $r^2 = 0.27$ ,  $p < 0.001$ ), LBM  
339 (boys:  $r^2 = 0.83$ ,  $p < 0.001$ ; girls:  $r^2 = 0.38$ ,  $p < 0.001$ ) and AOD (boys:  $r^2 = 0.85$ ,  $p < 0.001$ ;  
340 girls:  $r^2 = 0.19$ ,  $p < 0.01$ ).  $EPOC_{\tau_1}$  was positively correlated with age (boys:  $r^2 = 0.61$ ,  $p < 0.001$ ;  
341 girls:  $r^2 = 0.19$ ,  $p < 0.01$ ), BM (boys:  $r^2 = 0.70$ ,  $p < 0.001$ ; girls:  $r^2 = 0.28$ ,  $p < 0.001$ ) and LBM  
342 (boys:  $r^2 = 0.76$ ,  $p < 0.001$ ; girls:  $r^2 = 0.35$ ,  $p < 0.001$ ). Allometric scaling exponents are  
343 displayed by sex in Table 2.

344

345 - Please insert Table 2 near here -

346

### 347 **Accumulated oxygen deficit**

348 AOD values are displayed by age group and sex in Table 3. Two-way ANOVA showed a  
349 sex  $\times$  age group interaction effect for AOD ( $F_{(3, 64)} = 10.84$ ,  $p < 0.001$ ,  $\eta^2 = 0.33$ , power = 0.99).  
350 *Post-hoc* tests showed significantly higher values for AOD in boys than girls between 14.0 and  
351 17.9 years ( $p < 0.001$ ).

352

- Please insert Table 3 near here -

353

354 **Excess post-exercise oxygen consumption**

355

EPOC<sub>8</sub>, EPOC<sub>8</sub>/AOD ratio and EPOC<sub>τ<sub>1</sub></sub> are displayed by age group and sex in Table 3.

356

Two-way ANOVA revealed a significant sex × age group interaction effect for absolute EPOC<sub>8</sub>

357

( $F_{(3, 69)} = 13.05, p < 0.001, \eta^2 = 0.36, \text{power} = 0.99$ ). *Post-hoc* tests showed significantly higher

358

EPOC<sub>8</sub> with increasing age ( $p < 0.01$  at least) in both sexes. *Post-hoc* tests also showed

359

significantly higher values for absolute EPOC<sub>8</sub> in boys than girls between 14.0 and 17.9 years ( $p$

360

$< 0.001$ ). However, there was neither a significant age effect ( $F_{(3, 69)} = 0.97, p = 0.413, \eta^2 = 0.04,$

361

power = 0.25) nor a sex × age group interaction effect ( $F_{(3, 69)} = 1.25, p = 0.298, \eta^2 = 0.05,$

362

power = 0.32) for EPOC<sub>8</sub> allometrically scaled with BM + age. In the same way, there was

363

neither a significant age effect ( $F_{(3, 69)} = 1.01, p = 0.394, \eta^2 = 0.04, \text{power} = 0.26$ ) nor a sex ×

364

age group interaction effect ( $F_{(3, 69)} = 1.24, p = 0.303, \eta^2 = 0.05, \text{power} = 0.32$ ) for EPOC<sub>8</sub>

365

allometrically scaled with LBM + age. Two-way ANOVA also showed no sex × age group

366

interaction effect for EPOC<sub>8</sub>/AOD ratio ( $F_{(3, 64)} = 0.30, p = 0.827, \eta^2 = 0.01, \text{power} = 0.10$ ).

367

368

Two-way ANOVA revealed a significant sex × age group interaction effect for absolute

369

EPOC<sub>τ<sub>1</sub></sub> ( $F_{(3, 69)} = 9.99, p < 0.001, \eta^2 = 0.30, \text{power} = 0.99$ ). *Post-hoc* tests showed significantly

370

higher EPOC<sub>τ<sub>1</sub></sub> with increasing age for boys but not for girls ( $p < 0.001$ ). *Post-hoc* tests also

371

showed significantly higher values for absolute EPOC<sub>τ<sub>1</sub></sub> in boys than girls between 14.0 and 17.9

372

years ( $p < 0.001$ ). However, there was neither a significant age effect ( $F_{(3, 69)} = 0.41, p = 0.745,$

373

$\eta^2 = 0.02, \text{power} = 0.13$ ) nor a sex × age group interaction effect ( $F_{(3, 69)} = 2.36, p = 0.078, \eta^2 =$

374

0.09, power = 0.57) for EPOC<sub>τ<sub>1</sub></sub> allometrically scaled with BM + age. In the same way, there

375

was neither a significant age effect ( $F_{(3, 69)} = 0.61, p = 0.611, \eta^2 = 0.03, \text{power} = 0.17$ ) nor a sex

376  $\times$  age group interaction effect ( $F_{(3, 69)} = 1.56, p = 0.206, \eta^2 = 0.06, \text{power} = 0.39$ ) for  $\text{EPOC}\tau_1$   
377 allometrically scaled with LBM + age.

378

### 379 **Recovery time constant**

380 Oxygen uptake during and after the all-out 60-s rowing test in boys and girls is shown in  
381 Figure 1. Oxygen uptake recovery time constant ( $\tau_1\dot{V}O_2$ ) is displayed in Table 3. Two-way  
382 ANOVA revealed a significant main effect for sex ( $F_{(3, 69)} = 8.47, p < 0.01, \eta^2 = 0.11, \text{power} =$   
383  $0.82$ ) but not for age ( $F_{(3, 69)} = 0.52, p = 0.671, \eta^2 = 0.02, \text{power} = 0.15$ ). No significant sex  $\times$   
384 age group interaction effect was observed for  $\tau_1\dot{V}O_2$  ( $F_{(3, 69)} = 2.57, p = 0.061, \eta^2 = 0.10, \text{power}$   
385  $= 0.61$ ).

386 - Please insert Figure 1 near here -

387

## 388 **DISCUSSION**

389 The purpose of the present study was to determine during childhood and adolescence the  
390 effects of age and sex on oxygen uptake recovery after high-intensity exercise. The main results  
391 confirm our first hypothesis since the absolute amount of  $O_2$  consumed during recovery ( $\text{EPOC}_8$   
392 and  $\text{EPOC}\tau_1$ ) increased more extensively in boys than girls from the age of 14 years, and  $\text{EPOC}_8$   
393 and  $\text{EPOC}\tau_1$  were no longer significantly different with respect to age and sex when the effects  
394 of LBM + age were considered in allometric modelling. However, the results of the present study  
395 do not confirm our last hypothesis since we do not show a difference between girls and boys in  
396 the  $\dot{V}O_2$  recovery time constant ( $\tau_1\dot{V}O_2$ ) from 10 to 17 years old. Therefore, despite the more  
397 significant increase in EPOC in boys compared to girls from 14 years of age due to their greater  
398 LBM gain, the  $\dot{V}O_2$  recovery kinetics after high-intensity exercise were not different between  
399 sexes during childhood and adolescence.

400 The results of the present study show, for the first-time, a significant age  $\times$  sex  
401 interaction effect on EPOC<sub>8</sub>, indicating an increase in excess post-exercise oxygen consumption  
402 after high-intensity exercise from childhood into adolescence, with higher absolute values in  
403 boys from the age of 14 years. This result is likely explained by the sex-related changes in body  
404 size and composition between girls and boys with advancing age since a sex difference was no  
405 longer significant when EPOC<sub>8</sub> was analysed using a multiplicative allometric modelling  
406 including either BM + age or LBM + age. The absence of difference in results between BM +  
407 age and LBM + age as scaling factors is noteworthy because of the normally marked sex-related  
408 differences in LBM and fat mass from the age of about 14 years (7). This finding could be  
409 explained by the nature of rowing that is a BM-supported activity and where body composition  
410 (LBM vs fat mass) could have less effect on physiological responses during exercise than non-  
411 BM-supported activities such as running. Also, in the present study, girls exhibited no significant  
412 difference in fat mass between age groups probably due to their training activity (Table 1),  
413 thereby attenuating the effect of sex-related differences in body composition on EPOC. Another  
414 point of consideration in the present study is that, once age was controlled for, EPOC<sub>8</sub> increased  
415 proportionally more than BM and LBM in boys (b: 1.11 and 1.10, respectively). However, this  
416 was not the case in girls (b: 0.61 and 0.67, respectively). This is likely explained by the closer  
417 relationships obtained between age, BM, LBM and EPOC<sub>8</sub> in boys. Taken together, these results  
418 show that both age and body mass and composition play a major role in explaining sex-related  
419 differences in EPOC after high-intensity exercise from the age of 14 years. However, the greater  
420 EPOC<sub>8</sub> in boys from the age of 14 years could be also attributed to greater non-oxidative energy  
421 production (*i.e.*, AOD) incurred at the onset of high-intensity exercise via a greater mobilisation  
422 of LBM. Indeed, the results of our study show significant relationships between EPOC<sub>8</sub>, AOD  
423 and LBM, but with greater determination coefficients in boys than girls. From a physiological  
424 perspective, sex-related changes in EPOC<sub>8</sub> from the age of 14 years could be attributed to factors

425 accounting for the concomitant increase in AOD. These could include a higher production of  
426 androgen hormones (*e.g.*, testosterone) at the time of puberty in boys (17, 23), increasing more  
427 favourably muscle mass and the specific area of type II fibres and thereby the activity of non-  
428 oxidative metabolism during exercise and possibly EPOC<sub>8</sub> during recovery. However, these  
429 factors could act on EPOC<sub>8</sub> in the same proportions during childhood and adolescence since no  
430 significant sex × age group interaction effect for EPOC<sub>8</sub>/AOD ratio was found in the present  
431 study.

432

433         The results of the present study also show in boys a significant increase with age in the  
434 amount of O<sub>2</sub> required to replenish muscle phosphagens and reoxygenate myoglobin (*i.e.*,  
435 EPOC<sub>τ<sub>1</sub></sub>). This finding was not found in girls, which led to a sex difference in EPOC<sub>τ<sub>1</sub></sub> from the  
436 age of 14 years (Table 3). Multiplicative allometric modelling, however, highlighted that when  
437 age was considered concurrently with BM or LBM, the difference in EPOC<sub>τ<sub>1</sub></sub> between girls and  
438 boys was no longer significant ( $p = 0.079$  for BM + age;  $p = 0.206$  for LBM + age). Moreover,  
439 when age was considered in the allometric procedure, EPOC<sub>τ<sub>1</sub></sub> increased proportionally more  
440 than BM or LBM in boys (b: 1.03 and 1.13, respectively) but not in girls (b: 0.71 and 0.80,  
441 respectively). Accordingly, the amount of O<sub>2</sub> required for phosphagen replenishment and  
442 myoglobin reoxygenation would be influenced by the changes in LBM with age, but with less  
443 evidence in girls as indicated by their lower determination coefficients between LBM and  
444 EPOC<sub>τ<sub>1</sub></sub> (0.35 vs 0.76 in girls and boys, respectively). However, while EPOC<sub>τ<sub>1</sub></sub> increased with  
445 age and differed between both sexes from 14 years onwards, the  $\dot{V}O_2$  recovery time constant  
446 (*i.e.*,  $\tau_1 \dot{V}O_2$ ) did not significantly increase during childhood and adolescence in either boys or  
447 girls. This result does not seem to be in accordance with some previously published studies  
448 reporting faster  $\dot{V}O_2$  recovery kinetics in prepubertal children than adults (21, 40). However, in  
449 the present study, data were collected among a population aged 10 to 17 years, thus not including

450 adults. In girls, our data are consistent with those reported by McNarry et al. (28) showing no  
451 difference in the  $\dot{V}O_2$  recovery time constant obtained from a monoexponential model between  
452 11-12- and 14–15-year-olds following both cycle and upper body submaximal exercise.  
453 Therefore,  $\tau_1\dot{V}O_2$  could remain stable from childhood into adolescence for both girls and boys,  
454 and then increase in the transition to adulthood, but this still remains to be confirmed.

455

456         Due to the close inverse relationship between the initial phase of the  $\dot{V}O_2$  recovery  
457 kinetics and the phosphocreatine (PCr) resynthesis kinetics obtained from  $^{31}\text{P}$ -magnetic  
458 resonance spectroscopy ( $^{31}\text{P}$ -MRS) following exercise (24, 32),  $\tau_1\dot{V}O_2$  may be considered as a  
459 surrogate of PCr recovery rate, and thereby muscle oxidative capacity. In relation to this,  
460 Kappenstein et al. (22) showed following ten sets of 30-s high-intensity dynamic plantar flexion  
461 that the PCr recovery time constant obtained from a monoexponential function did not differ  
462 significantly between 9.4-year-old boys and girls and 26.1-year-old men and women. Likewise,  
463 Willcocks et al. (39) reported no significant effect of age, sex, and age  $\times$  sex interaction on the  
464 PCr recovery kinetics following fatiguing isometric quadriceps exercise in thirteen 13-year-old  
465 adolescents (6 males and 7 females) and fourteen 29-year-old adults (6 males and 8 females).  
466 Therefore, although this has yet to be confirmed due to the high interindividual variability in the  
467 PCr recovery kinetics,  $^{31}\text{P}$ -MRS data appear to show no significant age  $\times$  sex interaction on the  
468 PCr recovery time constant after exercise during childhood and adolescence, which supports our  
469 data obtained from  $\tau_1\dot{V}O_2$  from 10 to 17 years in both sexes.

470

471 Strengths and limitations

472         This study presents cross-sectional data and would have been enhanced with measures of  
473 maturity status. However, it has been demonstrated in longitudinal studies that once age and  
474 LBM have been controlled for in multiplicative allometric analyses, maturity status does not

475 make an additional, significant contribution to explaining the development of aerobic fitness,  
476 anaerobic fitness or ventilatory variables of 11–18-year-olds (1, 3, 4). In addition, even if the  
477 length of exercise training exposure was not determined and considered in the present study,  
478 peak oxygen uptake allometrically scaled with LBM + age was found to be comparable between  
479 age groups and sex, thereby indicating a similar level of aerobic fitness between boys and girls  
480 during childhood and adolescence.

481 A unique strength of the present study lies in the adoption for the first-time of allometric  
482 modelling to analyse oxygen consumption recovery, notably EPOC. This approach has provided  
483 new insights into the influence of age and sex and their interaction on EPOC and  $\tau_1 \dot{V}O_2$  during  
484 childhood and adolescence.

485

## 486 **CONCLUSION**

487 The results of the present study show, for the first-time, that oxygen consumption  
488 recovery after high-intensity exercise (quantified by EPOC) increased with age, with boys  
489 differing from girls from the age of about 14 years, likely an outcome of a greater gain in BM  
490 and LBM. Multiplicative allometric modelling showed that when age is considered concurrently  
491 with BM or LBM, the sex difference in EPOC is reduced during childhood and adolescence. In  
492 addition, despite a sex-related difference in the amount of O<sub>2</sub> required for phosphagen  
493 resynthesis and myoglobin reoxygenation (*i.e.*, EPOC $\tau_1$ ) in boys from 14 years of age onwards,  
494 the  $\dot{V}O_2$  recovery kinetics (*i.e.*,  $\tau_1 \dot{V}O_2$ ) is not altered during childhood and adolescence  
495 irrespective of sex.

496

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498

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599

600

601 **Table 1:** Participants' physical and fitness characteristics (n = 77).

	<b>Group 1 (n = 13)</b> <b>10 – 11.9 yr</b>		<b>Group 2 (n = 17)</b> <b>12 – 13.9 yr</b>		<b>Group 3 (n = 27)</b> <b>14 – 15.9 yr</b>		<b>Group 4 (n = 19)</b> <b>16 – 17.9 yr</b>	
	<i>Girls</i> (n = 6)	<i>Boys</i> (n = 7)	<i>Girls</i> (n = 6)	<i>Boys</i> (n = 11)	<i>Girls</i> (n = 14)	<i>Boys</i> (n = 13)	<i>Girls</i> (n = 8)	<i>Boys</i> (n = 11)
<b>Age</b> (yr)	11.4±0.7	11.5±0.4	12.7±0.7	13.2±0.4	15.0±0.6	15.0±0.7	16.8±0.9	16.7±0.5
<b>Height</b> (m)	1.55±0.05	1.53±0.11	1.63±0.09	1.63±0.08	1.66±0.04	1.79±0.07 ***	1.66±0.05	1.78±0.07 **
<b>BM</b> (kg)	48.7±4.6	41.9±7.5	58.8±11.8	51.6±8.9	58.7±6.4	66.7±9.7	56.6±4.3	70.0±5.8 **
<b>Body fat</b> (%)	24.9±6.1	17.6±4.1 *	25.2±5.0	13.7±6.1 ***	22.3±3.3	6.7±2.0 ***	23.2±2.1	10.4±2.0 ***
<b>LBM</b> (kg)	36.4±2.7	34.4±5.7	43.7±7.1	44.6±9.1	45.6±4.7	62.2±8.9 ***	43.4±3.6	62.7±4.9 ***
<b><math>\dot{V}O_{2peak}</math></b> (L·min <sup>-1</sup> )	2.0±0.2	2.2±0.4	2.3±0.2	2.8±0.8	2.7±0.3	4.2±0.6 ***	2.8±0.4	4.5±0.3 ***
<b><math>\dot{V}O_{2peak}</math></b> [L/(kg LBM <sup>b</sup> · exp(a + c · age))]	1.00±0.09	1.05±0.12	1.01±0.07	0.96±0.11	1.01±0.09	1.01±0.09	0.98±0.17	1.01±0.09

602 Values are presented as mean ± SD. BM: body mass; LBM: lean body mass;  $\dot{V}O_{2peak}$ : peak oxygen uptake;  $\dot{V}O_{2peak}$  [L/(kg LBM<sup>b</sup>· exp(a + c · age))]: peak  
603 oxygen uptake allometrically scaled with LBM + age as follows:  $\log(\dot{V}O_{2peak}) = b \cdot \log(\text{LBM}) + a + c \cdot \log(\text{age})$  (see section “Allometric modelling  
604 procedure” for further explanations). \*, \*\*, and \*\*\*: significantly different from girls within each age group at  $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ ,  
605 respectively.

606 **Table 2:** Allometric exponents obtained from multiplicative modelling of EPOC<sub>8</sub> and EPOC<sub>τ<sub>1</sub></sub> for body size  
 607 variables and age.

608

	Allometric coefficients	
	Girls	Boys
EPOC <sub>8</sub> :		
Proportionality coefficient	-1.83	-3.86 <sup>10</sup>
BM	0.61	1.11
Age	0.05	0.07 <sup>11</sup>
EPOC <sub>8</sub> :		
Proportionality coefficient	-1.80	-3.46 <sup>12</sup>
LBM	0.67	1.10
Age	0.05	0.05 <sup>13</sup>
EPOC <sub>τ<sub>1</sub></sub> :		
Proportionality coefficient	-3.45	-5.16 <sup>14</sup>
BM	0.71	1.03
Age	0.03	0.07 <sup>15</sup>
EPOC <sub>τ<sub>1</sub></sub> :		
Proportionality coefficient	-3.49	-4.91 <sup>16</sup>
LBM	0.80	1.13 <sup>17</sup>
Age	0.02	0.04 <sup>17</sup>

618 EPOC<sub>8</sub>: excess post-exercise oxygen consumption calculated for 8 minutes after a 60-s all-out rowing exercise;

619 EPOC<sub>τ<sub>1</sub></sub>: excess post-exercise oxygen consumption calculated until τ<sub>1</sub>  $\dot{V}O_2$  was reached; BM: body mass; LBM:

620 lean body mass.

621

622 **Table 3:** Parameters describing the oxygen uptake recovery kinetics and excess post-exercise oxygen consumption following an all-out 60-s rowing  
 623 exercise test in seventy-seven children and adolescents 10-17 years of age in both sexes.

	<b>Group 1 (n=13)</b> <b>10 – 11.9 yr</b>		<b>Group 2 (n=17)</b> <b>12 – 13.9 yr</b>		<b>Group 3 (n=27)</b> <b>14 – 15.9 yr</b>		<b>Group 4 (n=20)</b> <b>16 – 17.9 yr</b>	
	<i>Girls</i> (n=6)	<i>Boys</i> (n=7)	<i>Girls</i> (n=6)	<i>Boys</i> (n=11)	<i>Girls</i> (n=14)	<i>Boys</i> (n=13)	<i>Girls</i> (n=9)	<i>Boys</i> (n=11)
<b>EPOC<sub>8</sub></b> (L)	3.1±0.3	3.1±0.6	3.8±0.2	3.9±1.2 †	4.4±1.0	6.7±1.0 †††, ***	4.7±0.5 ††	7.6±0.8 †††, ***
<b>EPOC<sub>8</sub></b> [L/(kg BM <sup>b</sup> · exp(a + c · age))]	0.98±0.12	1.06±0.08	1.01±0.12	0.92±0.17	1.01±0.17	1.07±0.15	1.03±0.12	1.01±0.11
<b>EPOC<sub>8</sub></b> [L/(kg LBM <sup>b</sup> · exp(a + c · age))]	0.99±0.13	1.08±0.10	1.02±0.12	0.92±0.14	1.00±0.17	1.02±0.13	1.03±0.11	1.04±0.11
<b>AOD</b> (L O <sub>2</sub> Eq.)	1.9±0.4	1.9±0.6	2.4±0.4	2.7±0.7	2.8±0.6	4.6±0.9 †††, ***	2.9±0.6	5.2±0.7 †††, ***
<b>EPOC<sub>8</sub>/AOD ratio</b>	1.66±0.35	1.60±0.21	1.61±0.32	1.50±0.18	1.61±0.52	1.47±0.20	1.74±0.33	1.47±0.18
<b>τ<sub>1</sub>·<math>\dot{V}O_2</math></b> (s)	50±6	41±7	50±7	42±11	48±12	48±7	51±7	46±8
<b>EPOC<sub>τ<sub>1</sub></sub></b> (L)	0.7±0.1	0.7±0.1	0.9±0.2	0.8±0.3	0.9±0.2	1.5±0.3 †††, ***	1.0±0.2	1.5±0.2 †††, ***
<b>EPOC<sub>τ<sub>1</sub></sub></b> [L/(kg BM <sup>b</sup> · exp(a + c · age))]	1.02±0.12	1.07±0.20	1.03±0.2	0.94±0.27	0.97±0.15	1.12±0.18 ††, ***	1.06±0.17	0.97±0.14 †

<b>EPOC<math>\tau_1</math></b> [L/(kg LBM <sup>b</sup> · exp(a' + c' · age)]	1.03±0.10	1.09±0.16	1.03±0.19	0.94±0.26	0.95±0.15	1.06±0.16	1.08±0.15	1.01±0.15
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624 EPOC<sub>8</sub>: excess post-exercise oxygen consumption calculated for 8 minutes after a 60-s all-out rowing exercise; AOD: accumulated oxygen deficit;  
625 BM: body mass; LBM: lean body mass;  $\tau_1 \dot{V}O_2$ :  $\dot{V}O_2$  recovery time constant obtained from a bi-exponential model; EPOC $\tau_1$ : excess post-exercise  
626 oxygen consumption calculated until  $\tau_1 \dot{V}O_2$  was reached. Values are presented as mean ± SD. †, ††, †††: significantly different from the group 1 within  
627 each sex category at  $p < 0.05$ ,  $p < 0.01$ , and  $p < 0.001$ , respectively. \*\*\*: significantly different from girls within each age group at  $p < 0.001$ . AOD  
628 was calculated on one girl and four boys less for technical reasons.

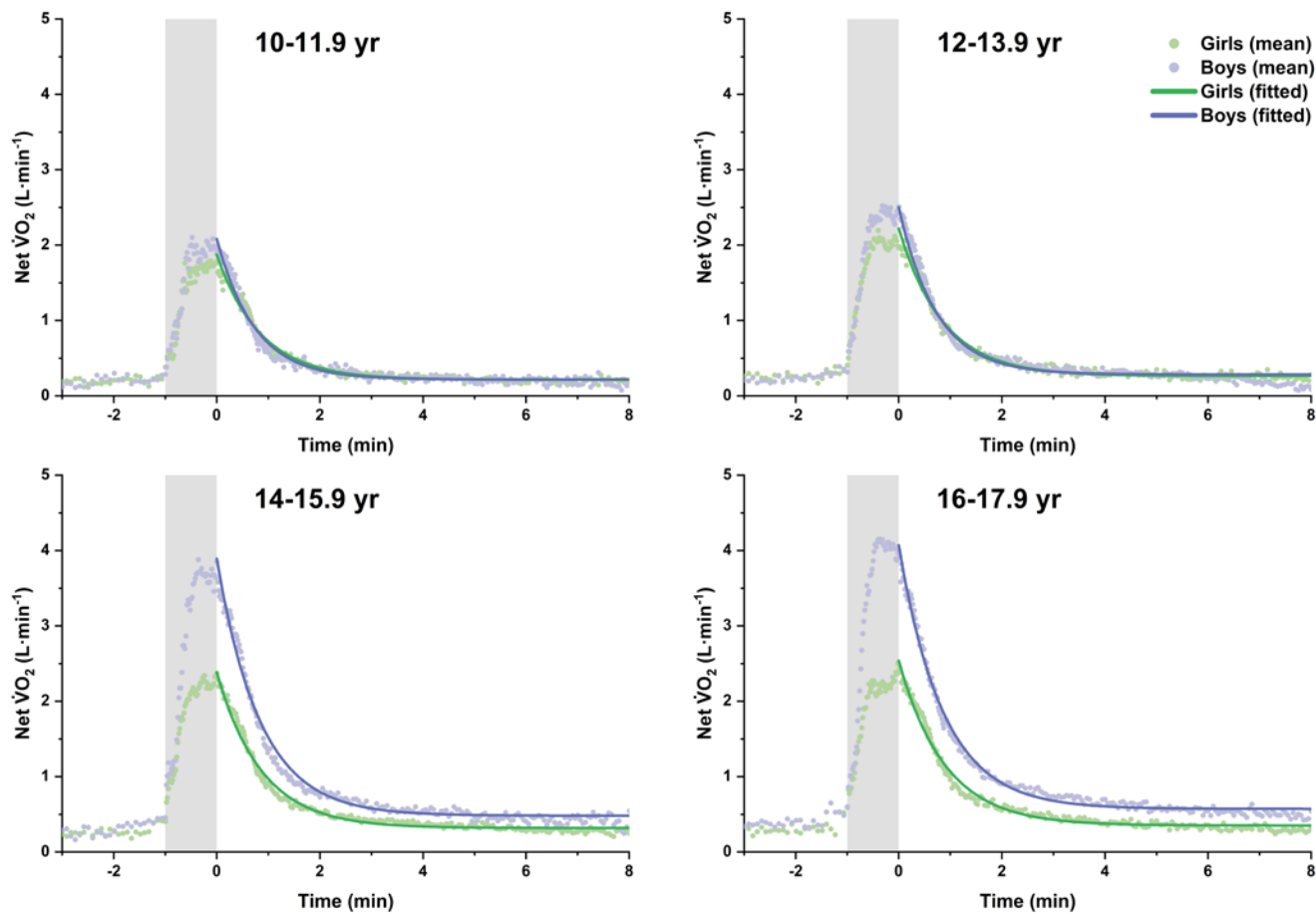
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631 **FIGURE LEGEND**

632 **Figure 1:** Oxygen uptake ( $\dot{V}O_2$ ) during and following an all-out 60-s rowing test in boys and girls 10-17 years  
633 of age.  $\dot{V}O_2$  recovery kinetics were modelled using a bi-exponential function.  $\dot{V}O_2$  values are presented as net  
634 values, *i.e.* minus baseline. Grey zone corresponds to the 60-s all-out rowing exercise.



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