

1 **Comments on the calculation of the specific growth rate in experiments with untagged**
2 **individuals**

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25 ABSTRACT

26 The specific growth rate, G , is widely used in articles dealing with the growth of aquatic
27 organisms under experimental conditions. When individuals are untagged, the arithmetic
28 mean of G for a group of animals must be calculated from weight geometric means, not from
29 arithmetic means. The type of weight mean used in articles to calculate the arithmetic mean of
30 G is usually not reported, and an extended use of weight arithmetic means is common. The
31 arithmetic mean of G so calculated is biased according to the increment in the squared
32 coefficient of variation of body weights. Another potential bias in the calculation of the
33 arithmetic mean of G is size-dependent mortality; this bias cannot be avoided when
34 individuals are untagged, but maximal and minimal values can be obtained. In summary, in
35 view of these analytical results, it seems prudent to calculate the arithmetic mean of G for a
36 group of untagged animals from geometric means of weights, and to estimate the maximal
37 error due to the possibility of size-dependent mortality whenever possible.

38

39 The specific growth rate, G , is currently used to investigate growth patterns and growth
40 correlates in both basic (Pelletier et al. 1995, Lefébure et al. 2011) and applied research
41 (Fontagné et al. 2009) on aquatic organisms. The index is based on the concept of
42 proportional growth and, for one individual, it can be defined as the arithmetic mean of the
43 instantaneous relative growth rate, dW/Wdt , over a finite time interval $[0, t]$. This simplicity
44 trades-off against a number of dependencies on internal (body weight, genetic background)
45 and environmental factors (temperature, diet) (Allen and Wootton 1982, Rabí and Maraví
46 1997, Björnsson and Steinarsson 2002, Lefébure et al. 2011). These dependencies make up
47 the core of a number of papers dealing, for example, with fish growth: in basic research, the
48 functional expressions connecting G and body size for a given species is frequently explored
49 by means of correlation analyses in order to obtain a model for the growth trajectory
50 (Björnsson and Steinarsson 2002); in applied research, G is widely used not to model growth,
51 but to assess the performance of different treatments *a posteriori* (Fontagné et al. 2009,
52 Collins et al. 2013).

53
54 Whatever the topic under investigation may be, it is necessary to calculate G according to its
55 definition. In our view, if G is based on mean body weights, it should be based on geometric
56 means of weight, otherwise the worked out value can be biased. The geometric mean for a
57 numerical series is always lower than or as large as the arithmetic mean for the same series,
58 the size of this difference approximately depending on the coefficient of variation for the
59 considered set of numbers; thus a change in the coefficient of variation of fish weights over
60 the experimental time can cause a bias in the calculation of G . The type of weight mean
61 inserted in the formula of G is not always clear in scientific literature. It is often stated that
62 averages are used, so that an appraisal of the effect of inserting arithmetic means of weight in
63 the formula of G seems to be prudent at the moment. In the case of experiments with tagged

64 or individually reared animals, no bias exists if G is obtained from individual growth rates,
65 but geometric means are necessary in the case of populations comprising untagged individuals
66 reared in groups.

67

68 We would like to address the present comment to researchers mainly concerned with
69 experimental designs on growth of aquatic organisms. No new growth index is proposed in
70 this note. On the contrary, it is intended to briefly show our point of view about two types of
71 biases potentially affecting the calculation of the well-known specific growth rate (biases that
72 cannot be corrected during the statistical analysis of data) and to suggest a few
73 recommendations in the calculation of such a growth index, mainly when conducting
74 experimentation on juvenile animals kept in small groups. Let us now consider two situations
75 of increasing complexity with untagged animals reared in the same population.

76

77 UNTAGGED FISH WITHOUT MORTALITY

78 Suppose a group of n untagged juvenile individuals in the same tank so that, as in many
79 experiments with fish, n is not very high and body weights can be easily recorded for all
80 animals at the first and the last samplings. In addition, suppose there is no mortality. In such a
81 simple experimental situation the arithmetic mean of individual specific growth rates, G , will
82 be,

83

$$84 \quad G = \frac{1}{n} \sum_i G_i = \frac{1}{n} \sum_i \frac{1}{t} (\ln W_{i,t} - \ln W_{i,0}) = \frac{1}{t} \left(\frac{1}{n} \sum_i \ln W_{i,t} - \frac{1}{n} \sum_i \ln W_{i,0} \right)$$

85

86 Since the summation of the logarithms of i numbers equals the logarithm of the product of
 87 those i numbers and, in addition, the product of a constant by a logarithm can be written as the
 88 logarithm of a power expression, it is now possible to write,

89

$$90 \quad G = \frac{1}{t} \left[\frac{1}{n} \ln \left(\prod_i W_{i,t} \right) - \frac{1}{n} \ln \left(\prod_i W_{i,0} \right) \right] = \frac{1}{t} \left[\ln \left(\sqrt[n]{\prod_i W_{i,t}} \right) - \ln \left(\sqrt[n]{\prod_i W_{i,0}} \right) \right]$$

91

92 By definition, the n -root of the product of i numbers is the geometric mean of those i
 93 numbers. Thus if μ_t and μ_0 denote the geometric means of the final and initial individual
 94 weights, the final expression of G becomes,

95

$$96 \quad G = \frac{\ln \mu_t - \ln \mu_0}{t} = \frac{\ln(\mu_t / \mu_0)}{t}$$

97

98 The above expression is very similar to that for the specific growth rate for one individual,
 99 except that individual weights have been replaced by geometric means. If initial and final
 100 arithmetic means of body weights are used instead of geometric means, a bias is produced in
 101 the calculation. The quantity of this bias will depend on the change in the squared coefficient
 102 of variation for body weights, as explained as follows. The geometric mean, μ , can be
 103 approximated by developing the terms $\ln W_i$, where W_i represents each individual weight, as a
 104 Taylor series centred at the value M , where M is the arithmetic mean of individual weights;
 105 then taking expectations, $E[\]$,

106

$$107 \quad \ln \mu = \ln M + \sum_{i=1}^{\infty} \frac{(-1)^{i+1}}{i M^i} E[(W_i - M)^i]$$

108

109 The Taylor series will be developed till the third term to obtain an approximation based on the
 110 arithmetic mean and variance of body weights; keeping in mind that the second term is zero,
 111 the looked for expression is (Jean and Helms 1983),

112

$$113 \quad \ln \mu \approx \ln M - 0.5 \frac{V_w}{M^2} = \ln M - 0.5 C^2$$

114

115 In the above approximation, V_w denotes the variance in fish weights and C sets for the
 116 coefficient of variation of fish weights. Now, substituting the above approximation into the
 117 expression of the true mean G ,

118

$$119 \quad G = \frac{\ln \mu_t - \ln \mu_0}{t} \approx \frac{\ln M_t - \ln M_0 - 0.5 (C_t^2 - C_0^2)}{t}$$

$$120 \quad G_M \approx G + 0.5 \frac{\Delta C^2}{t}$$

121

122 where G_M is the growth rate as affected by the bias due to the use of arithmetic means of fish
 123 weights. The following results are now apparent:

124

$$125 \quad \text{i) } \quad \Delta C = 0 \Rightarrow G_M = G$$

$$126 \quad \text{ii) } \quad \Delta C > 0 \Rightarrow G_M > G$$

$$127 \quad \text{iii) } \quad \Delta C < 0 \Rightarrow G_M < G$$

128

129 The relative bias, $100 \times (G_M - G)/G$, can be calculated as

$$130 \quad 100 \frac{G_M - G}{G} \approx 100 \frac{\Delta C^2}{2 \ln(M_t/M_0) - \Delta C^2}$$

131

132 For example, Petursdottir (2002) performed a series of experiments on the growth of tagged
133 individuals of the arctic charr *Salvelinus alpinus* (Linnaeus 1758); the ratio M_t/M_0 was in the
134 range 1.8-2.1, and the initial and final coefficients of variation of fish weights were
135 approximately 6.6% and 33%; if the experiments had been conducted with untagged fish, the
136 relative bias due to the arithmetic mean would have been in the range 7-10%.

137

138 UNTAGGED FISH WITH MORTALITY

139 Let us now think of a more complex but also more frequent experimental situation with
140 juvenile animals: a group of untagged fish in the same container, whose body weights are
141 recorded from time 0 to time t and with mortality in the same time interval; in addition,
142 suppose geometric means are used instead of arithmetic ones, so that the bias due to the
143 arithmetic mean can be ruled out. In this case, there is still a potential bias in the calculation
144 of G , because the first sampling includes both dead fish and fish surviving to time t . This fact
145 was early recognized in the field of fisheries research (Ricker 1975) and later on, and perhaps
146 inconspicuously, in the field of fish culture (Otterå 1992). Moreover, some authors have
147 followed the “mortality of the smaller” principle (Folkvord and Otterå 1993) to correct this
148 potential bias in G .

149

150 The size of the selective mortality bias can be expressed as a function of fish size in the
151 surviving and dead populations. This goal can be attained by splitting the factors within $\ln\mu_0$
152 (i.e. within the geometric mean of fish weights at time 0), into two groups according to the
153 survival or non-survival of each individual and then rewriting the expression of G ,

154

155
$$\ln \mu_0 = \ln \sqrt[n]{\prod_i W_{i,0}} = \frac{1}{n} \ln \left(\prod_{j \in \text{surviving}} W_{j,0} \right) + \frac{1}{n} \ln \left(\prod_{k \in \text{dead}} W_{k,0} \right)$$

156

157 Let s and d be the number of surviving and dead animals respectively, μ_s and μ_d the geometric
 158 mean weights at time 0 of the surviving and dead individuals in the interval $[0, t]$ respectively,
 159 and $m = d/n$ the proportional mortality, then,

160

$$\ln \mu_0 = \frac{s}{s} \frac{1}{n} \ln \left(\prod_{j \in \text{surviving}} W_{j,0} \right) + \frac{d}{d} \frac{1}{n} \ln \left(\prod_{k \in \text{dead}} W_{k,0} \right)$$

161

$$\ln \mu_0 = (1 - m) \ln \mu_s + m \ln \mu_d$$

162

163 Therefore, it is possible to obtain an analytical expression for the bias, $G_m - G$ (where G_m
 164 denotes the mortality-biased growth rate) as a function m , μ_s and μ_d . Firstly, consider the
 165 expression for G calculated irrespective of the mortality,

166

167
$$G_m = \frac{\ln \mu_t - \ln \mu_0}{t}$$

168 Secondly, substitute the expression of $\ln \mu_0$ in G_m ,

169

170
$$G_m = \frac{\ln \mu_t - \ln \mu_s + m (\ln \mu_s - \ln \mu_d)}{t}$$

171

172 At last, after some rearrangements, the relationship between G_m and G becomes,

173

174
$$G_m = G + m \frac{\ln \mu_s - \ln \mu_d}{t}$$

175

176 It is now apparent that, the potential bias is dependent on the quotient of geometric mean
177 weights of surviving and dying subpopulations. To our knowledge, this is a new result. Under
178 positive mortality, three statements can be derived from the above expression,

179

180 i) $\mu_s = \mu_d \Rightarrow G_m = G$

181 ii) $\mu_s > \mu_d \Rightarrow G_m > G$

182 iii) $\mu_s < \mu_d \Rightarrow G_m < G$

183

184 In practice, because the values of μ_s and μ_d remained unknown in experiments with untagged
185 fish, the size of the selective mortality bias, $G_m - G$, cannot be precisely estimated.
186 Nevertheless, in the case of a researcher interested in getting an approximation to the actual
187 value of G and acquainted with the exact mortality in the experiment, it can be suggested to
188 calculate a maximum G value assuming that only the largest animals at the initial time died
189 during the interval $[0, t]$, and also a minimum G value under the assumption that only the
190 smallest animals at the initial time died during $[0, t]$. Thus the following estimation for the
191 arithmetic mean of G can be useful for such an experimenter,

192

193
$$G = \frac{G_{\max} + G_{\min}}{2}$$

194

195 Except for the introduction of geometric means, the above expression is an extension of
196 Folkvord and Otterå (1993) correction, but it would be more appropriate when the validity of
197 the “mortality of the smaller” principle is not clear. If the researcher is also interested in
198 evaluate the goodness of the experimental measurement, the length of the semi-interval can be
199 proposed as the maximal value of the error:

200

$$201 \quad Error = \pm \frac{G_{\max} - G_{\min}}{2}$$

202

203 LIMITATIONS TO THE PROPOSED CORRECTIONS

204

205 It should be noted that in experimental scenarios where it is not possible to sample the whole
206 population, for example when working with larval stages, the uncertainty of the calculated
207 specific growth rate is also affected by the sampling error. Therefore, the uncertainty in G will
208 also depend on the statistical distribution of the selected metric variable, more specifically, on
209 the shape of the distribution of $\ln W$ or $\ln L$. On the other hand, when the mortality rate is
210 above zero, the calculation of G_{\max} and G_{\min} will in addition require knowing the true
211 distribution of the population, these complications being beyond the scope of this comment.

212

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