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On the exponent in the von Bertalanffy growth model

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Bertalanffy proposed the differential equation $m'(t) = p \times m(t)^a - q \times m(t)$ for the description of the mass growth of animals as a function $m(t)$ of time t. He suggested that the solution using the metabolic scaling exponent $a = 2/3$ (von Bertalanffy growth function VBGF) would be universal for vertebrates. Several authors questioned universality, as for certain species other models would provide a better fit. This paper reconsiders this question. Using the Akaike information criterion it proposes a testable definition of 'weak universality' for a taxonomic group of species. (It roughly means that a model has an acceptable fit to most data sets of that group.) This definition was applied to 60 data sets from literature (37 about fish and 23 about non-fish species) and for each dataset an optimal metabolic scaling exponent $0 \le a_{opt} < 1$ was identified, where the model function $m(t)$ achieved the best fit to the data. Although in general this optimal exponent differed widely from $a = 2/3$ of the VBGF, the VBGF was weakly universal for fish, but not for non-fish. This observation supported the conjecture that the pattern of growth for fish may be distinct. The paper discusses this conjecture.

1 **On the exponent in the von Bertalanffy growth model**

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8

9 **Abstract**. Bertalanffy proposed the differential equation $m'(t) = p \cdot m(t)^a - q \cdot m(t)$ for the description of the mass growth
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18 but not for non-fish. This observation supported the conjecture that the pattern of growth for fish may be distinct. The
19 paper discusses this conjecture.

20 **Keywords**: Akaike's information criteria (AIC), multi-model inference, von Bertalanffy growth function (VBGF),
21 metabolic scaling exponent, weak universality

1. Introduction

23 **Growth models**: Size at age is a key metric of productivity for any animal population (MacNeil
24 et al., 2017) and since Verhulst' (1838) seminal work about the logistic function a wide range of
25 growth models to describe the size of animals as a function of time has been developed. Amongst
26 applications are improved otolith analysis for age estimation (Ashworth et al., 2017, based on
27 Vigliola and Meekan, 2009) or stock assessments in fisheries management (Juan-Jorda et al.,
28 2015). The resulting information about life history and population structure has been applied e.g.
29 in ecology, where the age structure of coral reef destructing starfish populations was reconstructed
30 from size measurements and used to explain outbreaks (Pratchett, 2005).

31 Of particular interest are models based on biological principles. One class of such models was
32 developed by Bertalanffy (1957) and Pütter (1920), who formulated a differential equation of
33 ontogenetic growth (assuming $0 \le a < b$; this paper assumes in addition $b = 1$):

34   (1) $\frac{dm(t)}{dt} = p \cdot m(t)^a - q \cdot m(t)^b$

35 Equation (1) aims at explaining the allocation of metabolic energy between growth and sustenance
36 of an organism: If $m = m(t)$ is body mass (weight) at age t, then the body utilizes resources at a
37 metabolic rate $(p \cdot m^a)$ for growth, except for the resources allocated to the operation and
38 maintenance of existing tissue $(q \cdot m^b)$. The parameters p and q are positive scaling constants
39 obtained by fitting the model curve (1) to growth data. Growth functions described by equation (1)

40   with $a > 0$, $q > 0$ are bounded and of a sigmoid shape with an asymptotic weight limit $m_{max} =$
41   $(p/q)^{1/(b-a)}$; the inflection point is assumed, when body mass reaches the fraction $(a/b)^{1/(b-a)}$ of that
42   weight limit (the right hand side of the differential equation and its derivative, respectively,
43   vanish).

44   In general, the equation (1) can only be solved with elliptic functions (Ohnishi et al., 2014).
45   Bertalanffy (1957) provided an explicit solution of equation (1) for exponents $0 \le a < b = 1$ with
46   elementary functions (exp = exponential function):

47   $$(2) \quad \left(\frac{m(t)}{m_{max}}\right)^{1-a} = 1 - \left(1 - \left(\frac{m_0}{m_{max}}\right)^{1-a}\right) \cdot \exp(-q \cdot (1-a) \cdot t)$$

48   Formula (2) explains growth in terms of the asymptotic weight limit (mature body mass) m_{max} and
49   the initial value (neonate weight) $m_0 = m(0)$. This choice of parameters follows a recommendation
50   of Cailliet et al. (2006). Richards (1959) provided another solution of (1) for $b > a = 1$ to model
51   plant growth (e.g. Verhulst's model: $a = 1$, $b = 2$).

52   **Is there a true exponent?** This paper asks, if the growth of different species needs to be modeled
53   by different metabolic scaling exponents $a < 1$ in equation (2). The null hypothesis would state
54   that on the contrary a certain universal metabolic exponent would suffice.

55   To resolve this question, the growth model (2) was applied to 60 data sets and best fit exponents
56   a_{opt} together with suitable parameters m_0, m_{max} and q were determined, using nonlinear regression
57   by means of the method of least squares. As is illustrated by Figure 1, for certain data sets the
58   choice of the optimal exponent resulted in a clear improvement of the fit.

59   **INSERT Figure 1**: Comparing the fit of model (2) with different exponents to growth data

60   Several concrete values of the metabolic scaling exponent for the model (2) have been discussed
61   in literature and the question, if the true exponent would be $a = 2/3$ or $a = ¾$ has been a topic of
62   scientific controversy (Isaac and Carbone, 2010).

63   Bertalanffy (1934, 1949, 1957) suggested that model (2) with $a = 2/3$ would describe the growth
64   of vertebrates; this defines the classical von Bertalanffy growth function (VBGF). Bertalanffy
65   derived it from equation (1) by the following reasoning: Anabolism (synthesis for growth) would
66   be proportional to the $2/3^{th}$ power of body weight ($a = 2/3$), as the oxygen consumption would be
67   proportional to surface ($2/3^{th}$ power of volume), whereas catabolism (energy use for the
68   maintenance of biomass) would be proportional to body weight ($b = 1$). This choice of exponents
69   was supported e.g. by Banavar et al. (2002) and White and Seymour (2003).

70   Bertalanffy identified also species, where growth would be better described by model (2) with an
71   exponent $a = 0$. This is the model of bounded exponential growth, where $m_{max}-m(t)$ is described
72   by the model of exponential decay. Further, Bertalanffy observed that if mass growth is described
73   by the VBGF and if mass is assumed to be proportional to the third power of length, then the
74   growth of length is modeled by bounded exponential growth. And conversely, if length grows
75   according to the bounded exponential growth model, then mass growth is described by the VBFG.
76   In this sense these two models are equivalent and in literature both models are referred to as VBGF.
77   (For this paper, VBGF is defined by the exponent $a = 2/3 \approx 0.67$.)

78   West et al. (2001) proposed an alternative to the VBGF. They argued, that growth would better be
79   described by the model function (2) with exponent $a = \frac{3}{4}$, as the number of capillaries would be
80   proportional to the $\frac{3}{4}$th power of the number of cells. This model was supported by Darveau et al.
81   (2002). A metabolic exponent $a = \frac{3}{4}$ had been suggested already earlier by Kleiber (1947).

82   However, more recent literature observed that no single metabolic exponent may be exactly correct
83   and that perhaps the exponent may be unrelated to metabolism. (Noisy data may hide it; c.f. Batt
84   and Carpenter, 2012.) As Killen et al. (2010) and White (2010) observed, for different species
85   there were different optimal exponents a_{opt}. Also for the same species different data sets supported
86   different exponents. Amongst the stated reasons were environmental factors (e.g. food
87   composition, temperature); c.f. Kimura (2008), Porch (2002), Quince et al. (2008), Stewart et al.
88   (2013), or Yamamoto and Kao (2012). Further, asking for exponents that would be characteristic
89   for a species may be ill-posed. For, due to random fluctuations one can expect that the best fit
90   exponents for different samples for the same species might not be exactly the same. As Shi et al.
91   (2015) observed, for some data sets a near-optimal fit could be achieved by a wide range of
92   exponents, whence such fluctuations might lead to the identification of widely different optimal
93   exponents.

94   **INSERT Figure 2**: Akaike weights for different exponents, when compared to the optimal exponent

95   Thus, the identification of an optimal exponent alone may be misleading, if there is no additional
96   information about the achieved goodness of fit to the data. This paper applies Akaike's information
97   criterion (more specifically the Akaike weight) for this purpose. Given an optimal exponent a_{opt}
98   computed for a certain data set and a hypothesized universal exponent a_{univ}, the Akaike weight
99    $prob(a_{univ})$ is the probability that the model (2) using the universal exponent a_{univ} is true, when
100   compared with the optimal exponent a_{opt}. Figure 2 displays the Akaike weights for a certain
101   dataset.

102   **Problem of the paper**: Summarizing, the above informal question may be recast into the following
103   testable form. Given a data set, a metabolic exponent $0 \leq a < 1$ is refuted for this data set, if in
104   comparison to the optimal exponent for model function (2) its Akaike weight is below 2.5%. Given
105   a taxonomic group of species (e.g. 'all fish'), then an exponent is weakly universal for this group,
106   if with 90% confidence at least 90% of randomly chosen data sets from this group do not refute
107   that exponent.

108   Variants of the definition of 'weak universality' can be obtained with different thresholds; the
109   present percentages were used for the proof of principle, only. The notion of refutation remains
110   meaningful, if the Akaike weight is merely used as an index for the goodness of fit, as in that case
111   'below 2.5%' defines the 5% of the index values with the worst fit. Further, the use of confidence
112   limits in the definition leaves room for alternative models for exceptional species and it
113   acknowledges that certain data sets may not be appropriate for further analysis by growth models
114   of type (2), whence such exceptional data sets should not refute a universal exponent. In view of
115   the unknown distributions, this paper uses Clopper-Pearson confidence limits (Casella and Berger,
116   2001), which are conservative (higher confidence, than nominally stated) and also suitable for

117   small sample sizes (as for the proof of principle small samples suffice, whereby a sample consists
118   of different data sets).

119   Of particular interest is the question, if the exponent $a = 0.67$ of the VBGF is weakly universal for
120   fish. For, the VBGF is widely used to describe the growth of fish and many authors reported an
121   excellent fit (e.g. Koch et al., 2015). For instance, the FishBase database (Frose and Pauly, 2017)
122   presumes VBFG and lists growth parameters for 2320 species. A search in Google Scholar (August
123   2018: combining with AND the key phrases Bertalanffy, 'growth model', 'fish growth') identified
124   approximately 24,800 papers. Smart et al. (2016) surveyed the literature about growth of
125   elasmobranch species (e.g. sharks) and the VBGF (with or without prescribing an initial value for
126   size at $t = 0$) was studied twice as often as any other model.

127   ## 2.   Materials and methods

128   **Choice of the growth model**: Model (2) has been chosen for this study, as its metabolic scaling
129   exponent is believed to have a biological meaning. This distinguishes it from simpler models
130   recommended in literature for data interpolation, such as power-laws between size and age
131   (Katsanevakis and Maravelias, 2008).

132   Another feature is the sigmoid shape: For model (2) with exponent $a > 0$ the rate of mass growth
133   increases, as size increases, until it reaches a maximal rate (inflection point) and then decreases
134   towards zero as mass approaches the asymptotic weight limit m_{max}. Whether the growth data show
135   a sigmoid shape can be verified graphically by a Walford plot (Figure 3) of growth rate over size
136   (unimodal curve, peaking above the weight at the inception point).

137   Further, despite its dependency on merely three parameters plus the metabolic exponent, model
138   (2) is flexible enough to represent growth curves of different sigmoid shapes and it is amenable to
139   data fitting by means of spreadsheets. Spreadsheets may be used also for more complex models, if
140   numerical solutions of differential equations (e.g. Leader, 2004) are used, but then numerical errors
141   would require further analysis.

142   In literature there are different parametrizations of model (2). In relation to the parameters of
143   equation (1), assuming $b = 1$ and using the formula for m_{max}, $p = q \cdot m_{max}^{1-a}$. The constant in the
144   exponent of (2), $q \cdot (1-a)$, corresponds to the 'growth coefficient' k. Further, several papers used a
145   time shift t_0 to eliminate the multiplicative constant in (2). However, t_0 might not have a biological
146   meaning (Schnute and Fournier, 1980). The main difference between the model curves (2) for
147   different exponents was the weight at the inflection point, varying between 0% and 37% of m_{max}
148   (limits of $a^{1/(1-a)}$ for exponents $a \rightarrow 0$ and $a \rightarrow 1$).

149   **INSERT Figure 3**: Weight increase and its approximation by a VBGF

150   **Data sources**: The authors considered only age-mass or age-length (for most fish) data. The main
151   sources were Parks (1982), Ogle (2017) and the supporting information of West et al. (2001). The
152   authors supplemented them by data from other literature sources or from data obtained by personal
153   communications. Data in diagrams were retrieved by means of digitalization (Digitize-It of
154   Bormisoft®).

155　For easier identification, data sets were numbered as follows.

156　The original published sources of the data for fish were Cubillos et al. (2001) for #1 Anchoveta
157　(*Engraulis ringens*), #2 Araucanian Herring (*Strangomera bentincki*) and #26 Sardine
158　(*Strangomera bentincki*); Jørgensen (1992) for #3 Atlantic (Arctic) Cod (*Gadus morhua*); Maceina
159　(2007) for #5 Blue Catfish (*Ictalurus furcatus*); Stewart et al. (2013) for #6-7 female and male
160　Australian Bonito (*Sarda australis*); Abad (1982) for #9 Sea (Brown) Trout (*Salmo trutta fario*);
161　Parker et al. (2007) for #10 Bull Trout (*Salvelinus confluentis*), whereby the authors removed an
162　outlier; Mooij et al. (1999) for #13 European Perch (*Perca fluviatilis*); Brown and Rothery (1993)
163　for #14 time-weight data of Guppy (*Poecilia reticulate = Lebistes reticulatus* in the source);
164　Yildirim (2003) for #16 Jonubi (*Chalcalburnus mossulensis*); Jobes (1946) for the meanwhile
165　extinct #20 Longjaw Cisco (*Coregonus alpenae = Leucichthys alpenae* in the source) at two
166　locations; Vaughan & Helser (1990) for #21 Red Drum (*Sciaenops ocellatus*); Moreau (1979) for
167　#22 Redbreast Tilapia (*Coptodon rendalli = Tilapia rendalli* in the source); Wolfert (1980) for #23
168　Rock Bass (*Ambloplites rupestris*); Bailey (1963) for #24 Round Whitefish (*Prosopium
169　cylindraceum*); West et al. (2001) for #25 time-weight data of Sockeye Salmon (*Oncorhynchus
170　nerka*); Grabowski et al. (2012) for #29 Spotted Sucker (*Minytrema melanops*); Krüger (1973) for
171　#30 Atlantic Bluefin Tuna (*Thunnus thynnus*); House and Wells (1973) for #31 Troutperch
172　(*Percopsis omsicomaycus*); Ianelli et al. (2011) for #33 Walleye Pollock (*Theragra
173　chalcogramma*); Araujo and Martins (2007) for #34-35 female and male White Grunt (*Haemulon
174　plumierii*); Gomez-Requeni et al. (2010) for #36 time-weight data of male Zebrafish (*Danio rerio*)
175　and Kaushik et al. (2011) for #37 Zebrafish larvae.

176　Further fish data originated from other resources of Ogle (2017) for #4 female Black Drum
177　(*Pogonias cromis*), #8 Sea (Brown) Trout (*Salmo trutta*) and Rainbow Trout (*Oncorhynchus
178　mykiss*), #11 Cabezon (*Scorpaenichthys marmoratus*), #12 Atlantic Croaker (*Micropogonias
179　undulatus*), #15 Jackass Morwong (*Nemadactylus macropterus*), #17 Lake Erie Walleye (*Sander
180　vitreus*), #18-19 female and male Arctic Lake Trout (*Salvelinus namaycush*), #27-28 female and
181　male Siscowet Lake Trout (*Salvelinus namaycush*), and #32 Virgina Spot (*Leiostomus xanthurus*).

182　The original published sources of the data for non-fish species were Brody (1945) for #38 Cattle
183　(*Bos primigenius taurus*), #40 Chicken (*Gallus gallus domesticus*) and #57 Rat (*Rattus rattus*);
184　Grossmann (1969) for #42 Rhode Island chicken, Ricard (1975) for #44-46 about chicken strains
185　X33, X38 and X44; Elke Schläger (personal communication) for #47 Rhodesian Ridgeback dog
186　(*Canis lupus familiaris*), Renner-Martin et al. (2016) for #50 Domestic Pig (*Sus scrofa domestica*);
187　Sturm (2003) for Cricket larvae #51 (*Acheta domesticus*), #52 (*Gryllus assimilis*) and #53
188　(*Teleogryllus commodus*); Owen (1960) for #54 Heron (*Ardea cinerea*) and #58 Robin (*Erithacus
189　rubecula*); Fabian Bader (personal communication) for #55 Ball Python (*Python regius*); Forsyth
190　(1976) for #59 Shrew (*Sorex cinereus*); and Rudstam (1989) for #60 Shrimp (*Mysis mixta*).

191　Further non-fish data originated from unpublished resources of Parks (1982) for #39 Friesian
192　cattle, #41 and #43 about Apollo and Ross Fryer chicken, #48-49 female and male Great Dane
193　dogs, and #56 albino rats.

194   **Data selection and preprocessing**: Only data sets with $N = 6$ or more points of time were
195   considered, regardless of how many animal observations were available for each point of time.
196   Amongst data sets removed for this reason were Channel Darter (*Percina copelandi*) and Creek
197   Chub (*Semotilus atromaculatus*) from Ogle (2017) based on Reid (2004) and Quist et al. (2012).

198   For non-fish species, the authors did not consider (hunting or capturing) data of wildlife (e.g. Read
199   et al., 1993, for Bottlenose Dolphin; Pei, 1996, for Muntjak Deer; or Smuts, 1975, for Burchell's
200   Zebra), where animal age was estimated. However, for fish, data sets using age estimates were not
201   removed. Consequently, for fish spawning time caused age uncertainties (Datta and Blanchard,
202   2016).

203   In order to use data of the same format, data were transformed into mean-weight-at-time data.
204   Most data for non-fish species were of this form. For fish, most data were about length. Empirical
205   evidence suggested that for fish mass may be related to length by an allometric power relation $m(t)$
206   $= c \cdot l(t)^p$ with $2.5 < p < 3.5$ and some constant c (Pauly, 1979; Anderson and Neumann, 1996). The
207   paper approximated mass for all time-length data by the third power of length. This convention
208   was in line with Bertalanffy (1934, 1957) and it avoid mixing up information from different
209   sources about time-length and length-mass relations. The direct comparison of length data between
210   e.g. fish and birds was avoided, as 'length' was ambiguous (e.g. Holden and Raid, 1974: standard
211   length, fork length, total length).

212   Further, the search for data was confined to data of the growth from an early point in life (birth)
213   till the end of the growth phase (e.g. sexual maturation). For otherwise, as is illustrated by Figure 4,
214   a data set might not capture the full phase of growth, and the modeling of a growth curve would
215   depend on extrapolation. This has been an issue for one data set (Figure 5).

216   **INSERT Figure 4**: Dependency of the optimal exponent on which phase of growth was observed

217   **INSERT Figure 5**: Weight increase and approximation by a logistic model, i.e. (1) with $a = 1$, $b = 2$

218   **Statistical methods**: Generally, computations were done in Microsoft® EXCEL. Casella and
219   Berger (2001) was used as a standard reference for statistics and XL-Stat of Addinsoft® for
220   statistical computations.

221   For Clopper-Pearson confidence limits, given a sample of size M (here the number of data sets)
222   and amongst them m ones with a specific property (here the number of data sets not rejecting a
223   certain exponent), then using the beta distribution and EXCEL notation, the one-sided lower 90%-
224   confidence limit and the upper 90%-confidence limit for the frequency of this property in the
225   population were $1–\text{BETA.INV}(0.9; M–m+1; m)$ and $\text{BETA.INV}(0.9; m+1; M–m)$.

226   **Data fitting**: The paper used nonlinear regression by means of the method of least squares. Given
227   an exponent in $0 \le a < 1$, optimal parameter values m_0, m_{max}, and $q > 0$ for model (2) were sought
228   to minimize the sum of squared residuals, *SSR*, between the data points and the model function.
229   (Recall that the squared residual for the nth data point (t_n, m_n) is $(m_n–m(t_n))^2$.) Optimization used
230   the SOLVER Add-In of Microsoft EXCEL, which implemented an iterative optimization method
231   (Newton's method).

232   Next, the paper sought to obtain an optimal exponent, where $SSR = SSR(a)$ was minimal; the
233   desired accuracy for the exponent was 1/100. Therefore, using a macro the optimization was
234   repeated for each exponent $a = 0$, 1/100, 2/100, … 99/100 and the resulting minimal values of
235   $SSR(a)$ were tabulated. Summarizing, this defined an optimal exponent $a_{opt} < 1$ and optimal
236   parameter values m_0, m_{max}, and q for this exponent.

237   **INSERT Figure 6**: Transformation of time-mass-data and a regression line for the transformed data set

238   A disadvantage of the present method, when applied to the considered data, was numerical
239   instability. Therefore, optimization was done in two steps, whereby in the first step good initial
240   estimates of the optimum parameters were computed by adapting a graphical method (Figure 6),
241   the Bertalanffy-Beverton plot (Bertalanffy, 1934). It aims at an optimal fit of the weight-time data
242   to the inverse function of (2), described by equation (3) for $t = t(m)$; ln is the natural logarithm
243   function:

244   $$(3) \quad t = \frac{f(m_0) - f(m)}{q} \text{ where } f(x) = \frac{\ln\left(1 - (x/m_{max})^{1-a}\right)}{1-a} \text{ for } x > m_{max}$$

245   Collecting terms not depending on m, this is simplified to equation (4):

246   $$(4) \quad t = A + B \cdot f(m) \text{ with } A = f(m_0)/q, \ B = -1/q$$

247   Assuming a given exponent and a given asymptotic weight limit m_{max}, a linear regression line $t =$
248   $A + B \cdot u$ was fitted to transformed data $(u_n, t_n) = (f(m_n), t_n)$, using the function f of equation (3) and
249   computing A and B with the LINEST function of EXCEL (Figure 6). Its goodness of fit was
250   evaluated by the sum of squared residuals $SSR_{inv}(m_{max})$; it was dependent on m_{max}.

251   Next, the exponent was kept fixed and m_{max} was allowed to vary: The function $SSR_{inv}(m_{max})$
252   decreased rapidly for m_{max} near the observed maximum and was flat for larger values of m_{max}
253   (Figure 7). The SOLVER Add-In minimized this function iteratively (a starting value 1% above
254   the observed maximum weight was chosen). As the optimization used exact formulae for A, B and
255   was done in one dimension (seeking m_{max} with minimal SSR_{inv}), it could be performed fast and
256   with high precision.

257   For a given exponent, this optimization defined m_{max}, A and B, from which $q = -1/B$ and m_0
258   $= m_{max} \cdot (\exp(A \cdot (a-1)/B) - 1)^{1/(1-a)}$ were computed.

259   These values were used as starting values for the second step, the iterative optimization of SSR.
260   Given an exponent a and starting with the above parameter values m_0, m_{max}, and q, these values
261   were successively improved to compute the minimal $SSR(a)$.

262   **INSERT Figure 7**: Optimizing the asymptotic weight limit (fit to weight-time data)

263   The two optimization steps compare as follows: The second step assumed that age was controlled
264   and that the weight observations came from a random sample of animals with a given age; this
265   was the traditional approach towards nonlinear regression. The first step assumed that age was
266   random for a given weight. Piner et al. (2012) compared these methods and recommended the first
267   step as a viable alternative to the traditional approach. Also Sparre and Venema (1988) suggested
268   this method. However, this paper used the traditional approach, as all non-fish data were controlled

269   for age. As for a computationally simpler method, there is a large body of literature using the
270   Walford plot for data fitting (e.g. Espino-Barr et al., 2015), which was explained in Figures 3 and
271   5. However, that method did not always provide good initial estimates.

272   In order to retain m_{max} as an asymptotic limit (and as otherwise the transformed data would not be
273   defined), the constraint that m_{max} should exceed the maximal observed mass was added. As for
274   some data sets the optimal m_{max} was extremely high without substantially improving on SSR_{inv},
275   another constraint was added, that m_{max} should not exceed hundred times the maximal observed
276   mass.

277   **Model comparison**: In order to compare the goodness of fit, for each data set the 100 models
278   corresponding to different exponents $a < 1$ were assessed by means of the Akaike information
279   criterion (Akaike, 1974; Burnham and Anderson, 2002; Motulsky and Christopoulos, 2003), using
280   an index AIC_c for small sample sizes. It was computed from $SSR(a) =$ the sum of squared residuals,
281   $N =$ number of data points, and $K = 4 =$ number of optimized parameters (namely m_0, m_{max}, q and
282   implicitly SSR). The number of data points essentially counted, for how many points of time there
283   were data. (If there were several observations for the same point of time, as e.g. for reported
284   average values, then this was counted as one data point.)

285   $\quad$ (5) $AIC(a) = N.\ln\left(\frac{SSR(a)}{N}\right) + 2 \cdot K + \frac{K \cdot (K+1)}{N-K-1}$

286

287   $\quad$ (6) $prob(a) = \frac{e^{-\Delta/2}}{1+e^{-\Delta/2}}$, where $\Delta = AIC(a) - AIC(a_{opt}) > 0$

288   Formula (6) gives the probability $prob$ (Akaike weight: see Figure 2) that the model with exponent
289   a was true, when compared with the better fitting model with exponent a_{opt}, assuming that either
290   a or a_{opt} would be the true exponent. However, neither exponent may be true and the paper makes
291   no assumption thereabout, as this is not needed for the criterion of refutation: If a model (defined
292   from an exponent a) is refuted, as it fares poorly amongst its 'peers', it is sensible to refute it also
293   for any larger group of models.

294   **Data quality**: Data quality is an elusive concept. This paper quantified it by the indicator FNR,
295   the fraction of non-refuted exponents for model (2). Recall that that 100 exponents $a = 0, 0.1, …,$
296   0.99 were compared and that an exponent was refuted, if $prob(a) < 2.5\%$. If High and Low were
297   the highest and lowest non-refuted exponents (c.f. Tables 1 and 2 below), then FNR was the
298   difference between High and Low plus 0.01.

299   This definition will be justified below by a discussion of certain issues about data quality, which
300   translated into longer intervals of non-refuted exponents.

3.   Results

302   Tables 1 and 2 summarize the fit of model (2) to the 60 fish and non-fish data and Figure 8 plots,
303   for each exponent, confidence intervals for the percentages of non-rejection.

304   **INSERT Table 1**. Optimal exponents and interval of non-refuted exponents for fish data

305   **INSERT Table 2**. Optimal exponents and interval of non-refuted exponents for non-fish data

306 **INSERT Figure 8**: Confidence intervals for the percentage of fish data sets not rejecting an exponent

307 Contrary to the assumption that the metabolic exponent may be characteristic for a species, the
308 best fitting metabolic exponents could differ widely for female and male fish of the same species.
309 (For F and M of Lake Trout in #18-19 of Table 1 the best exponents were 0.69 and 0.28,
310 respectively.) The concept of non-rejection relativized these differences. For, amongst the
311 considered data sets the non-rejection intervals of female and male animals of the same species
312 were overlapping, allowing for the selection of a common exponent suitable for both sexes.

313 Figure 8 generalized this reasoning by counting, for each exponent $0 \leq a < 1$, for how many fish
314 data sets (as percentage) this exponent was not rejected. (Thus, it was counted, for how many lines
315 of Table 1 the exponent was between Low and High.) There was a first peak for exponents 0.66
316 and 0.67, which were not rejected for 36 data sets (97% of 37 data sets). Further, exponents $a \geq$
317 0.9 were not rejected for 97% of the data sets. Under the assumption, that the data sets and species
318 were selected at random from the universe of all fish data sets, statistical reasoning could be
319 applied: For these peak exponents the lower one-sided Clopper-Pearson confidence limit (90%
320 confidence) was 90%. Specifically, with 90% confidence the VBGF (exponent $a = 0.67$) should
321 not be rejected by at least 90% of fish data sets.

322 Hence, based on the present data set, it could be concluded that the VBGF was weakly universal
323 for fish.

324 Notably, for the exponent $a = 0.75$ proposed by West et al. (2001) weak universality for fish could
325 not be established. For the non-fish data, no weakly universal exponent could be identified. Both
326 observation may be explained by the too low number of data sets (resulting in broader confidence
327 intervals).

328 Considering the upper one-sided confidence limits (90% confidence) for the fish data, for
329 exponents $a \leq 0.5$ these were below 89%, whence such exponents might not be weakly universal
330 for fish. For non-fish data the upper confidence limit was below 89% for exponents $a \leq 0.88$
331 whence the VBGF ($a = 0.67$), and more generally any exponent $a \leq 0.88$, might not be weakly
332 universal for non-fish species.

4. Discussion and conclusion

334 **Do fish grow differently from non-fish species?** As noted above, the universality of the VBGF
335 seems to distinguish fish from non-fish species. The authors therefore hypothesized that the pattern
336 of mass growth may differ between fish and non-fish species.

337 **INSERT Table 3**. Contingency of the rejection of the VBGF on the taxonomic group

338 An analysis of the optimal exponents (a_{opt}) provided support for this hypothesis. As the distribution
339 of optimal exponents was unknown, a non-parametric location test was applied (Mann-Whitney
340 test: computations in XL-Stat); it indicated with 95% significance (*p*-value 4.7%) that the mean
341 value of the optimal exponents for fish (0.61) was stochastically lower than the mean value for
342 non-fish (0.79). Further, Table 3 displayed a 99.99% significant contingency for the fit of the
343 VBGF on the taxonomic group (fish or non-fish species).

344   **Review of the data**: The unusual high significance for an ambitious hypothesis not yet found in
345   literature led to the question, if there was some non-biological peculiarity of the fish data that made
346   the refutation of the VBGF more difficult for fish.

347   An obvious difference between fish and non-fish data was the transformation of length to weight,
348   which was needed for most fish. This paper used a power-law transformation $m(t) = l(t)^p$ with $p =$
349   3 for fish. As Figure 9 illustrates, this convention could have affected refutations, but it could not
350   explain a systematic bias towards easier or more difficult refutations. (In the figure, higher/lower
351   values of p make refutations easier/more difficult. However, for some data, the 'true' p was below
352   3 and for others it was above 3.) Further, the VBGF was not rejected for the three time-weight fish
353   data sets (#14 Guppy, #25 Salmon, and #36 Zebrafish).

354   **INSERT Figure 9**: Effect on the Akaike weights of using different length-mass relations

355   **INSERT Figure 10**: Effect of outliers on the Akaike weights

356   Data with outliers are obviously of poor data quality. For such data, the refutation of exponents
357   turned out to be more difficult, i.e. FNR became larger; Figure 10 illustrates this. Therefore, in
358   order to remove non-refutations caused by poor data quality, obvious outliers had to be removed.
359   (The authors removed an outlier from a data set.)

360   Further, while for non-fish species the data for females and males of the same species were
361   collected separately, this was not the case for all fish. In case that these groups had a different
362   growth pattern (different optimal exponents), the combination of data could result in higher
363   residuals, making refutations more difficult and increasing FNR (Figure 11). This effect was
364   particularly extremal for the Black Drum (*Pogonias cromis*) data from Ogle (2017), where the
365   combined data did not allow to refute any exponent and also the sigmoid growth pattern was lost
366   (optimal exponent $a = 0$ for the combined data), whereas the Akaike weights for females showed
367   a clear peak. (The Akaike weights for males were not meaningful by lack of data.) The
368   phenomenon of sex change was not considered, but literature did not report problems for the fit of
369   a VBGF (c.f. Taylor and Pardee, 2017).

370   **INSERT Figure 11**: Effect of combining males and females on the Akaike weights

371   Where fish came from different locations (e.g. different water temperatures for the Lake Trout data
372   #18-19 and #27-28), a different pattern of growth was expected for biological reasons. However,
373   for other data, e.g. of Longjaw Cisco (*Coregonus alpenae*) from Ogle (2017) and Jobes (1946),
374   the combination of data from two locations of the same lake did not seem to have notable effects
375   (the paper used the combined data).

376   Another difference was related to how data were gathered: Data were either growth data for
377   individual animals or average values. In the latter case, either the same group of animals was
378   observed over a certain time span (e.g. feeding experiments), or completely different animals were
379   observed (e.g. hunting data; these displayed the largest variations). Most non-fish data were about
380   pets, farmed animals or laboratory animals, whose age was known, whose food intake was
381   controlled and where the animals could easily be grouped by objective factors (e.g. sex, strain).
382   For fish, comparable data were conceivable only for aquarium fish, such as Guppy or Zebrafish.

383 **Implications about data quality**: Summarizing, there were differences in the data quality between
384 fish and non-fish data. Consequently, for the fish data refutations may have become more difficult
385 (larger FNR) and this could have been the reason, why the VBGF was not refuted for most fish
386 data. This is tested below.

387 With 99.99% significance (Mann-Whitney test: p-value below 0.01%, computed in XL-Stat) the
388 average FNR for fish (0.8) was stochastically larger than the average FNR for non-fish (0.38).
389 Thereby FNR = 1 for 18 data sets, 17 of them for fish. Thus, apparently the larger FNR for fish
390 was the reason for the high level of non-refutation of the VBGF for fish and the contingency in
391 Table 3. However, there were also fish with good data quality in this sense; thus for Artic Cod (#3
392 in Table 1) a minimal FNR = 0.1 was observed.

393 The indicator FNR may also explain the different location of the optimal exponents for fish and
394 non-fish, as with 99.99% significance the optimal exponents (a_{opt}) were negatively correlated with
395 FNR (t-test: p-value below 0.01%, computed in XL-Stat). Thus, the lower optimal exponents for
396 fish were related to a higher FNR.

397 Thereby, for 48% of the considered data sets it was conceivable that model (2) was not true, as the
398 optimal exponent was found on the boundary of the considered domain. Thereby, for five data sets
399 $a_{opt} = 0$ (indicating that growth was rather not sigmoid); these data sets were for fish and for them
400 FNR =1. For 24 of the 60 data sets (12 fish) the optimal exponent was maximal ($a_{opt} = 0.99$) and
401 of them FNR = 1 for only four data sets (all fish).

402 **Conclusion**: The paper argued that the question, whether there exists a universal metabolic scaling
403 exponent, may be ill-posed and it developed a mathematical definition of weak universality to
404 reformulate this question in an empirically testable way. Applying this notion to 60 data sets about
405 the growth of fish and non-fish species the data seemed to support the hypothesis that there would
406 be a difference between fish and non-fish; for the former VBGF would be weakly universal.
407 However, this ambitious hypothesis could not be maintained, as there were systematic differences
408 between fish and non-fish in data quality, and these differences could have hindered the refutation
409 of the VBGF for fish-data.

410 It may thus be concluded: The VBGF did adequately describe the growth of 97% of data sets for
411 fish. Therefore, where the purpose of data fitting is the condensation of information to summarize
412 growth data about wildlife by means of a few parameters, then the VBGF appears to be adequate.
413 However, the reason for its adequacy may not be the 'inherent truth' of the VBGF, but rather a not
414 so good quality of wildlife data in general.

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Figure 1

Comparing the fit of model (2) with different exponents to growth data

Figure generated in Microsoft EXCEL, based on (time-length) data of Arctic Cod (*Gadus morhua*) from Jørgensen (1992), approximating weight by length^3 and determining the least squares fit to these data of model (2) with exponents $a = 0.67$ (VBGF = dashed line) and $a = 0.99$, the optimal exponent.
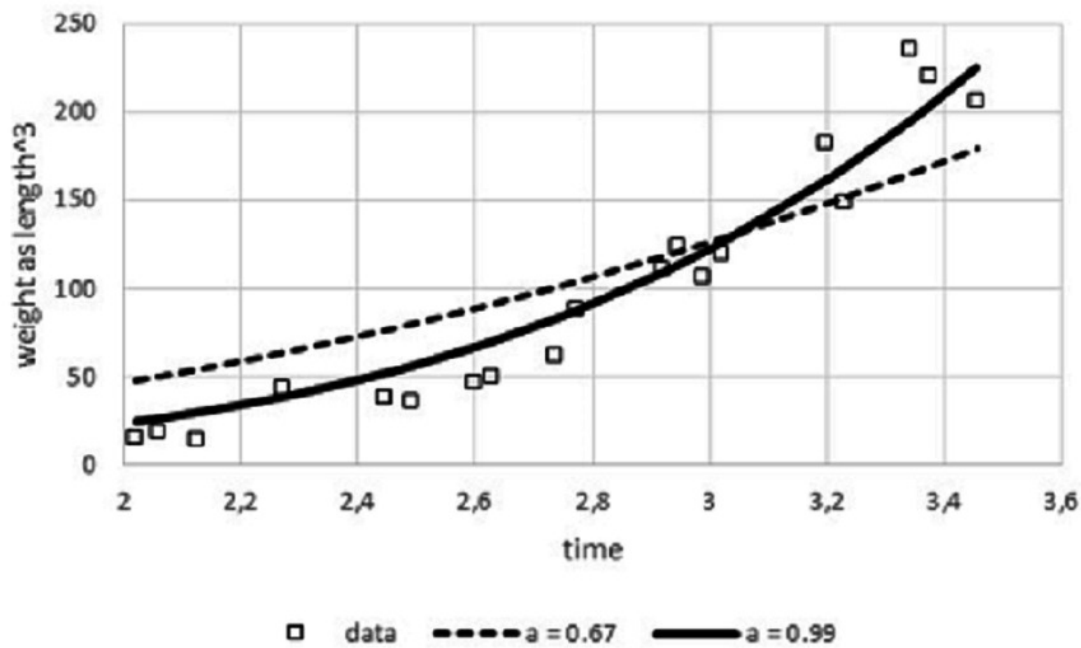
Figure 2

Akaike weights for different exponents, when compared to the optimal exponent

Graphical multi-model comparison, generated in Microsoft EXCEL, based on time-length data of Sea Trout (*Salmo trutta fario*) from Abad (1982), approximating weight by length^3. The Akaike weight *prob*(*a*) for the generalized von Bertalanffy model with exponent *a* was computed in comparison with the optimal exponent a_{opt} = 0.66. The figure highlights also the Akaike weight (50%) of the VBGF (*a* = 0.67). The comparison presumes, that one of the two exponents *a* or a_{opt} is true (*prob*(*a*) + *prob*(a_{opt}) = 100%) and that *prob*(*a*) ≤ *prob*(a_{opt}), whence *prob*(*a*) ≤ 50%. As is suggested from this figure, exponents *a* < 0.5 may be refuted. For, either model (2) is false and then all exponents refuted. Or the model is true. Then even under the assumption that one of the exponents *a* < 0.5 or a_{opt} = 0.66 would be true, the probability for the truth of any exponent *a* < 0.5 would be negligible.
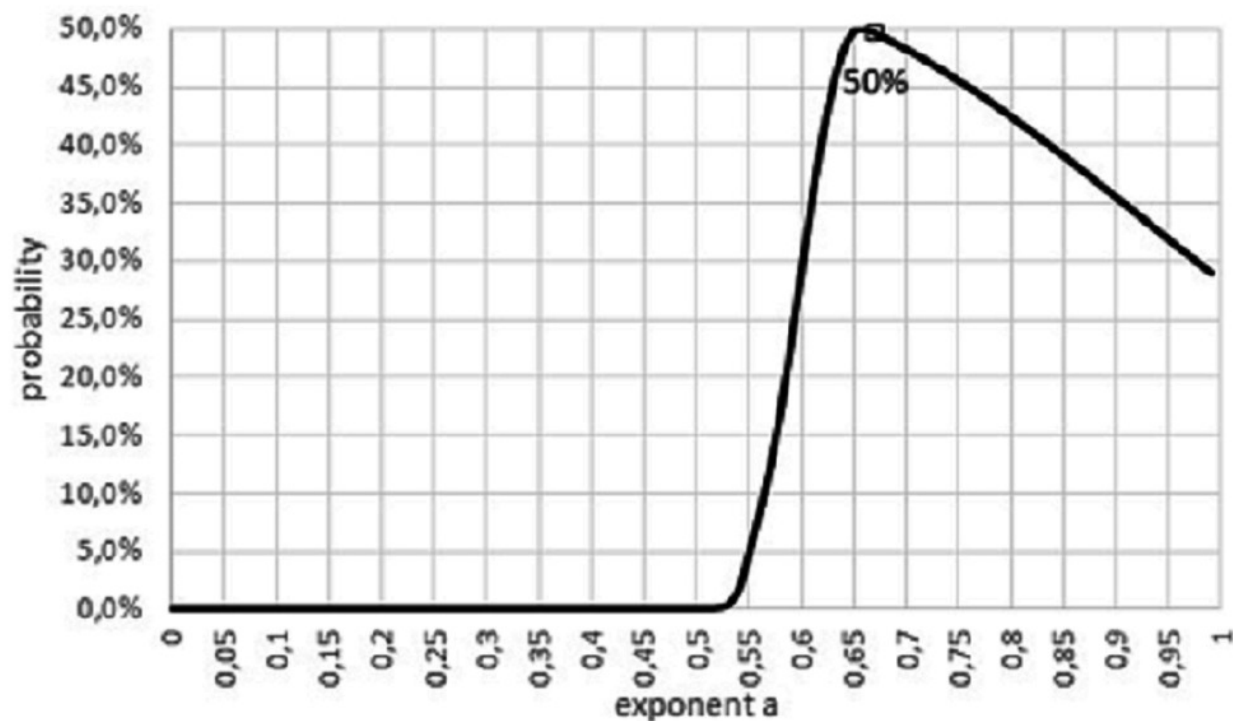
Figure 3

Weight increase and its approximation by a VBGF

Modification of the Walford plot (Walford, 1946; other modifications: Ford, 1933; Gulland, 1964) generated in Microsoft EXCEL, based on (time-length) data of Bull Trout (*Salvelinus confluentis*) from Ogle (2017) and Parker et al. (2007) with *dm/dt* computed from the data by numeric differentiation (quadratic interpolation to take care of unequal *dt*-interval length: Burden and Faires, 1993). The model curve is right hand side of (1), with *p, q* obtained from a linear fit (LINEST function applied to *dm/dt*, m^a, m^b with $a = 2/3$, $b = 1$).
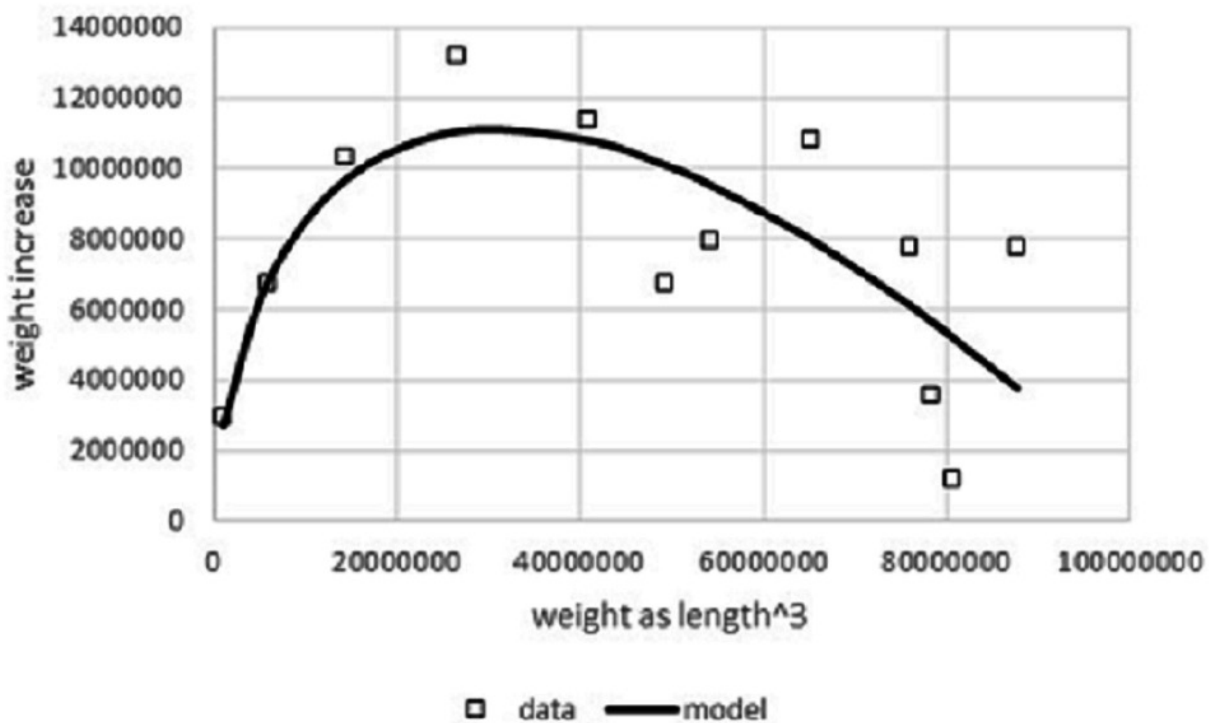
Figure 4

Dependency of the optimal exponent on which phase of growth was observed

The figure illustrates a) the general form of VBGF showing a characteristic S-shape over its whole range; b) missing end-data, which suggest unbounded growth; and c) missing data at the beginning, which suggests exponential bounded growth (exponent $a = 0$).

a) full growth   b) initial phase   c) final phase
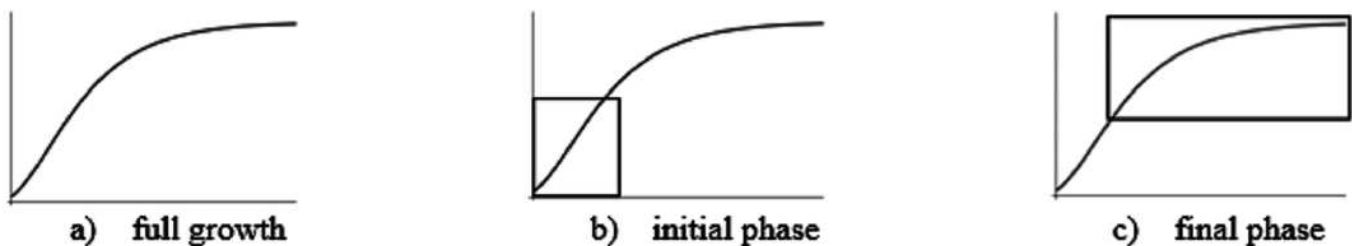
Figure 5

Weight increase and approximation by a logistic model, i.e. (1) with $a = 1$, $b = 2$

Modified Walford plot generated in Microsoft EXCEL, based on (time-length) data of Freshwater Drum (*Aplodinotus grunniens*) from Ogle (2017) and Bur (1984), and model curve computed as in Figure3. This data set was removed, as no data point supported the estimation of m_{max} (selection criterion from Knight, 1968).
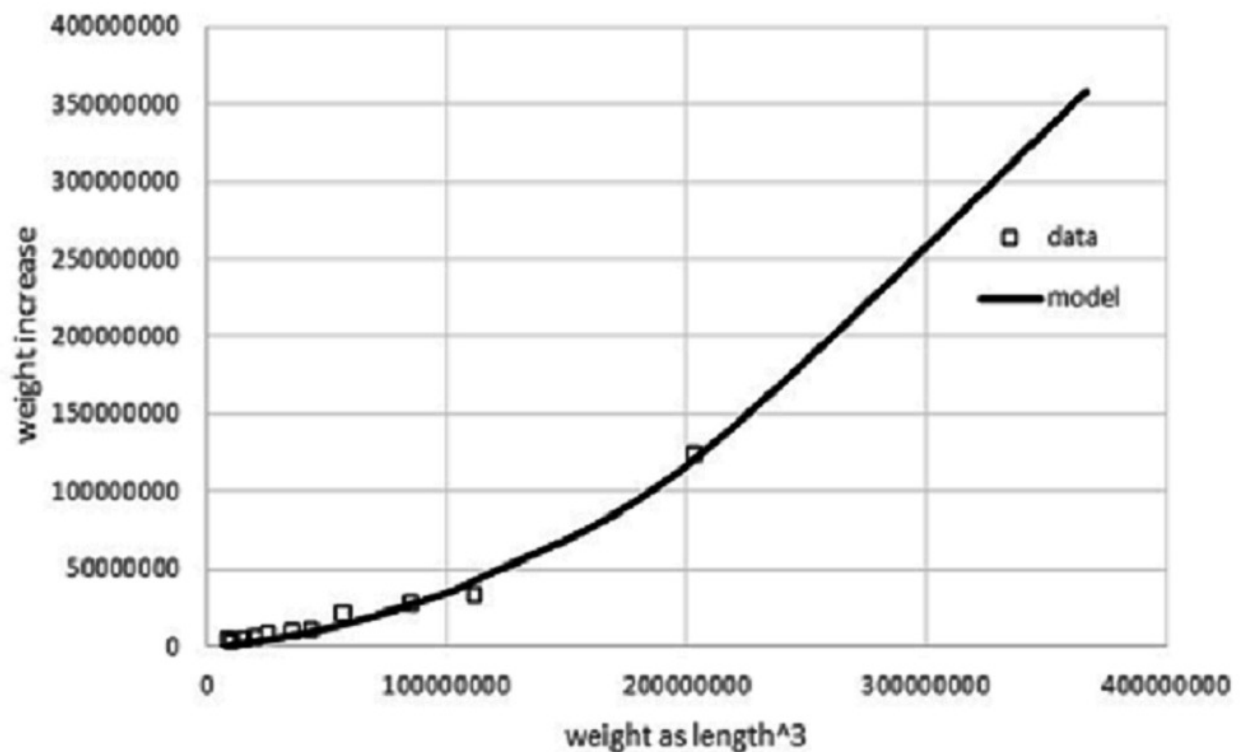
Figure 6

Transformation of time-mass-data and a regression line for the transformed data set

Generalized Bertalanffy-Beverton plot generated in Microsoft EXCEL, based on (time-mass) data of male Zebrafish (*Danio rerio*) from Gomez-Requeni (2010), transforming the time-mass data (t,m) into $(u,t) = (f(m),t)$ and fitting a regression line $t = A+B{\cdot}u$ with $A = 22.486$ and $B = 3.438$ to the transformed data. The function f was defined in equation (3) using the exponent $a = 0.67$ and assuming an asymptotic weight limit $m_{max} = 345$mg. The transformation required m_{max} to exceed the maximal observed weight (344.4mg), as otherwise the transformation would not be defined for all data points.
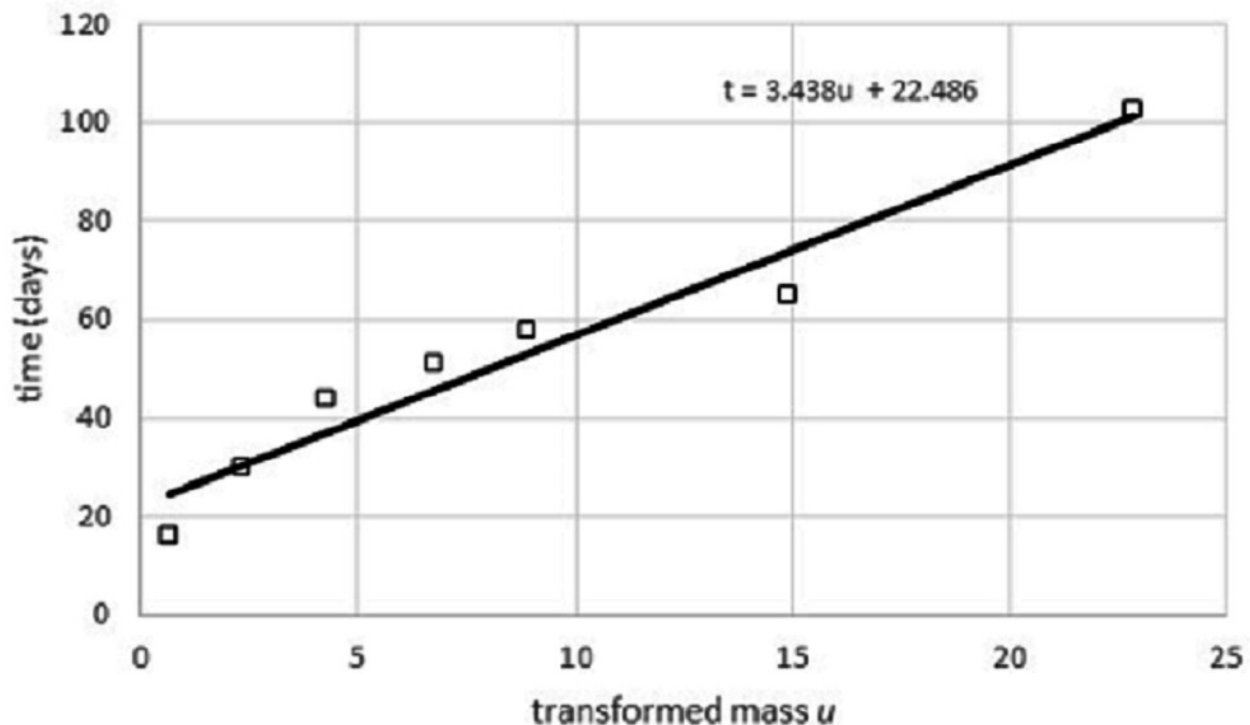
Figure 7

Optimizing the asymptotic weight limit (fit to weight-time data)

Figure generated in Microsoft EXCEL, based on (time-mass) data of Guppy (*Poecilia reticulata*) from West et al. (2001), referring to Brown and Rothery (1993): 14 data points (average weights) from days 0 to 88 with a maximal observed weight of 0.145g. Assuming an exponent $a = 0.67$, the sum of squared residuals SSR_{inv} was plotted in dependency on m_{max}. The minimum was attained for $m_{max} = 0.165g$, resulting in $q = 0.1$/day and $m_0 = 0.03g$. This was used as a starting value for the minimization of SSR for the fit of function (2) to the time-weight data. The resulting optimal parameters (for $a = 0.67$) were $q = 0.139$/day, $m_0 = 0.002g$ and $m_{max} = 0.149g$.
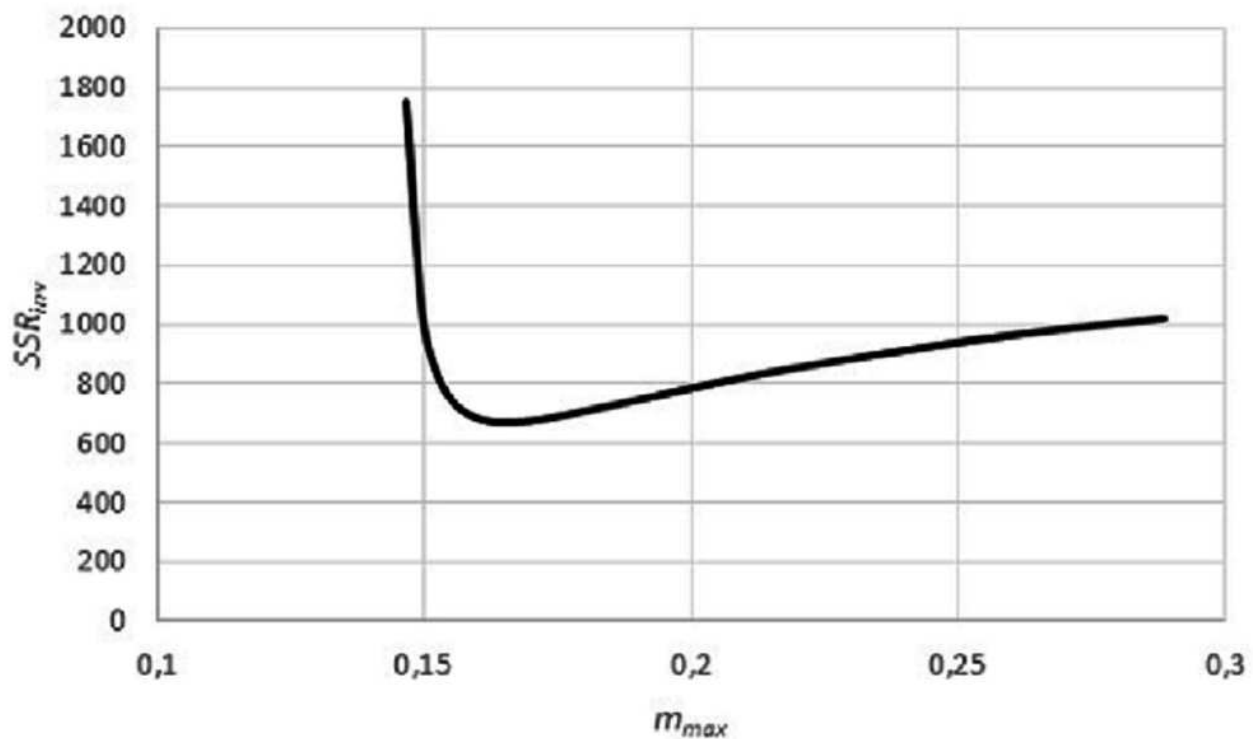
Figure 8

Confidence intervals for the percentage of fish data sets not rejecting an exponent

Figure generated in Microsoft EXCEL, counting the percentage of how many of the 37 fish data sets of Table1 did not reject the exponent on the *x*-axis together with the upper and lower one-sided Clopper-Pearson confidence limits (90% significance). The lower limit mattered for the weak universality criterion.
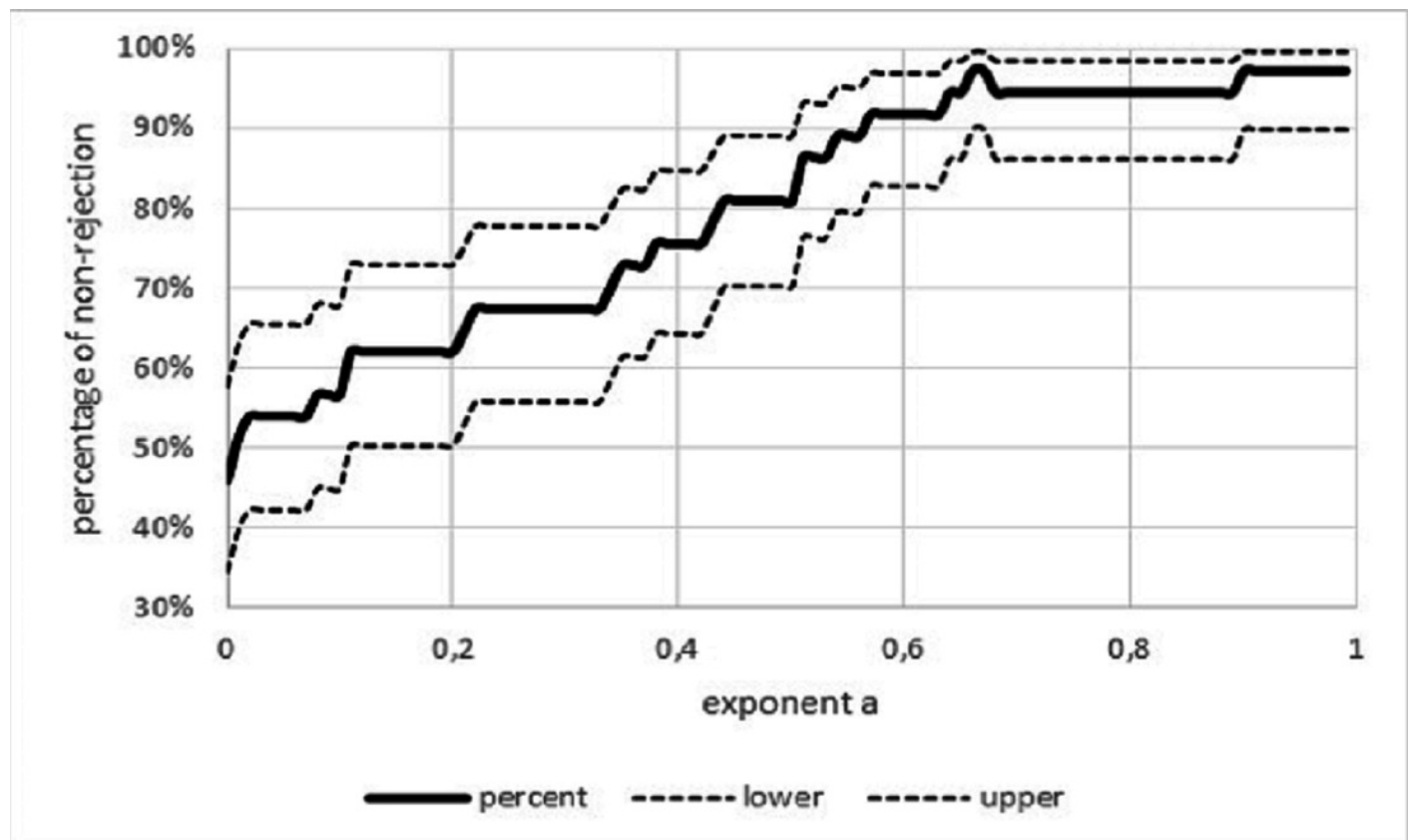
Figure 9

Effect on the Akaike weights of using different length-mass relations

Figure generated in Microsoft EXCEL, based on time-length data of Araucanian Herring (*Strangomera bentincki*) from Ogle (2017) and Cubillos et al. (2001), using different powers of length to estimate mass.
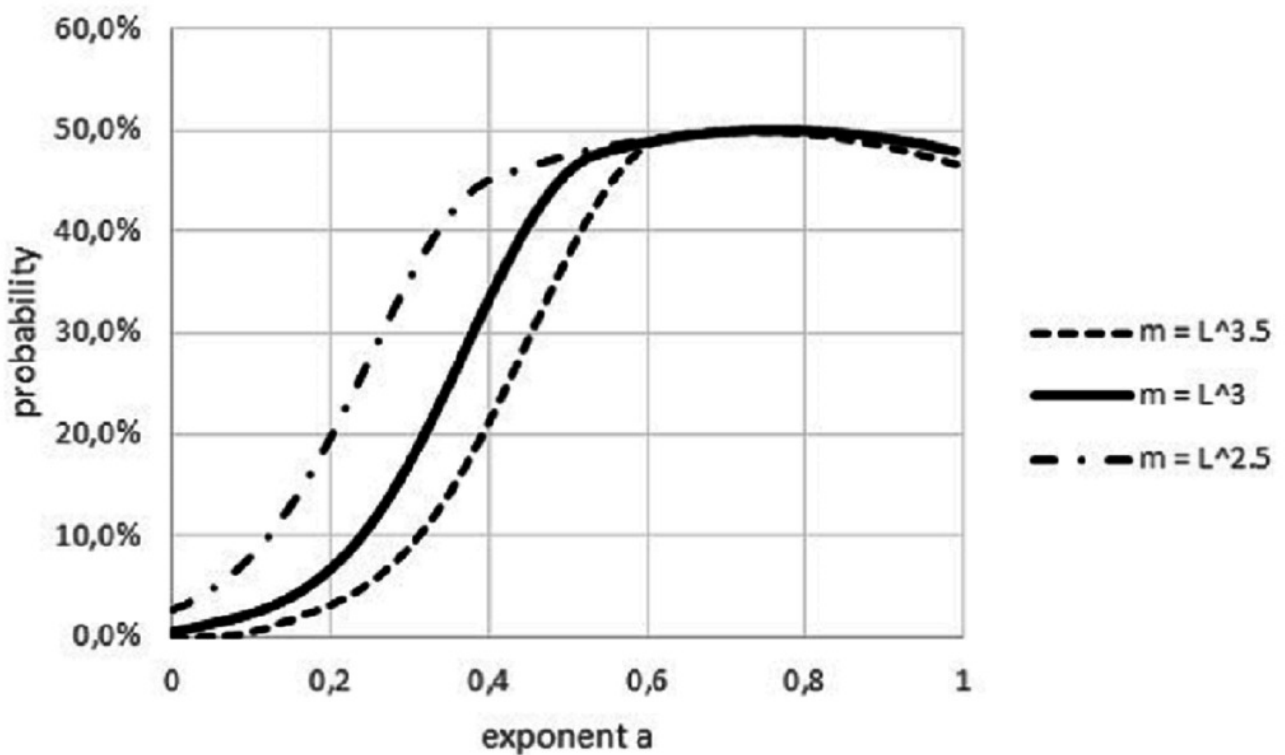
Figure 10

Effect of outliers on the Akaike weights

Figure generated in Microsoft EXCEL, based on (time-length) data of Bull Trout (*Salvelinus confluentis*) from Ogle (2017) and Parker et al. (2007), whereby for the correction one outlier was removed from the data. Data from the Arctic Long Term Ecological Research, separated by sex and combined.
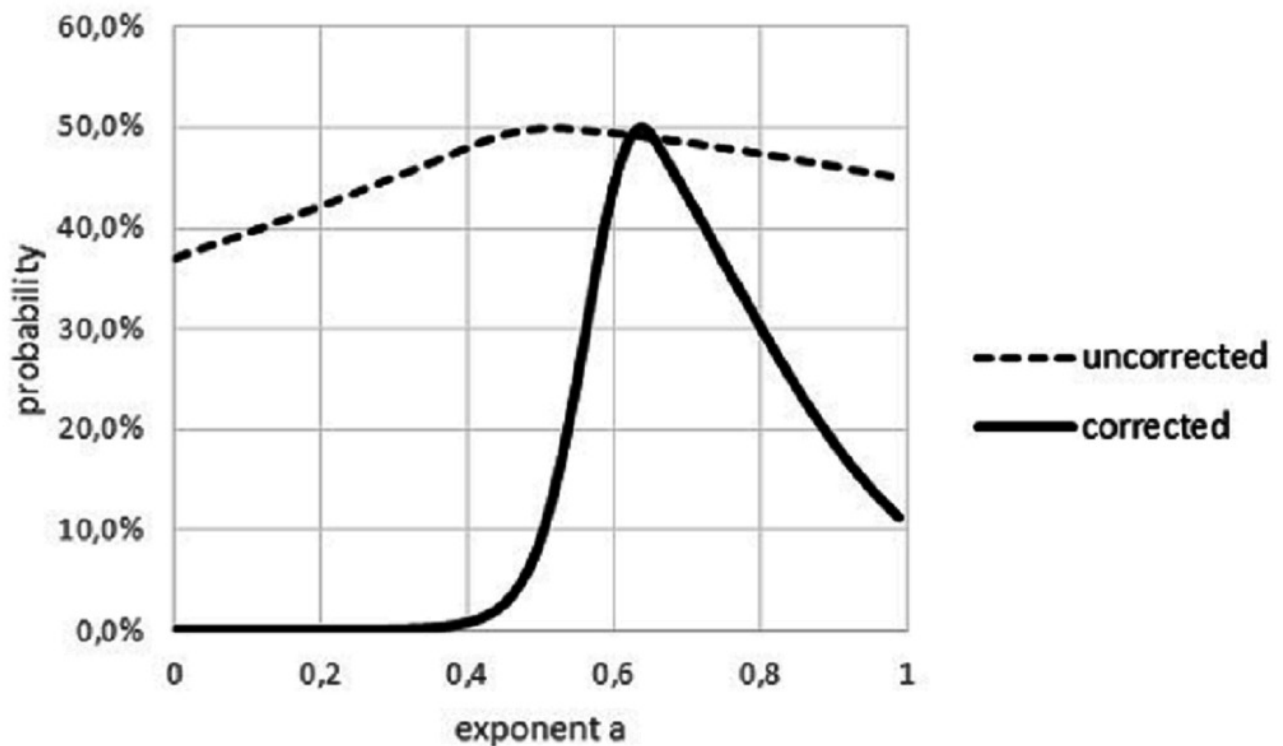
Figure 11

Effect of combining males and females on the Akaike weights

Figure generated in Microsoft EXCEL, based on time-length data of Lake Trout (*Salvelinus namaycush*) from Ogle (2017), based on data from the Arctic Long Term Ecological Research, separated by sex and combined.
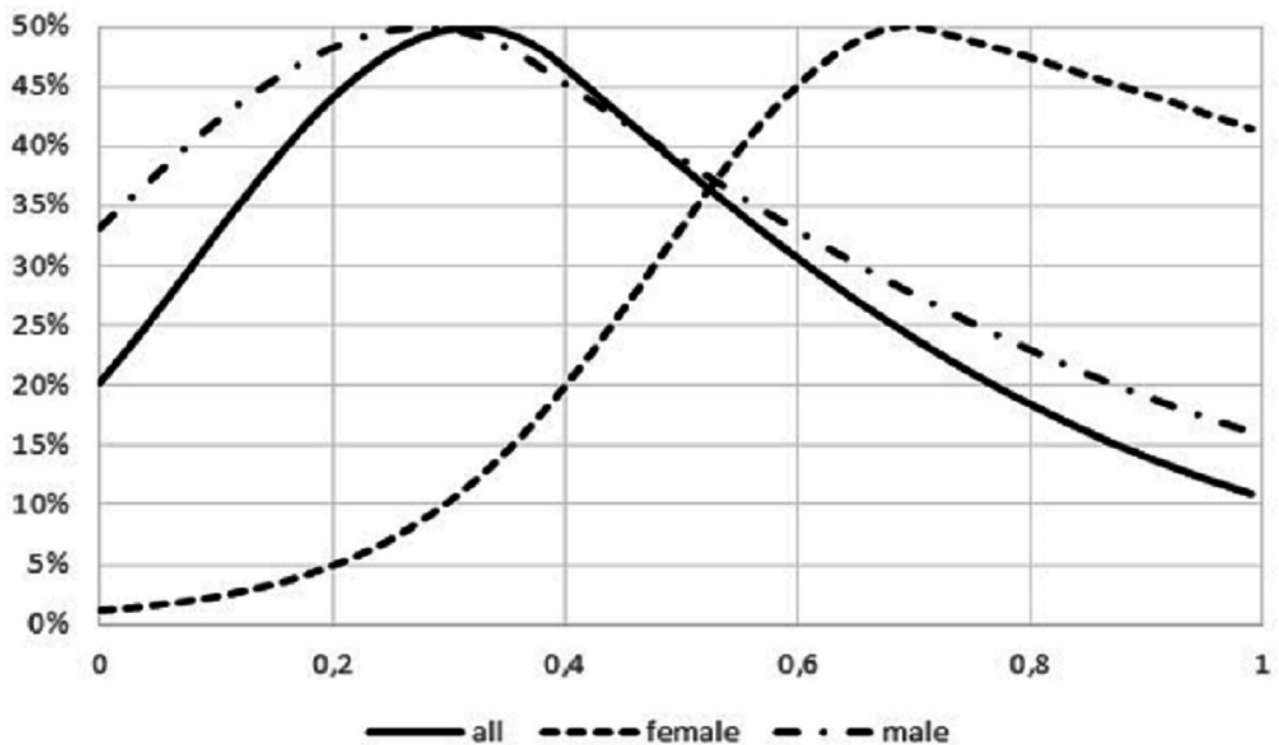
Table 1(on next page)

Optimal exponents and interval of non-refuted exponents for fish data

Data sets abbreviated (details in the text); F and M denotes data for females and males; a_{opt} = metabolic scaling exponent with the best fit of model (2) to the data; non-refutation defines the lower and upper bounds of the interval consisting of those of metabolic exponents that in comparison to a_{opt} could not be refuted (Akaike weight 2.5% or higher).

1   **Table 1**. Optimal exponents and interval of non-refuted exponents for fish data

No	Data set	a_{opt}	Non-refutation		No	Data set	a_{opt}	Non-refutation	
			Low	High				Low	High
1	Anchoveta	0.83	0.43	0.99	**20**	Cisco	0.99	0.38	0.99
2	Herring	0.76	0.11	0.99	**21**	Red Drum	0	0	0.99
3	Cod	0.99	0.9	0.99	**22**	Tilapia	0.62	0.51	0.99
4	Black Drum (F)	0.39	0.21	0.99	**23**	Rock Bass	0.57	0	0.99
5	Blue Catfish	0.75	0	0.99	**24**	Whitefish	0.51	0.35	0.99
6	Bonito (F)	0	0	0.99	**25**	Salmon	0.91	0.64	0.99
7	Bonito (M)	0	0	0.99	**26**	Sardine	0.99	0.34	0.99
8	Trout (various)	0.99	0	0.99	**27**	S. Trout (F)	0.91	0.01	0.99
9	Sea Trout	0.66	0.54	0.99	**28**	S. Trout (M)	0.99	0.02	0.99
10	Bull Trout	0.64	0.44	0.99	**29**	Sucker	0.99	0	0.99
11	Cabezon	0.6	0	0.99	**30**	Bluefin Tuna	0.11	0	0.99
12	Croaker	0	0	0.99	**31**	Troutperch	0.19	0	0.99
13	European Perch	0.8	0	0.99	**32**	Spot	0.99	0	0.99
14	Guppy	0.99	0.51	0.99	**33**	Pollock	0.37	0.22	0.67
15	Morwang	0.99	0	0.99	**34**	Grunt (F)	0.01	0.01	0.99
16	Jonubi	0.99	0.08	0.99	**35**	Grunt (M)	0	0	0.99
17	Walleye	0.21	0	0.99	**36**	Zebrafish	0.99	0.66	0.99
18	Lake Trout (F)	0.69	0.11	0.99	**37**	Zebrafish	0.99	0.57	0.99
19	Lake Trout (M)	0.28	0	0.99					

2   **Notes**: Data sets abbreviated (details in the text); F and M denotes data for females and males; a_{opt} = metabolic scaling
3   exponent with the best fit of model (2) to the data; non-refutation defines the lower and upper bounds of the interval
4   consisting of those of metabolic exponents that in comparison to a_{opt} could not be refuted (Akaike weight 2.5% or
5   higher).

Table 2(on next page)

Optimal exponents and interval of non-refuted exponents for non-fish data

Explanations as for Table1.

1   **Table 2**. Optimal exponents and interval of non-refuted exponents for non-fish data

No	Data set	a_{opt}	Non-refutation		No	Data set	a_{opt}	Non-refutation	
			Low	**High**				**Low**	**High**
38	Cattle	0.24	0	0.54	50	Pigs	0.45	0.37	0.93
39		0.2	0.02	0.38	51	Crickets	0.99	0.8	0.99
40	Chicken	0.17	0	0.99	52		0.94	0.75	0.99
41		0.85	0.65	0.99	53		0.99	0.89	0.99
42		0.99	0.75	0.99	54	Heron	0.99	0.78	0.99
43		0.99	0.79	0.99	55	Python	0.99	0.57	0.99
44		0.88	0.78	0.99	56	Rats	0.14	0	0.52
45		0.99	0.9	0.99	57		0.78	0.55	0.99
46		0.99	0.85	0.99	58	Robin	0.99	0.16	0.99
47	Dogs	0.83	0.68	0.99	59	Shrew	0.99	0.3	0.99
48		0.84	0.58	0.99	60	Shrimp	0.99	0.76	0.99
49		0.99	0.68	0.99					

2   **Notes**: Explanations as for Table 1.

Table 3 (on next page)

Contingency of the rejection of the VBGF on the taxonomic group

The contingency table was based on the count of the number of rejections of the exponent a = 0.67 (VBGF). For all common tests (chi-squared, chi-squared with Yates continuity correction, Fisher exact test, simulation) the fish data of this paper differed from the non-fish data with 99.99% confidence (p-value below 0.01%). The odds ratio comparing the odds of non-rejection for fish with the odds for non-rejection of non-fish was (36/1)/(8/15) = 67.5 and its 95% confidence limits were 10.8 and 422.8. (The computations used XL-Stat.)

1   **Table 3**. Contingency of the rejection of the VBGF on the taxonomic group

Number of data sets	Fish	Non-Fish	Sum
VBGF not rejected	36	8	44
VBGF rejected	1	15	16
Sum	37	23	60

2   **Notes**: The contingency table was based on the count of the number of rejections of the exponent $a = 0.67$ (VBGF).
3   For all common tests (chi-squared, chi-squared with Yates continuity correction, Fisher exact test, simulation) the fish
4   data of this paper differed from the non-fish data with 99.99% confidence (p-value below 0.01%). The odds ratio
5   comparing the odds of non-rejection for fish with the odds for non-rejection of non-fish was $(36/1)/(8/15) = 67.5$ and
6   its 95% confidence limits were 10.8 and 422.8. (The computations used XL-Stat.)