Do herring grow faster than orange roughy?

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In growth studies it is common to find the statement "P grows faster than Q". However, it is much less common to find a clear definition of what the author means by that statement. What is it about two sets of growth parameters, or two growth curves, that should make us conclude that "P grows faster than Q"? In this note I will show that this is not as simple a question as it may seem. There are several plausible ways of answering it and these have very different consequences. Thus, the statement "P grows faster than Q" is ambiguous and it is important for authors to be specific about what they mean by it. I will also give reasons for preferring one of the possible meanings.

In what follows it will sometimes be convenient to refer to the two entities being compared as "species P" and "species Q." However, my conclusions are the same whether the growth comparison is made within species (e.g. males vs. females [Horn, 1993; Hostetter and Munroe, 1993; Kitagawa et al., 1994; Collins et al., 1995], one time period vs. another [Raspopov, 1993; Collins et al., 1995], or one area vs. another [Horn, 1993; Savard et al., 1994]), or between species (Arkhipkin and Nekludova, 1993; Gorny et al., 1993; Milton et al., 1993; Potts and Manooch, 1995).

Before proceeding, it is useful to restrict the scope of the question being considered. First, only the mean growth for a "species" is considered; therefore between-individual variability in growth is ignored. Second, I will assume that we have perfect knowledge about the growth of P and Q; i.e. statistical uncertainty is ignored. Third, I will consider only unqualified comparisons such as "P grows faster than Q," comparisons that apply only to a portion of the life history (e.g. "P grows faster than Q up to age 1") are excluded. The purpose of these restrictions is to allow for a simpler presentation. Without them, the picture is more complex, but the results given below will still apply, although not in precisely the same form.

Six methods of growth comparison

There are at least six plausible methods for comparing growth (Table 1). With method 1, we would say that P grows faster than Q if $L_{t,P} > L_{t,Q}$ for all t, where $L_{t,P}$ and $L_{t,Q}$ are the lengths at age t for species P and Q, respectively. The rationale behind this method is that $L_{t,P} > L_{t,Q}$ implies that P must have grown faster than Q (at least on average) over the period up to age t. Now, rather than comparing average growth rates over a period of time it may be more sensible to compare instantaneous growth rates. This is the reason for method 2. However, it may be argued that method 2 makes no sense when $L_{t,P}$ is very different from $L_{t,Q}$. For example, a growth rate of 10 cm/yr is fast for an animal of size 20 cm but slow for an animal of size 200 cm. There are two ways to deal with this difference: we can either insist that the comparison be made when the animals are of the same size (method 3), or we can standardize the growth rates by dividing by length (methods 4 and 5). (Method 5 is included here for completeness, but it is easy to show that it is exactly equivalent to method 3.) Method 6 could be appropriate where growth is asymptotic and the asymptotes for P and Q are different. Here the species that approaches its asymptote faster is said to grow faster. Of course, this method is not fully defined until we specify what we mean by "the rate at which the asymptote is approached."

To illustrate the difference between these methods we will assume that growth is adequately described by the von Bertalanffy equation with $t_0 = 0$, i.e.

$$L_t = L_\infty(1 - e^{-kt}).$$

Table 1

Six methods for comparing the mean growth of two species or populations. The absolute growth rate is the slope of the length-at-age curve (with dimension length/time) and the relative growth rate is this slope divided by the length (dimension 1/time).

Method 1:	compare lengths at each age
Method 2:	compare absolute growth rates at each age
Method 3:	compare absolute growth rates at each length
Method 4:	compare relative growth rates at each age
Method 5:	compare relative growth rates at each length
Method 6:	compare rates at which the asymptotic size is approached

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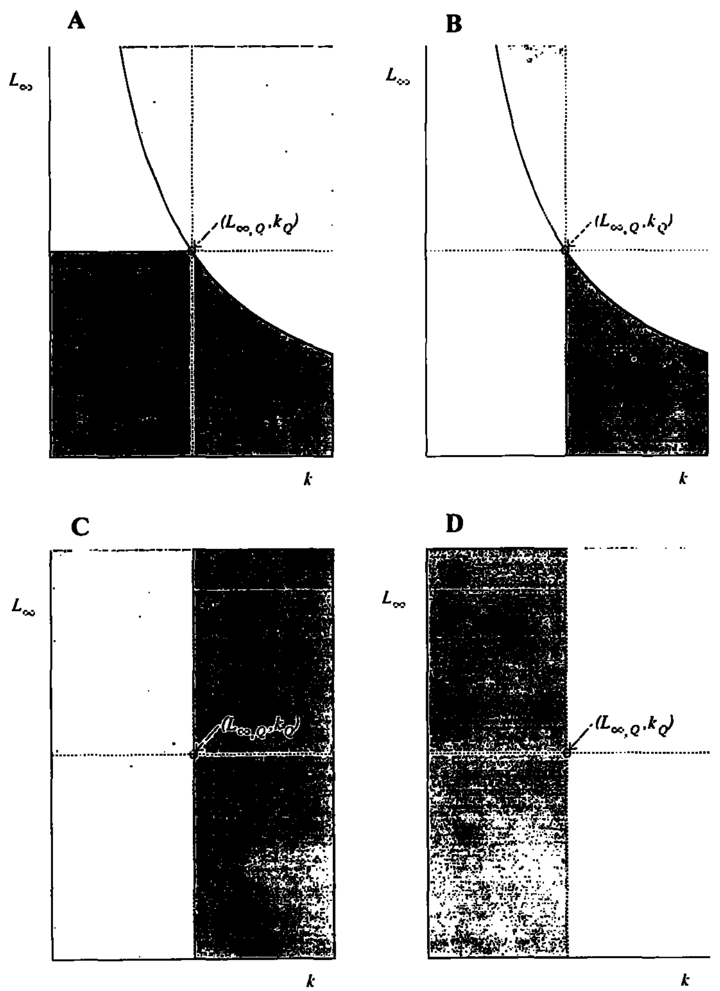

Figure 1

Illustration of the six methods of growth comparison in Table 1 when growth follows the von Bertalanffy equation. In each panel, the central point, 'o', represents the growth parameters for species Q, $(L_{\infty,Q}, k_Q)$. Species P is said to grow faster (or slower) than species Q if the point $(L_{\infty,P}, k_P)$ lies in the light (or dark) shaded area of the graph. In the unshaded areas, no comparison can be made over the whole life history (so P may be faster than Q at one age [or length] and slower at another). Comparisons are for (**A**) methods 1, 3, and 5; (**B**) method 2; (**C**) method 4; and (**D**) method 6. See Table 1 for definitions of methods. The curved line in panels A and B is $L_\infty = L_{\infty,Q} k_Q / k$. (Details of the derivation of this Figure are available from the author).

With this assumption, method 6 is fully defined because the parameter k determines the rate at which the asymptote is approached; the bigger k is, the faster the asymptote is approached. Thus, according to method 6, P grows faster than Q if $k_P > k_Q$.

Now, given growth parameters $L_{\infty,Q}, k_Q$ for Q, we are in the position to address the question, "What range of values can $L_{\infty,P}, k_P$ take if we are to say that P grows faster (or slower) than Q?". Figure 1 shows that the answer to this question depends strongly on which of the six methods of comparison is used. Methods 1, 2, and 5 give identical answers, but these are very different from the answers from the other methods. Methods 4 and 6 give completely opposite answers. For methods 4 and 6, we can always say either "P grows faster than Q" or "Q grows faster than P" (as long as the growth rates are not identical). However, for all other methods in Table 1, it will sometimes not be possible to make either of these statements without qualification. For example, in the unshaded areas of Figure 1A, P grows faster than Q at some ages (or lengths) and slower than Q at others (according to methods 1, 3, and 5).

Method 6: A comparison of rates at which the asymptotic size is approached

I suggest that method 6 is the most "natural" method of growth comparison, in the sense that it produces common-sense results. To see why, consider the question in the title of this paper. Orange roughy, *Hoplostethus atlanticus*, is described as "very slow-growing" (Fenton et al., 1991) and herring, *Clupea harengus*, is generally considered to be fast-growing; therefore the answer to this question should be "yes." Given growth parameters for orange roughy ($L_{\infty,Q}$=40 cm, k_Q=0.044/yr; Fenton et al., 1991) and any of the sets of herring parameters given by Pauly (1980) (range: $L_{\infty,P}$=19.4 – 36.0 cm, k_P = 0.21– 0.48/yr), the point $(L_{\infty,P}, k_P)$ would lie in the right-hand unshaded space in Figure 1A (and in the corresponding position in the other panels of Figure 1). This means that with methods 1, 2, 3, and 5 there would be no clear-cut difference in growth rates between these species and that with method 4 herring would grow slower than orange roughy. Only method 6 reaches the common-sense conclusion.

Another reason to prefer method 6 is that it ignores asymptotic size (L_∞). It seems to me that comparisons of this parameter determine only whether one species is bigger than another, not whether growth is faster or slower. In other words L_∞ describes size, not growth rate. But note that, for the methods covered by Figure 1, A and B, P cannot be judged to grow faster than Q unless $L_{\infty,P} > L_{\infty,Q}$. This confusion between measures of size and growth rate is illustrated by Figure 2. Method 6 ranks curve P as the slowest-growing because it is the slowest of the three in approaching its asymptote; with methods 1, 2, 3, and 5, the ranking is reversed because of the influence of L_∞ (it is also reversed for method 4, but not because of L_∞).

So far, method 6 has been defined only where growth follows the von Bertalanffy equation with $t_0 = 0$. This definition works equally well even if $t_0 \neq 0$ (this parameter simply determines the horizontal position of the growth curve and is therefore irrelevant in describing the speed of growth). The definition also extends naturally to the Gompertz and logistic growth equations as long as growth is considered only to the right of the inflection point. Both these equations have a rate parameter precisely analogous to k (this is the parameter g in equations 3 and 4 of Schnute, 1981). However, more complex growth models (e.g. the four-parameter model of Schnute, 1981) are so flexible that it seems difficult to rank growth curves along a single dimension, from slower to faster. A simple solution, which is consistent with method 6, would be to determine the age at which a species reaches 90%, say, of L_∞. The younger this is, the faster-growing is the species.

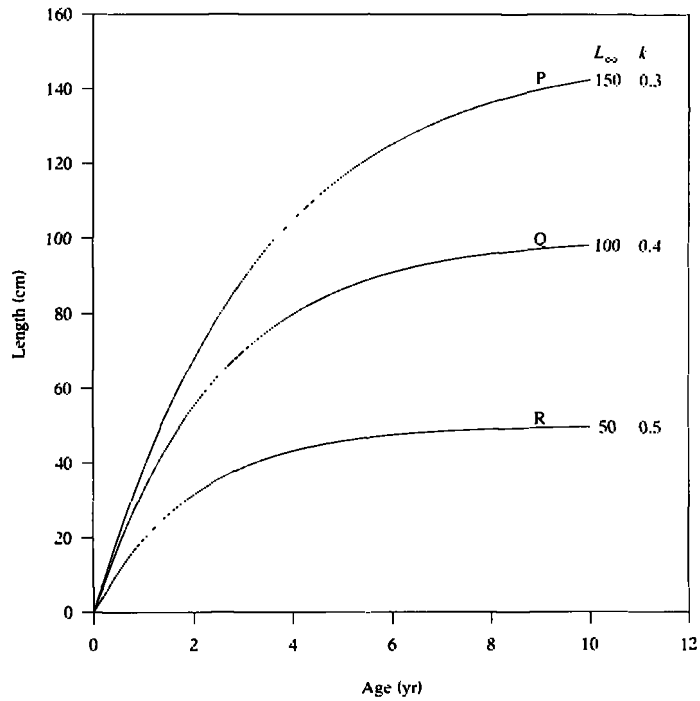

Figure 2

Example of three von Bertalanffy growth curves whose ranking, from slowest- to fastest-growth, is P, Q, and R for method 6 but the reverse for all other methods in Table 1.

Conclusions

The main conclusion of this paper is that statements like "P grows faster than Q" are ambiguous unless the method of growth comparison (e.g. one of the methods in Table 1) is specified. To some extent it does not matter which method is used as long as this is clearly stated. However, I have given some reasons to believe that method 6 is the most natural method. Amongst these reasons is the observation that, for von Bertalanffy growth, it is the parameter k that describes growth rate; L_∞ merely describes (eventual) size.

In order to make a point, the title of this paper refers to comparisons between disparate species. However, my main conclusion applies whether the growth comparison is made within or between species. I am happy to agree with an anonymous referee who asserted (forcefully) that some authors may not share my preference for method 6 (particularly for within-species comparisons).

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