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Dimensionless invariants for the optimal size (age) of sex change

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ABSTRACT

Optimization models have been widely and successfully used in evolutionary ecology to predict the attributes of organisms; perhaps the greatest quantitative success is in the area of sex allocation (sex ratio, sperm versus eggs for hermaphrodites, time as a male [female] for a sex changer), where the fact of having only one mother and one father makes Darwinian fitness a simple product of gain-via-male times gain-via-female. Previous work on sex change used the maximization of this male–female product to successfully predict the direction and age (size) for sex change, and that age has been shown to imply a breeding sex ratio biased towards the first sex. This paper unites recent advances in the comparative demography of organisms with indeterminate growth with the theory of optimal sex change to predict some new invariance rules for the *relative* age (size) of sex change. One of these rules is strikingly confirmed in a long-term study of the size-at-sex-change in the northern shrimp, *Pandalus borealis*, off Iceland.

Keywords: dimensionless analysis, evolutionarily stable strategy, life history, sex allocation.

It has recently been shown that interesting general rules exist for life histories if they are viewed in a dimensionless way (Charnov, 1993). For example, measure the average adult life span (E) as a ratio of the age-of-first-reproduction (a); then E/a is (approximately) invariant within a closely related taxon like mammals. After removing absolute scale (e.g. age), the life histories of, say, elephants and squirrels look much alike. Evolutionary life-history theory can be used to predict when such dimensionless invariance is to be expected (Charnov, 1993).

Sex allocation theory applied to sex change usually predicts the age/size of sex change (Charnov, 1982). The goal of this paper is to develop a dimensionless theory for optimal sex change. Our efforts are stimulated by three recent developments. First, Charnov and Bull (1989) proposed a dimensionless theory for sex change by looking at the breeding sex ratio. They showed that, at the evolutionarily stable strategy (ESS), the breeding sex ratio almost always favours the first sex. Although this qualitative invariance rule is quite general

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(and supported by comparative data), there are at least two additional ways to non-dimensionalize sex change (body size, age). We are also looking for dimensionless rules that are quantitative. Our second reason is that other dimensionless invariants (e.g. E/a) are known to hold within various taxa (Charnov, 1993). Some of these (dimensionless) numbers also appear in the formula for the ESS age/size of sex change (Charnov, 1979), and we wish to ask if they imply anything interesting about sex change itself.

The third development is shown by the data displayed in Fig. 1. Skúladóttir and Pétursson (1999) studied the northern shrimp, *Pandalus borealis*, for 7 years (1988–95) at 21 locations in Icelandic waters. Although the locations may not represent 21 separate breeding populations, they do represent three to four quite distinct growth regimes. The shrimp is a protandrous sex changer, and Skúladóttir and Pétursson estimated (for each year and location) the size-at-sex-change (L_{50} = carapace length at which 50% are females) and the maximum female carapace length (L_{max}). In all, about 900,000 shrimp were sized and sexed. Figure 1a shows the natural logarithm of the (time) average of L_{50} versus L_{max} for the 21 locations: the correlation is almost perfect with a slope of 1, indicating that L_{50}/L_{max} is a constant equal to about 0.79. Figure 1b is an arithmetic plot of L_{50} versus L_{max} and shows the 95% confidence interval for the intercept, which clearly includes zero. Our conclusion of proportionality would be unaltered under major axis regression (Ricker, 1973), which assigns equal error variance to L_{50} and L_{max} ; the correlations are just too strong for the regression model to matter. Other ways of testing for proportionality also yield the same result (see figure caption). So, the shrimp are changing sex at a constant proportion of their maximum length, a size invariant for sex change. The average of L_{50}/L_{max} for the 125 data points (years times locations) is $L_{50}/L_{max} = 0.80$, the same as we would conclude from Fig. 1. We explain below why we think the time average at a location is the appropriate measure for the relative size of sex change.

In the next paragraph, we develop sex change theory and use it to attach meaning to the invariance in L_{50}/L_{max} across populations. We will refer to shrimp, but the arguments probably apply to many other sex changers, since the growth model, and so forth, are widely applicable.

Shrimp growth is well described by the Bertalanffy equation $L = L_{\infty} (1 - e^{-k \cdot x})$, where L is length, L_{∞} is asymptotic length, x is age and k is the growth coefficient. Female fecundity is proportional to L^3 (references cited in Charnov, 1979). Let a be the age of first breeding (as a male), τ the age of sex change and M the adult instantaneous mortality rate. The optimal age of sex change (in a stationary population; Leigh *et al.*, 1976; Charnov, 1979, 1982) maximizes the *product* of the reproductive gain over the male period ($a \rightarrow \tau$) times the gain over the female period ($\tau \rightarrow \infty$), or

$$\max \left(\int_a^{\tau} e^{-M \cdot x} \cdot Q(x) dx \right) \left(\int_{\tau}^{\infty} e^{-M \cdot x} \cdot L_{\infty}^3 \cdot (1 - e^{-k \cdot x})^3 \cdot B dx \right) \tag{1}$$

$Q(x)$ is male fertility as a function of male age, while B converts L^3 to eggs per year.

It is plausible that $Q(x)$ is also a power function of $L(x)$. Assume $Q(x) = H \cdot L^{\delta}$; then, the maximization is of the *product*

$$\left(\int_a^{\tau} e^{-M \cdot x} \cdot H \cdot L_{\infty}^{\delta} \cdot (1 - e^{-k \cdot x})^{\delta} dx \right) \cdot \left(\int_{\tau}^{\infty} e^{-M \cdot x} \cdot B \cdot L_{\infty}^3 \cdot (1 - e^{-k \cdot x})^3 dx \right) \tag{2}$$

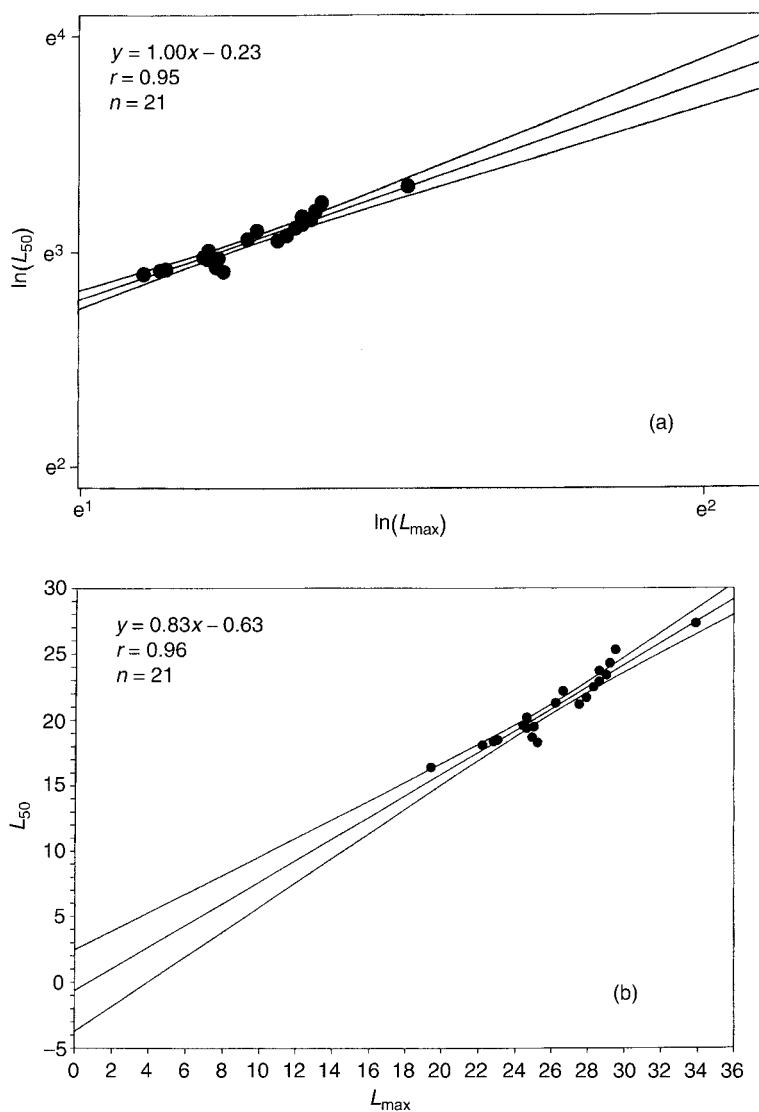


Fig. 1. Size at sex change (L_{50}) versus maximum size (L_{\max}) for Icelandic shrimp. (a) Log plot for the 21 locations (95% confidence intervals also shown). (b) Arithmetic plot for the 21 locations; the 95% confidence intervals on the intercept include zero. Size is carapace length. Other ways of testing proportionality include the following. Sixteen of the 21 locations represent three distinct growth regimes (in increasing order of L_{50} : inshore (9), offshore (6) and Denmark Strait (1)). If we calculate L_{50}/L_{\max} for each year and location, we get a grand average for each of the three growth regimes for the 7-year period. These time averages are: inshore 0.793, offshore 0.806, Denmark Strait 0.804. They are clearly the same numbers.

We find the optimal τ by setting $\partial(\text{product})/\partial\tau = 0$ and solving for τ .

But inspection of the product shows two interesting facts. First, the integration over ages (x) means that only the ages a and τ will appear in the final answer. Second, the optimal

τ will thus be a function only of a , M , k and δ ; because we maximize a *product*, H , B and L_∞ do not affect the optimal τ .

τ and a have units of time, M and k have units of $(\text{time})^{-1}$, and δ is a dimensionless number. Of course, this means that, at the optimal τ , the dimensionless product of $\tau \cdot k$ is solely a function of the dimensionless numbers k/M , $a \cdot M$ and δ . This is because if the optimal $\tau = \varphi_1(a, M, k \text{ and } \delta)$, we have four numbers with the dimension of time (τ , a , M^{-1} , k^{-1}), and dimensional analysis (Stephens and Dunbar, 1993) tells us that we can always eliminate time and write an equivalent function in terms of the dimensionless variables: $k \cdot \tau = \varphi_2(a \cdot M, k/M \text{ and } \delta)$.

Thus, all shrimp populations with the same $a \cdot M$, k/M and δ numbers are predicted to change sex at the same $k \cdot \tau$ value. The size at sex change is $L_\tau = L_\infty (1 - e^{-k \cdot \tau})$, so L_τ/L_∞ will be the same for all populations that have the same $k \cdot \tau$ value. $a \cdot M$ and k/M were shown to be approximately invariant in a worldwide study of pandalid shrimp growth, maturation and demography (Charnov, 1979, 1982, 1993). If δ is similarly invariant across populations, pandalid shrimp are predicted to change sex at an invariant relative size ($L_\tau/L_\infty = \text{constant across populations}$). Of course, the argument generalizes to other sex changers provided their $a \cdot M$, k/M and δ are invariant across populations/species with otherwise different absolute time scales. While we have no knowledge of how invariant δ might be, several comparative studies suggest that $a \cdot M$ and k/M may well be expected to be invariants *within* various taxa (Charnov, 1993).

There are two additional invariance rules here. First, species with the same $a \cdot M$, k/M and L_τ/L_∞ values will also have the same τ/a ratio. To see this, write $L_\tau/L_\infty = 1 - e^{-k \cdot \tau}$, then

$$L_\tau/L_\infty = 1 - e^{-(k/M)(\tau/a)(M \cdot a)} \quad (3)$$

Second, with a constant instantaneous mortality rate of M , the sex ratio (δ/φ) among the breeders will also be invariant (see also Charnov and Bull, 1989). To see this, note that

$$\delta/\varphi = \frac{\int_0^\tau e^{-M \cdot x} dx}{\int_\tau^\infty e^{-M \cdot x} dx} \quad (4)$$

After integration, only $M \cdot \tau$ and $a \cdot M$ will remain in the ratio, and both are invariants.

Our theoretical analysis simplifies the life history in two ways worthy of note. First, we assume a *stationary* population (i.e. unchanging in size with a stable age distribution). Second, we approximate the adult life table with a single instantaneous mortality rate (M). These simplifications are common in life-history analysis (Charnov, 1991, 1993) and have been used in earlier analyses of shrimp sex change (Charnov, 1979, 1982). Pandalid shrimp are known to alter the pattern of sex change in the face of temporal variation in the age (size) distribution (Charnov *et al.*, 1978). An earlier analysis (Charnov, 1979) looked carefully at the *stationary* and *constant M* assumptions and concluded that neither greatly altered the sex change predictions from those obtained under more realistic life table and population dynamics assumptions, at least for the prediction of an average over several years.

Dimensionless invariance under change in scale has been shown to be a common feature of life histories within many taxa (Charnov, 1993; Gemmil *et al.*, 1999). There are, of course, other kinds of invariance or symmetry rules that are also useful in understanding

life histories (e.g. allometry and trade-off-invariance; Charnov, 1991, 1997; Charnov and Downhower, 1995; Enquist *et al.*, 1999). Figure 1 strongly suggests that constant or invariant relative size-at-sex-change (L_{50}/L_{\max}) holds across shrimp populations with otherwise quite different individual growth rates (i.e. L_{\max} varies consistently with factors such as temperature; Skúladóttir and Pétursson, 1999); it is much more difficult to estimate the breeding sex ratio or the relative age-at-sex-change (τ/a). It will undoubtedly prove worthwhile to apply these invariance ideas to other sex changers.

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