



















vice-versa. Froese (2000) points out that if several weight-length relationships are available for a species, then a plot of  $\log a$  over  $b$  will form a straight line and can be used to detect outliers. For example, 25 estimates of weight-length relationships were available for the gila trout, *Oncorhynchus gilae* (Miller, 1950), from various streams in the Gila River system in New Mexico (Propst and Stefferud, 1997). Parameter  $a$  is log-normally distributed with geometric mean  $a = 0.0099$ , 95% confidence limits of 0.0072–0.0137, and total range of values from 0.002 to 0.086. Exponent  $b$  is normally distributed with mean  $b = 3.012$ , 95% confidence limits of 2.948–3.075, and total range of values from 2.60 to 3.32. The 95% confidence limits of the mean include 3.0 and thus the overall growth pattern of the species is isometric. A robust regression analysis of  $\log a$  over  $b$  identifies one outlier and after its removal linear regression explains 99% of the remaining variance (Fig. 8). In other words, the strong interrelationship between parameters  $a$  and  $b$  is linearized in a plot of  $\log a$  over  $b$  and helps in detecting WLRs that are questionable because of e.g. narrow size range, few data with high variance, or outliers in the respective sample. In some cases, outliers could be a misidentification of a similar-looking species, or a population that differs in body shape from the others.

Froese (2000) and Kulbicki et al. (2005) show multi-species plots of  $\log a$  over  $b$  to demonstrate the interdependence of these parameters. Here I repeated this plot (Fig. 9) using the means of the parameters per species to avoid bias towards well-studied species with many estimates, and to reduce the effect of intra-specific variability referred to above. Also, similar to Kulbicki et al. (2005), I used different symbols for different body shapes obtained from FISHBASE. A dotted line at  $b = 3.0$  was inserted to indicate the areas of negative-allometric, isometric and positive-allometric growth. Note that, as discussed above in the context of Fig. 6, many points below  $b = 2.5$  and above  $b = 3.5$  are based on only very few WLRs and are likely to move closer to the centre of the graph when more estimates become available for these species.

As can be seen from the distribution of the different symbols relative to the regression line in Fig. 9, the variation in  $\log a$  is largely a function of the body shape of the respective species. A robust multiple regression of  $\log a$  as a function of  $b$  and body shape as a categorical variable explains 82% of the variance in Fig. 9 and results in:

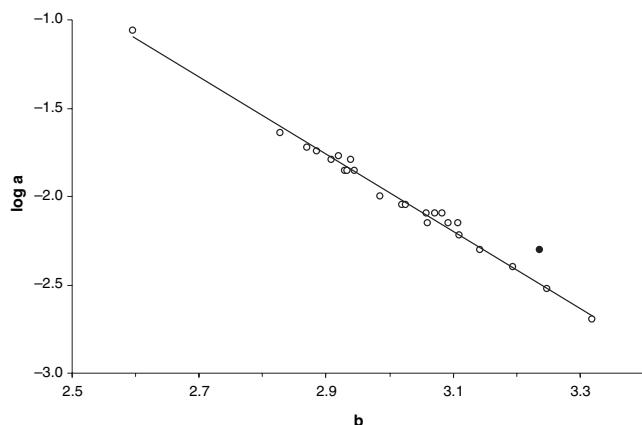


Fig. 8. Plot of  $\log a$  over  $b$  for 25 weight-length relationships of *Oncorhynchus gilae*. Black dot identified as outlier (see text) by robust regression analysis (robust weight = 0.000). Regression line:  $\log a = 4.544 - 2.174b$ ,  $n = 24$ ,  $r^2 = 0.9902$ ,  $CV = -0.0167$

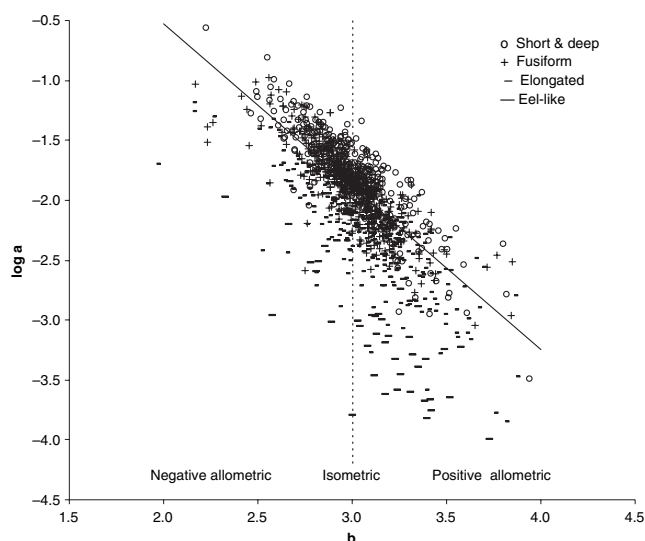


Fig. 9. Scatter plot of mean  $\log a$  (TL) over mean  $b$  for 1223 fish species with body shape information (see legend). Areas of negative allometric, isometric and positive allometric change in body weight relative to body length are indicated. Regression line based on robust regression analysis for fusiform species, with  $n = 451$ , intercept =  $2.322 - 0.133 = 2.189$ , and slope as in Eqn 17

$$\log a = -1.358b + 2.322 - 1.137(1 \text{ if eel-like, else } 0) - 0.3377(1 \text{ if elongated, else } 0) - 0.1331(1 \text{ if fusiform, else } 0), \quad (17)$$

robust multiple regression of  $\log a$  as a function of  $b$  and body shape as categorical variable, with  $n = 1223$ , slope =  $-1.358$ , 95% CL =  $-1.405$  to  $-1.311$ ,  $r^2 = 0.8225$ , and coefficient of variation =  $-0.0876$ .

One can interpret Eqn 17 as having the same slope as the regression line shown in Fig. 9 but being moved up or down along the dotted line, depending on the body shape of the fishes under consideration. Thus, most of the considerable variance in Fig. 9 can be accounted for by differences in body shape, allometric vs isometric growth patterns, and insufficient data for reliable estimation of mean values for  $a$  and  $b$  for some species.

**Form factor**

The slope of  $\log a$  vs  $b$  can be used to estimate for a given WLR the value that coefficient  $a$  would have if exponent  $b$  were 3 (Eqn 18). This value ( $a_{3,0}$ ) can be interpreted as a form factor of the species or population.

$$a_{3,0} = 10^{\log a - S(b-3)}, \quad (18)$$

form factor  $a_{3,0}$  of a species, where  $S$  is the slope of the regression of  $\log a$  vs  $b$ .

If not enough WLRs are available for the species or population in question for estimating the regression of  $\log a$  vs  $b$ , then the mean slope  $S = -1.358$  from Eqn 17 can be used as proxy for estimating the form factor.

The form factor  $a_{3,0}$  can be used to determine whether the body shape of a given population or species is significantly different from others. For example, FISHBASE 12/2005 contained nine weight-length relationships for *Gadus morhua* from the North Sea and four from the Baltic. If we had a hypothesis that body shape of cod in the Baltic were different from the North Sea, we would calculate the respective form factors from

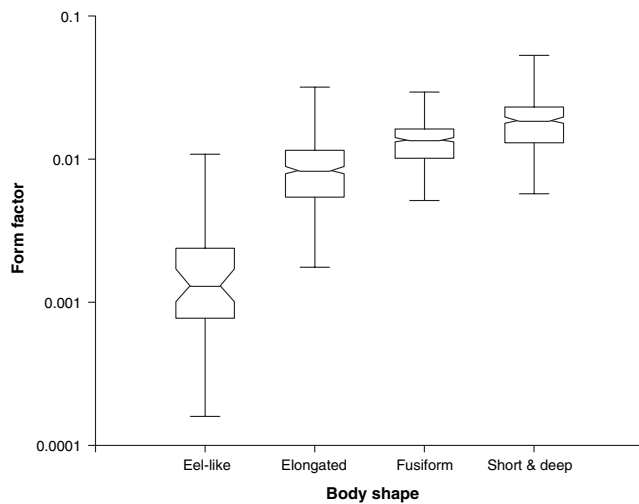


Fig. 10. Distribution of form factor  $a_{3,0}$  by body shape for 1,316 fish species. Form factor calculated from Eqn 18 using across-species slope of  $S = -1.358$  from Eqn 17

Table 1  
Relationship between body shape and form factor  $a_{3,0}$  for 1316 fish species

Body shape	Median $a_{3,0}$	95% CL	5th–95th Percentile	n
Eel-like	0.00131	0.00099–0.00165	0.00032–0.0139	45
Elongated	0.00838	0.00775–0.00906	0.00293–0.0178	403
Fusiform	0.0137	0.0131–0.0140	0.0061–0.0240	451
Short and deep	0.0187	0.0172–0.0193	0.0077–0.0336	324

Eqn 18 and perform a two-sample t-test on  $\log a_{3,0}$ . This results in the null-hypothesis being accepted [ $t$ -value = 0.6263, prob. level = 0.5439, power (0.05) = 0.08844], i.e. there is no significant difference in body shape between these populations.

In Fig. 10 the relationship of the form factor with body shapes of fishes is explored. There is a clear and significant increase of median  $a_{3,0}$  from eel-like to elongated, fusiform and short or deep body shapes (Table 1). This confirms the interpretation of  $a_{3,0}$  as a form factor and as an indicator of the body shape of fishes, but note the overlap of ranges, which does not allow assigning body shape based only on the form factor.

As pointed out by Kulbicki et al. (2005), there seem to be viability limits as to how elongated or spherical a fish can be. From the 5th percentile of eel-like fishes in Table 1 we can derive a lower ‘thinness’ limit of the form factor  $a_{3,0}$  of 0.00032, which is about 0.03% of the volume given by the cube of body length. Similarly, from the 95th percentile of short and deep fishes in Table 1 we can derive an upper ‘plumpness’ limit of the form factor  $a_{3,0}$  of 0.0361, which is about 4% of the length cubed. The latter appears low and would increase if we had considered standard length instead of total length, i.e. excluding the length of the caudal fin from calculating the cube of length.

Kulbicki et al. (2005) analysed body proportions and weight-length relationships for 396 species of fishes from New Caledonia. They provided guidance for estimating preliminary WLRs for fishes where none were available, based on seven measurements that could be taken from suitable

pictures, plus a classification as to whether the species is flat or laterally compressed, oval, or round in cross-section. Here I provide a simplified version of that approach, i.e. a very preliminary WLR for a species where none exists can be derived by using the median value of parameter  $a_{3,0}$  based on the respective body shape of the species from Table 1, and setting exponent  $b$  to 3.0. A better preliminary estimate can be obtained if at least one specimen within the size-range of interest is available, length and weight are measured, exponent  $b$  is set to 3.0, and the coefficient  $a$  is obtained from  $a = W/L^3$ .

#### Condition factor

Heincke (1908) established the usefulness of Fulton’s condition factor (Eqn 1) for comparing seasonal changes in nutritional condition. This is best done by a double-logarithmic plot of condition over length, where the connected points will form a more or less straight line. Alternatively, respective WLRs can be transformed to condition at length using Eqn 4. For example, the comber *Serranus cabrilla* (Linnaeus, 1758) in the Aegean Sea has seasonal WLRs with spring  $a = 0.0326$ ,  $b = 2.601$ ; summer  $a = 0.0207$ ,  $b = 2.767$ ; autumn  $a = 0.0126$ ,  $b = 2.955$ ; and winter  $a = 0.0135$ ,  $b = 2.914$  (Moutopoulos and Stergiou, 2002). In all seasons reported here, large specimens have lower condition than small specimens, as indicated by exponent  $b < 3$  and shown in Fig. 11. This trend is least expressed in autumn and winter, when small and large specimens have about the same condition, and is most expressed in spring during the spawning season. The dotted line is based on geometric mean  $a$  and mean  $b$  (see below) of all WLRs of this species, including other areas. It shows that the Aegean Sea population, except for small specimens in spring and large specimens in autumn and winter, has a lower condition than the average for this species.

Exploring the relevance of seasonal changes in condition is not a priority in current stock assessment work, probably because the general pattern in adult fishes is well known: a decrease during times of low temperatures and/or low availability of food, an increase towards the spawning season, a sharp decline after spawning, especially in females, and a second increase after spawning (e.g. see Fig. 8 in Le Cren, 1951). However, with the recent goal of ecosystem-based fisheries management (Pikitch et al., 2004), sustainable catches are to be

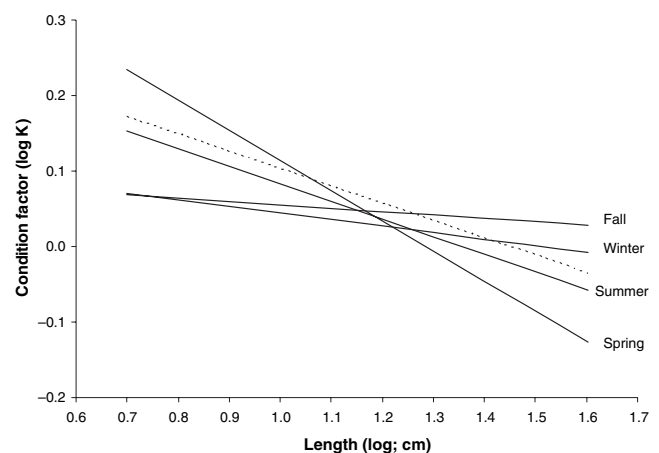


Fig. 11. Log-log plot of condition vs length calculated from weight-length relationships of *Serranus cabrilla* taken in spring, summer, autumn and winter in the Aegean Sea, respectively. Dotted line shows condition factors associated with geometric mean  $a$  and mean  $b$  across all available WLRs for this species

taken with the least impact on respective stocks. This can be done by catching fish only at an optimum size where, for a given cohort, the product of survivors times mean individual weight reaches a maximum (Beverton, 1992; Froese and Binohlan, 2000; Froese, 2004) and thus the proportion of specimens to be taken from the stock, to obtain a certain catch, is minimal.

$$L_{\text{opt}} = L_{\text{inf}} \frac{3}{3 + M/k}, \quad (19)$$

estimation of optimum length  $L_{\text{opt}}$ , where  $L_{\text{inf}}$  and  $k$  are parameters of the von Bertalanffy growth function, and  $M$  is the instantaneous rate of natural mortality.

If no growth or mortality information is available,  $L_{\text{opt}}$  can be obtained from an empirical equation by Froese and Binohlan (2000) (Eqn 20), and  $L_{\text{inf}}$  can be obtained from a good estimate of maximum length ( $L_{\text{max}}$ ), such as the mean length of the three largest specimens caught over the previous 10 years (Eqn 21).

$$L_{\text{opt}} = 10^{1.0421 \log L_{\text{inf}} - 0.2742}, \quad (20)$$

empirical equation for estimation optimum length ( $L_{\text{opt}}$ ) from asymptotic length ( $L_{\text{inf}}$ ), after Froese and Binohlan (2000).

$$L_{\text{inf}} = 10^{0.044 + 0.9841 \log L_{\text{max}}}, \quad (21)$$

Empirical equation for estimating asymptotic length ( $L_{\text{inf}}$ ) from maximum length ( $L_{\text{max}}$ ), after Froese and Binohlan (2000).

For most iteroparous fishes  $L_{\text{opt}}$  falls between the first and second spawning, thus making overfishing theoretically impossible, because all fish had a chance to spawn before being caught (Myers and Mertz, 1998). But as Heincke (1908) already pointed out, a further increase of e.g. 16% in mussel weight per specimen of North Sea plaice can be obtained if fish are caught when condition is highest in the non-spawning season. For example, if we assume a maximum total length of the comber in the Aegean Sea of 28 cm, we obtain from Eqn 21 an asymptotic length of 29.4 cm and from Eqn 20 the length at optimum size as 18.0 cm, which is about the same as the size of females at first maturity (Papaconstantinou et al., 1994). Using Eqn 4 with optimum length and the seasonal WLRs presented above, we obtain the following mean condition factors: spring  $K = 1.03$ , summer  $K = 1.06$ , autumn  $K = 1.11$ , and winter  $K = 1.05$ . Spawning season for this species is in spring and summer. Catching comber in the Aegean Sea only around 18 cm total length in autumn would thus deliver specimens in best condition (5–8% more weight per specimen than in other seasons), with least impact on the stock.

#### Relative condition and relative weight

Le Cren's (1951) relative condition factor (Eqn 5) is suitable for comparing condition within a given sample. Wege and Anderson's (1978) relative weight (Eqn 9) is useful for comparing condition across populations and species; however, their decision to take as a reference point a value larger than mean weight at length makes it arbitrary to calculate and use. Rather, I suggest deriving relative weight by comparison with a mean weight ( $W_m$ ) derived from a mean length–weight relationship representative of the species as a whole. I suggest using geometric mean  $a$  ( $a_m$ ) and mean  $b$  ( $b_m$ ) across all available, non-questionable weight–length estimates for a species as parameters of the mean weight–length relationship.

The relative weight ( $W_{\text{rm}}$ ) of a specimen with weight  $W$  and length  $L$  is then given by:

$$W_{\text{rm}} = 100 \frac{W}{a_m L^{b_m}}, \quad (22)$$

estimation of relative weight as percentage of mean weight derived from a mean weight–length relationship for the respective species.

For example, if we revisit the seasonal condition estimates for *Serranus cabrilla* in the Aegean Sea (Fig. 11), we can now express these as relative weights of a medium-size fish of 20 cm total length and find that these were 89.3% in spring, 93.2% in summer, 99.7% in autumn and 94.5% in winter. Medium size specimens in this Aegean Sea population apparently do not reach and surpass 100% of mean weight, confirming a hypothesis by Stergiou et al. (1997) that fishes in the oligotroph eastern Mediterranean have lower weight at length than those in the central and western Mediterranean.

#### Recommendations

Within-species variance in weight–length relationships can be substantial, depending on the season, the population, or annual differences in environmental conditions. As a result, differences in weight estimated from length can be two-fold or more, depending on which relationship is chosen. Thus, if at all possible, one may want to re-estimate weight–length relationships for the specimens under study. The following guidelines for data collection and analysis of weight–length relationships can be given:

- 1 Make certain that the gear used for collecting specimens do not introduce a bias with respect to length or weight, such as can be the case if only one size of gill net is used; gill nets tend to select fat fish among the shorter ones and thin fish among the longer ones, thus introducing a bias in  $b$  (Kipling, 1962).
- 2 When selecting specimens for measuring weight–length data, strive to include the size range to which the relationship will later be applied. Do not include early juveniles, such as fry and fingerlings, which in most fishes have not yet obtained adult body shape (Le Cren, 1951; Carlander, 1969; Murphy et al., 1991; Safran, 1992). If needed, estimate separate length–weight relationships for different development phases or growth stanzas (see Fig. 3). Also, do not include very old specimens, which often have distorted body forms with unusually high proportions of fat. Obviously aberrant specimens that are unusually thin or that are stunted or otherwise distorted should not be included.
- 3 Strive to include about equal numbers of randomly selected small, medium-size and large specimens. There is no need to measure large numbers of abundant medium-size specimens, as these have little influence on the relationship. For example, 10 small, 10 medium-size and 10 large specimens will normally suffice to establish a reliable length–weight relationship. If specimens are rare, lower numbers will also be acceptable.
- 4 If only one or few specimens of similar size are available, set  $b = 3$  and determine  $a$  from  $a = W/L^3$ ; take the geometric mean of  $a$  in case of several specimens.
- 5 When planning data collection, try to sample as many months as possible. Analyse samples by month to detect seasonal variation.

- 6 Test for differences between sexes. If such differences are significant, present separate relationships for males, females, and both sexes.
- 7 When selecting published weight-length relationships for use elsewhere, choose a relationship where data were sampled in the same season in the same or adjacent areas. If such studies are not available, take a study with parameters close to the median of  $a$  and  $b$  over all available studies. Alternatively, use geometric mean  $a$  and mean  $b$  across all available studies.
- 8 When discussing within-species variation in weight-length relationships, first do a  $\log a$  vs  $b$  plot to detect and exclude outliers. Then focus on variation in condition, which is likely to be driving variation in parameters  $a$  and  $b$ , e.g. with the help of a  $\log K$  vs  $\log L$  plot (Fig. 11). Try to find and explain e.g. seasonal, geographic, climatic or other patterns in the variation of the condition factor.
- 9 When exploring relative condition of individuals within a sample, use Le Cren's (1951) relative condition factor (Eqn 5). When exploring relative condition across populations or species, use relative weight in relation to mean weight (Eqn 22).
- 10 When exploring isometric vs allometric growth, use mean  $b$  and discuss whether the available length-weight studies cover a wide-enough seasonal and geographical range to be representative for the species. If strong allometric growth is found, try to find the reasons for such significant changes in body proportions.
- 11 When discussing across-species variation in length-weight relationships, use mean values of  $b$  and  $\log a$  by species. You would expect the overall mean of  $b$  to be close to 3.0, but there may be, for example, phylogenetic or functional groups of fishes with a tendency for allometric growth. You may want to calculate and discuss the general form factor (Eqn 18), which is likely to differ between phylogenetic or functional groups of fishes, or between riverine or lacustrine habitats.
- 12 When presenting weight-length relationships, make sure to indicate the number of specimens processed, range and type of length measurements, units (preferably grams and centimetres, to reduce the number of digits in  $a$  and facilitate comparisons between studies), parameters  $a$  and  $b$  with their respective 95% confidence limits, and the coefficient of correlation. Make your WLRs available to FISHBASE (<http://www.fishbase.org>), so that they can be archived and used by others.

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**Author's address:** Rainer Froese, Leibniz Institute of Marine Sciences IfM-GEOMAR, Düsternbrooker Weg 20, D-24105 Kiel, Germany.  
E-mail: rfroese@ifm-geomar.de