Growth, natural mortality, length-weight relationship, maximum length and length-at-first-maturity of the coelacanth *Latimeria chalumnae*

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Synopsis

Based on the re-interpretation of published data, the von Bertalanffy growth function parameters of the coelacanth, *Latimeria chalumnae,* are estimated as L_∞ = 218 cm total length, s.e. 23; K = 0.059 (year^{-1}), s.e. 0.012; t_0 = -3.3 (year), s.e. 0.5, corresponding to a life span of 48 years. The length-weight relationship of the form W = a * TL^b, with wet weight (W) in g and total length (TL) in cm, is estimated as a = 0.0278, b = 2.89, r^2 = 0.893, n = 87, range = 42.5–183 cm TL. Using extreme value theory, the maximum length for female coelacanths is estimated as 199 cm TL (95% confidence interval = 175-223 cm TL) and for males as 168 cm TL (95% confidence interval 155-180 cm TL). Based on data from seven females with embryos or mature eggs, the length-at-first-maturity for females is estimated to be about 150 cm TL, corresponding to an age of about 16 years. Based on the value of t_0 = -3.6 years and on the presence of three scale rings found in a newborn coelacanth, the period of embryogenesis lasts for about three years, the longest known in vertebrates. The natural mortality rate is estimated at M = 0.12. Population food consumption is found to be 1.4 times the existing biomass per year, and gross food conversion efficiency indicates that only 10% of the consumed food is utilized for somatic growth.

Introduction

The recent discovery of a new species of coelacanths in the Sulu Sea, Indonesia, over 10,000 km from the known occurrence of *Latimeria chalumnae,* Smith 1939 in the Comoro archipelago, Mozambique Channel, and South Africa has renewed the interest in this living fossil (Erdmann et al. 1998). Coelacanths seem to have survived millions of years rather unchanged but are now considered endangered (Bruton & Stobbs 1991, IUCN 1996). This study revisits the information published on life-history parameters of *Latimeria chalumnae,* re-analyses growth and length-weight relationships, and provides new estimates for maximum length, length and age-at-first-maturity, gestation period, natural mortality, life span, population food consumption, and gross food conversion efficiency. Thus expanding on our understanding of coelacanths, as recently summarized in Forey (1998).

Materials and methods

Data on length and weight as well as on eggs and embryos of *Latimeria chalumnae* were extracted from the Coelacanth Inventory (Bruton & Coutouvidis 1991, Bruton 1992, Bruton 1993a+b, Bruton 1999). The data set is available in FishBase (Froese & Pauly 1998) and on the Internet at http://www.fishbase.org. For the purpose of this study we assumed that all known coelacanths from the western Indian Ocean belong to one population, that catches of coelacanths more than one meter long have been random without size selectivity, and that fishing mortality has been negligible (see Bruton & Armstrong 1991 for a discussion of these issues).

The length-weight relationship of the form logW = loga + (b * logTL), in which W = wet weight in g and TL = total length in cm, was estimated using the linear regression algorithm of the MS Excel 97 software. All following length measurements refer to total length.

Estimates of maximum lengths (L_{max}) were obtained using the data described above and the extreme value theory (Gumbel 1954, Formacion et al. 1991), as implemented in the FiSAT software (Gayanilo et al. 1996, Gayanilo & Pauly 1997).

To estimate growth we re-interpreted length-at-age data presented in Hureau & Ozouf (1977); Pauly (1978) had identified this earlier analysis as misleading (see also Bruton & Armstrong 1991). For the purpose of this study we assumed that an apparently newborn specimen of 42.5 cm exhibited age 0 and that the common birth date of all specimens was August. This was based on the birth date of the specimen mentioned above and also the female (CCC no. 162) caught in August containing 26 embryos with fully absorbed yolk sacs. August is in the period between the southerly and northerly monsoons in the Comoros (Stobbs & Bruton 1991), when presumably a lack of strong currents would favor parturition. We also assumed that one scale ring as reported by Hureau & Ozouf (1977) indicated one year of age, as suggested by Balon et al. (1988). We used the non-linear fitting routine of FiSAT (Gayanilo et al. 1996, Gayanilo & Pauly 1997) to estimate the parameters of the von Bertalanffy growth function (VBGF) from the resulting data (Table 1).

Table 1. Length, sex, month of capture, and observed scale rings of *Latimeria chalumnae* as stated in Hureau & Ozouf (1977). Age was re-estimated in this study. The record marked with an asterisk was excluded from the subsequent analysis. Numbers of the Coelacanth Inventory (Bruton and Coutouvidis 1991) are given as cross-reference.

CCC No.	Length (cm)	Sex	Month of capture	Scale rings	Age (years)
29.5	30.5	embryo	Jan.	2	-0.5
94	42.5	female	Aug.	3	0
76	85	female	Apr.	8	5.67
105	89.9	unsexed	Sept.	9	6.08
7	120	male	Sept.	13	10.08
6	126	male	Feb.	13	10.50
5	127	male	Jan.	15	12.42
3	129	male	Sept.	15	12.08
19	132	male	Oct.	15	12.17
24	140	female	Jul.	18	15.92
13	154	female	May	20	17.75
71	160	female	Nov.	21	18.25
20*	180	female	Jan.	23	20.42

Results and discussion

Of the 151 available occurrence records of *Latimeria chalumnae*, 87 contained information on length and weight (Figure 1). The heaviest specimen was a female of 179 cm and 98 kg. The largest male measured 160 cm TL and weighed 77 kg. Coelacanths are not obviously sexually dimorphic (Bruton & Coutouvidis 1991; McAllister & Smith 1978). The resulting combined-sex length-weight relationship was:

$$W = 0.0278 * TL^{2.89} , r^2 = 0.893, TL = 42.5 - 179 \text{ cm}, n = 87$$

The double-logarithmic version of this relationship (Figure 1) explains 89% of the observed variance and thus appears to be suitable for estimating weight from length observations within the given range, despite the heterogeneous origin of the data and the warning of Bruton & Coutouvidis' (1991, p. 373) that 'some of the weight estimates are likely to be inaccurate'. The exponent of the relationship (b = 2.89) is close to 3, indicating that adult coelacanths follow a roughly isometric growth pattern, as suggested by McAllister & Smith (1978). Coelacanths have a relatively high value of a = 0.028 (with weight in g and length in cm), as is found in 'sturdy' fishes such as bonefishes and triggerfishes, whereas fusiform fishes such as scombrids have an average a = 0.01, and eels have an average a = 0.001 (see data in FishBase, Froese & Pauly 1998). Our length-weight relationship for the coelacanth is similar to that of Bruton & Armstrong (1991), who gave a log intercept = -4.8964, b = 3.05, r^2 = 0.921 for a group of 84 specimens. Note, however, that the log value of the intercept given here probably refers to weight in

kg (as stated in the text) and not in grams (as stated in Table 2 of Bruton & Armstrong 1991). Thus, using weight in kg at log intercept of -1.8964 results in a value of a = 0.0127. We used essentially the same data as did Bruton & Armstrong (1991). However, we included the smallest and the largest specimens known to date, in order to make the equation applicable over a wider size range.

Table 2 shows the available information on the reproductive status of coelacanth specimens. Of the female specimens ranging in size from 42.5 to 179 cm, two (142 and 145 cm TL) were approaching maturity and nine specimens of 160-179 cm carried eggs or embryos. It appears that all females larger than 160 cm were mature. The length (L_m) at which 50% of the females reach maturity then falls between 145 and 160 cm, with L_m = 150 cm probably being a reasonable estimate. Bruton & Armstrong (1991) estimated the length at first maturity at 125 cm TL, based on a hypothetical population structure, and expressing their hope that this '...will stimulate further research' (p. 306). We believe the data in Table 2 support our current estimate.

Table 2. Information on the reproductive status of female coelacanth specimens available in the Coelacanth Inventory (Bruton & Coutouvidis 1991).

CCC No.	Length (cm)	Date of capture	Reproductive status
173	133	August 1995	The gonad is small and the sex is not apparent.
8	142	November 1954	Immature female with maturing eggs.
141	145	November 1986	Immature female.
29	160	January 1962	Female with 5 embryos with half-resorbed yolk-sacs.
146	161	June 1987	Female with 30 eggs.
79	163	January 1972	Female with 19 mature eggs.
159	164	April 1994	Female with 67 small eggs in early oogenesis.
171	165	March 1995	Ovary with numbers of developing egg follicles.
10	166	March 1955	Female discovered with eggs during dissection.
154	168	June 1989	Female with 59 eggs.
166	178	December 1991	Female with 10-12 pups of about 28 cm.
162	179	August 1991	Female with 26 embryos with resorbed yolk-sacs.

A preliminary empirical relationship between asymptotic length and length-at-first-maturity (Binohlan 1998, data also available at http://www.fishbase.org) suggests that fishes of about 200 cm maximum size mature at about 100 cm. The value of L_m = 150 cm estimated in this study is significantly higher. The observed reproductive load, i.e., the ratio between L_m and L_∞ of 0.69, is typically found in much smaller fishes of about 50 cm asymptotic length (Binohlan 1998). Pauly (1984) suggested that L_m and L_∞ are both determined by the species-specific gill surface area. As illustrated in Figure 3 (based on Pauly 1998 and Hughes 1972, 1976), the relative gill surface area of coelacanths is clearly lower than in other fishes of this size and resembles that typically found in much smaller fishes with similar reproductive load (to 0.69). The low gill surface area also explains the slow growth found in this study in line with Pauly's theory of oxygen as a limiting factor for the growth of fish (Pauly 1981, 1984). It further explains the observed energy-saving behavior of the nocturnal, drift-feeding coelacanths described by Fricke et al. (1987) and the suggestion of Hughes & Itazawa (1972) and Hughes (1976) that coelacanths would have breathing difficulties in warm waters; the latter relationship is consistent with Uyeno's (1991) observation that a temporarily released live specimen became more active in deeper and supposedly cooler water with more oxygen. It also suggests that oxygen-demanding organs such as the brain will be relatively small, as is confirmed in Figure 4 (see also Locket 1980, Pauly et al. 1998), making it less likely that coelacanths have well-developed electrosensing capabilities (suggested, e.g. by Northcutt 1980), that usually are associated with large brains. Note,

however, that lampreys also have very small brains but posses electro-receptors (Fritzsch & Moller 1995).

The results of fitting the VBGF to the re-interpreted length-at-age data of Hureau & Ozouf (1977) are shown in Figure 5. We excluded the 180-cm specimen (CCC no. 20) because it seemed to be an outlier, having the largest residual value and leading to an unrealistic estimate of $L_\infty = 270$ cm, if included. Also, it is well known that scale readings become unreliable with increasing age (e.g., O'Gorman et al. 1987), and future studies using otolith data may show an even slower growth rate. The resulting VBGF parameters were $L_\infty = 218$ cm, s.e. 23; K = 0.059 (year^{-1}), s.e. 0.012; $t_0 = -3.3$ (year^{-1}), s.e. 0.5. Our asymptotic length is higher than the 200 cm estimated by Pauly (1978), but within the confidence limits (175 - 223 cm) of the independent estimate of L_{max} (see above). We did not calculate separate growth parameters for males and females because of the limited number of length-at-age data, especially for males. The given parameters will apply better to females, while males can be expected to have a lower asymptotic length and a slightly higher K (see Figure 5).

Taylor (1958) suggested that the life span of fishes could be calculated as the age at 95% of L_∞ from the equation:

$A_p = t_0 - \ln(1 - p)/ K,$

in which A_p is the life span in years, t_0 and K are VBGF parameters, and p is a fraction of L_∞ (in this case 0.95). This results in a life span of coelacanths of 48 years, supporting Bruton & Armstrong's (1991) opinion that coelacanths may live 40-50 years. It is incompatible, however, with two previous estimates, namely 11 years for a 180 cm female (Hureau & Ozouf 1977) and 7-8 years for an individual of 170 cm (Uyeno 1984). Applying the same equation to the reproductive load of 0.69 leads to a female age at first maturity which is three years more than the estimate of Bruton & Armstrong (1991).

The gestation period for coelacanths was predicted to last more than 13 months by Hureau & Ozouf (1977). Normally, the VBGF parameter $t_0 = -3.3$ (year) cannot be interpreted biologically, because fish larvae do not grow according to the VBGF, which describes the growth of gill-breathing animals (Pauly 1981). However, in live-bearers such as coelacanths, the oxygen demand of the embryos is provided ultimately through the gills of the mother, and thus VBGF applies to the growth of the embryos. This suggests that the gestation period of coelacanths is about three years (see also Figure 5), exceeding the longest known gestation period in vertebrates of two years recorded for piked dogfish, *Squalus acanthias*, with a calculated longevity of nearly 100 years, a maximum length of 160 cm TL, and maturation between 10 and 35 years of age (Compagno 1984, Nammack et al. 1985, see data in FishBase, Froese & Pauly 1998). Our gestation time estimate for coelacanths is supported by the two rings found on the 30.5 cm embryo and the three rings found on the 42.5 cm newborn specimen (see Table 1), assuming that scale rings in embryos are formed by the same process that forms the annual scale rings of the mother.

Beverton (1992) pointed out that there is an intermediate age t_{opt} at which the biomass (and egg production) of a year-class reaches a maximum. The corresponding length L_{opt} can be calculated from:

$$L_{opt} = L_\infty * 3 / (3 + M / K),$$

in which M is the natural mortality rate.

Solving this equation for M results in:

$$M = K * (3L_\infty/L_{opt} - 3).$$

To obtain an estimate of L_{opt} we grouped the available length data in size classes of 20 cm. For specimens without weight data, we used the above length-weight relationship to calculate the corresponding weight. We then summed up the weight in each length class, resulting in a maximum weight of 183 kg in the 120-139 cm length class, suggesting an L_{opt} of 130 cm (Figure 6). The ratio of L_{opt} to L_∞ of 0.59 compares well with the average ratio of 0.61 found by Froese & Binohlan (in press)[1] for 243 different fish species. Solving the equation above with $L_{opt} = 130$ cm and L_∞ and K as estimated above results in M = 0.1198, which equals the estimate of M = 0.12 derived from Pauly's (1980) empirical equation, with L_∞ and K as above, and a temperature of 14°C, commonly encountered off the Comoros in depths of about 170 m (Balon et al. 1998).

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[1] Froese, R. & C. Binohlan. Empirical relationships to estimate asymptotic length, length at first maturity, and length at maximum yield per recruit in fishes. J. Fish Biol. (in press).

Based on McCosker (1979), Bruton & Stobbs (1991) and Forey (1998), the coelacanth is a carnivore, feeding mainly on benthic snappers, cardinal fishes, mesopelagic lanternfishes, and cuttlefish. Based on the 9 known food items listed in Forey (1998), a Montecarlo routine in FishBase 99 (in prep.)[2] estimated an average trophic level of 4.5, s. e. of 0.76.

The population food consumption per unit biomass was estimated using the empirical equation of Palomares & Pauly (1998) for carnivorous fish, viz.:

$$\log Q/B = 7.964 - 0.204 \log W_\infty - 1.965\ T' + 0.083\ A,$$

in which Q/B is the food consumption per unit biomass; W_∞ the asymptotic weight; T' the mean annual temperature of the water body expressed as $T' = 1000/\text{Kelvin}$ (Kelvin = °C+273.15); A is the aspect ratio of the caudal fin which was set to 1.0 for this study, assuming that the caudal fin and epicaudal lobe form a functional unit and roughly fill a square of the height of the caudal fin. With the length-weight relationship and L_∞ estimated above, we calculated a W_∞ of 159288 g. Following the discussion in Balon et al. (1988), we assumed an average temperature of 14°C during most of the digesting phase.

The parameters lead to a Q/B estimate of 1.39, suggesting that the coelacanth population consumes the equivalent of 1.4 times its biomass per year, a rather low value as compared with other large fishes living at similar temperatures (Table 3), and providing another suggestion of slow growth.

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[2] Froese, R. and D. Pauly. (Editors). Bailly, N. and M.L.D. Palomares (Translators). FishBase 99. Concepts, structure et sources des données. ICLARM, Manila, Philippines. In preparation.

The life-history parameters obtained above were used to estimate the gross food conversion efficiency (GE), a key input in trophic models (e.g., Christensen & Pauly 1992a). Two methods for estimating GE were used. The first method expresses GE as a ratio between production (P) and consumption (Q) (Christensen & Pauly 1992b) as a function of the biomass (B) of the population. The second method predicts GE using the empirical equation of Palomares & Pauly (1998) for carnivorous fishes, viz.:

$$\log GE = -5.847 + 0.720 \log Z + 0.152 \log W_\infty + 1.360\, T' - 0.062\, A,$$

where GE is the gross conversion efficiency of the population, W_∞, T' and A are as defined above, and Z is the total mortality. Assuming that there is no active coelacanth fishery and that Z = M. The value of M = 0.12 year^{-1} estimated above was used for both methods. The first method yielded a GE value of 0.086 while the second lead to a value of 0.09. These estimates are practically similar and suggest that coelacanths turn only about 10% of their food consumption into somatic growth. This value falls within the lower end of the range of 10-30% established by Christensen & Pauly (1992b) and is particularly low when compared with other carnivorous fishes which have GE values of 20-30% (Villy Christensen, personal communication).

Table 3. Population food consumption Q/B for *Latimeria chalumnae* obtained from this study as compared with Q/B and related values for 5 other populations of large, cold-water fishes (adapted from Palomares & Pauly 1998).

Species	Locality	T (°C)	W_∞ (g)	K (year^{-1})	M (year^{-1})	A	Q/B (year^{-1})
Oncorhynchus kisutch	marine pop.	13	10,541	0.65	0.68	2.40	4.08
Thunnus thynnus	Japan	15	622,000	0.41	0.20	6.70	3.94
Gadus morhua	Western Baltic	10	12,356	0.16	0.23	0.77	2.59
Gadus morhua	North Sea	12	15,714	0.30	0.20	0.77	2.26
Esox lucius	England	15	13,312	0.23	0.36	1.50	2.03
Latimeria chalumnae	marine pop.	14	159,288	0.059	0.12	1.00	1.39

Summarizing our findings leads to the following tentative conclusions: Coelacanths have a significantly smaller gill surface area than other fishes of their size. This restricts their occurrence to cold, oxygen-rich waters and suggests that specimens that were captured alive died of hypoxia in warm surface waters. Limited oxygen supply explains the tranquil lifestyle in specific habitats (nocturnal drift-feeding on benthic, deep-water fishes over rocky slopes at depths of 100-400 m), correlates with low food consumption and slow digestion rates (e.g., during their diurnal rest in caves), and results in slow growth, late maturity, and a long gestation period. Restricted distribution, small population size, slow growth, late maturity, and low fecundity make coelacanth populations vulnerable to external disturbances, such as being by-catch of artisanal fisheries, being targeted for science and the curio trade, or being out-competed by a fishery on their preferred food organisms.
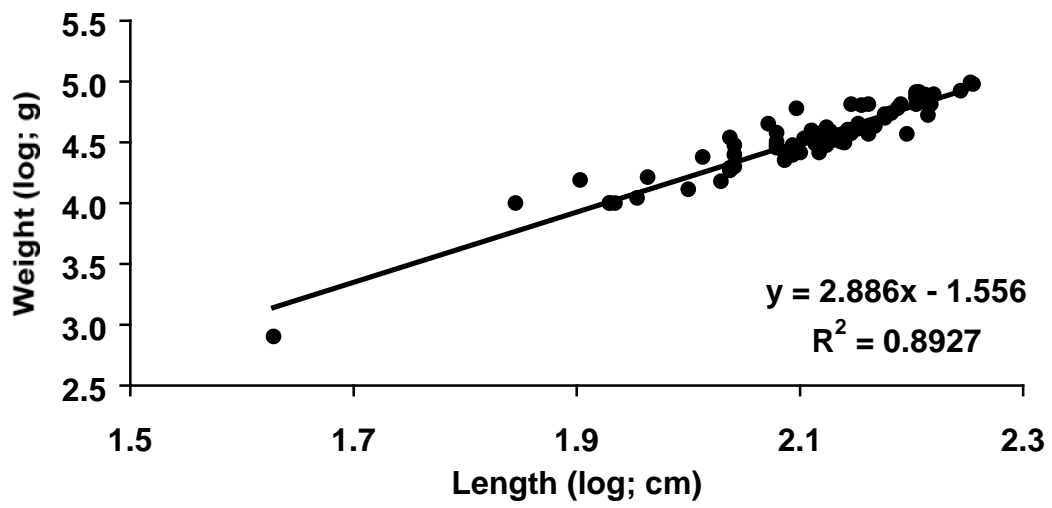
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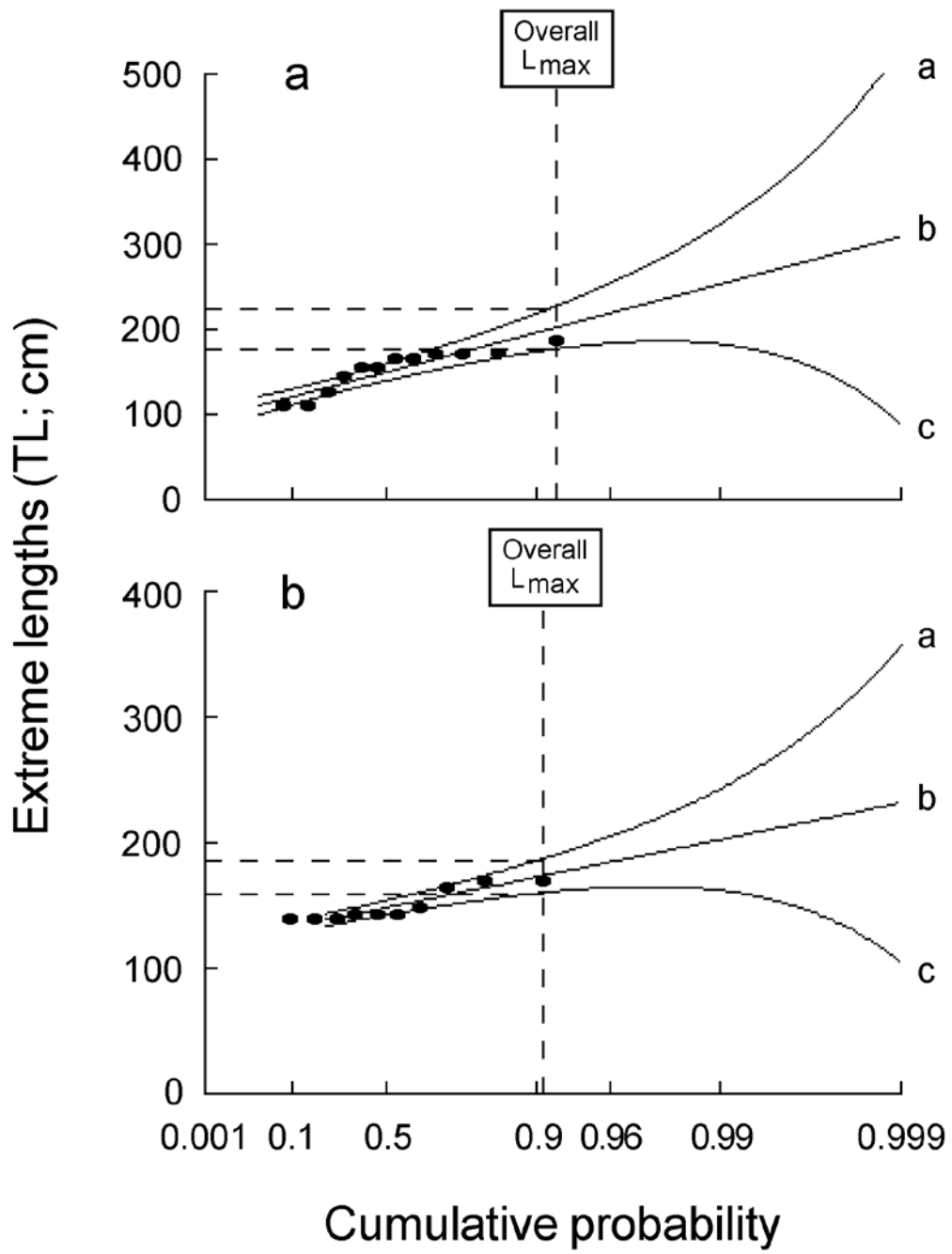
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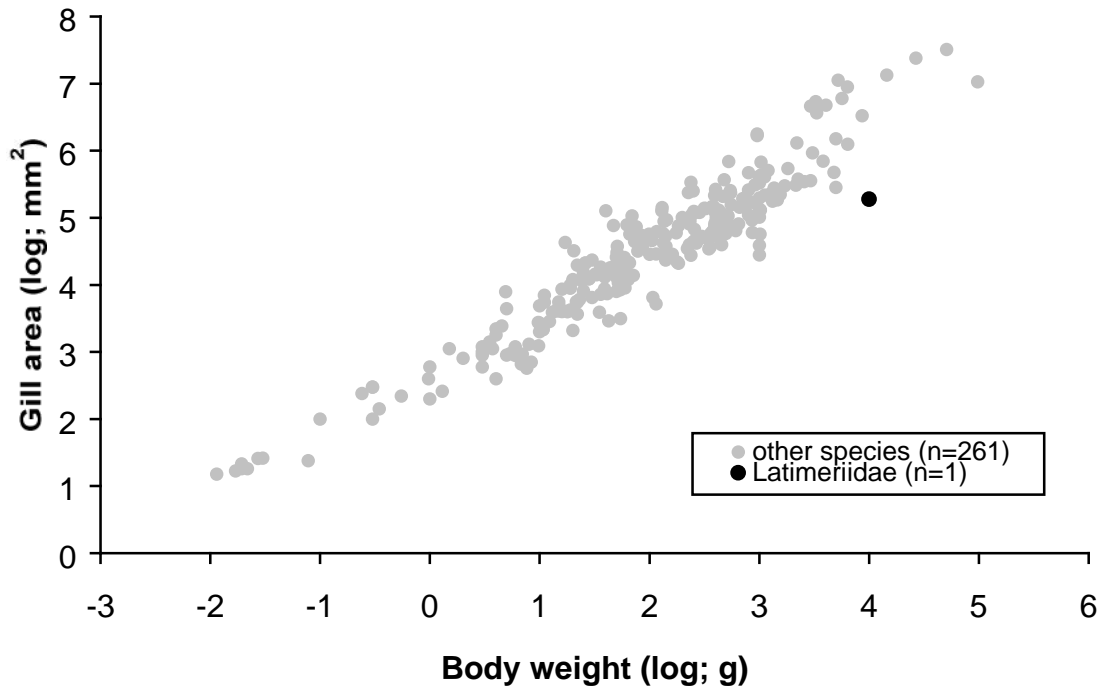
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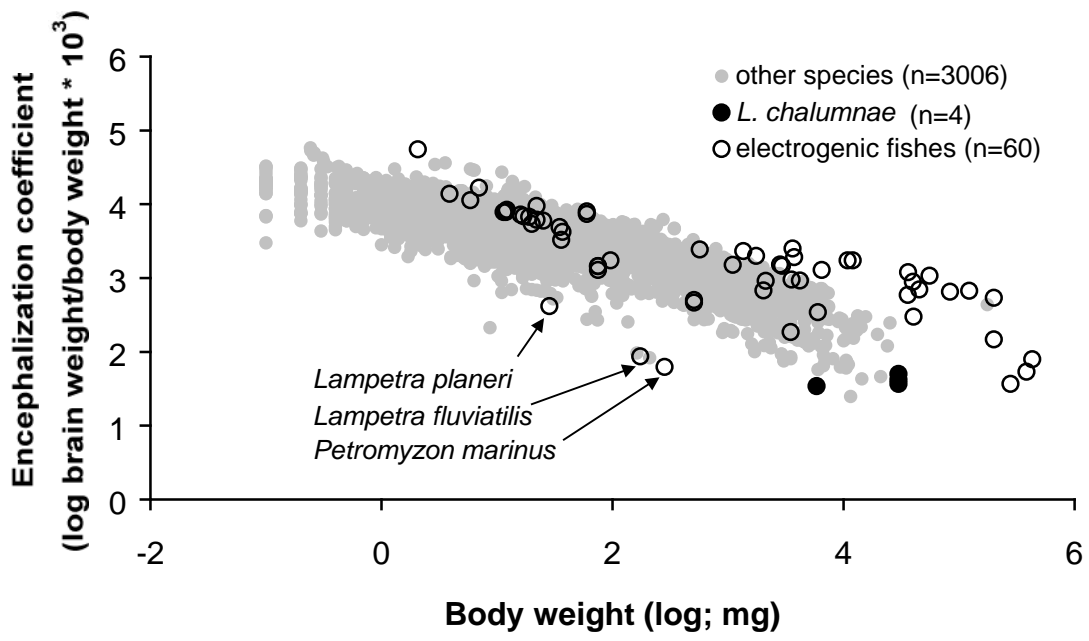
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$$y = 2.886x - 1.556$$
$$R^2 = 0.8927$$

Encephalization coefficient (log brain weight/body weight * 10^3) vs Body weight (log; mg)

- other species (n=3006)
- *L. chalumnae* (n=4)
- electrogenic fishes (n=60)

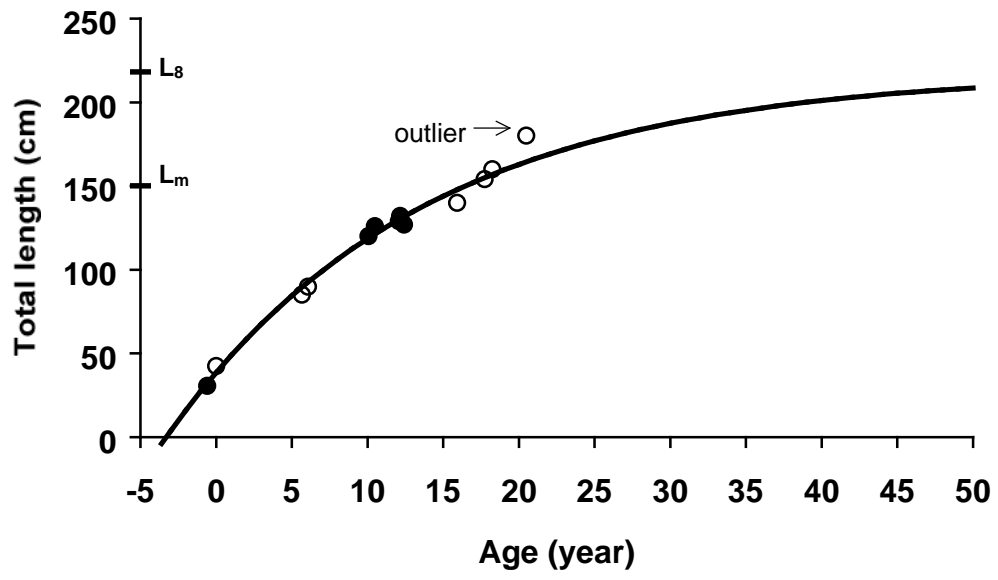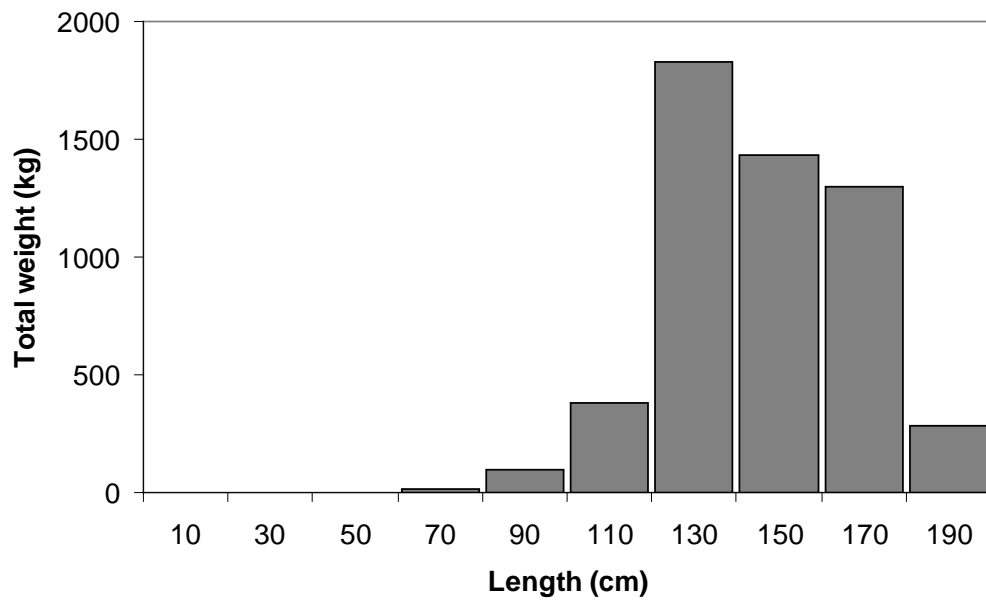*Lampetra planeri*
Lampetra fluviatilis
Petromyzon marinus

Figure legends

Figure 1. Length-weight relationship of *Latimeria chalumnae* based on 87 observations: source, FishBase (Froese & Pauly 1998).

Figure 2. Predicted maximum lengths for female (a) and male (b) *Latimeria chalumnae* based on occurrence data in FishBase (Froese & Pauly 1998) and on extreme value theory (Formacion et al. 1991). The predicted maximum length values and their 95% confidence intervals are obtained from the intersection of overall maximum length with the line b, and a, c, respectively.

Figure 3. Gill surface area of *Latimeria chalumnae* compared with that of other fishes: source, FishBase (Froese & Pauly 1998).

Figure 4. Relative brain size of *Latimeria chalumnae* (black dots) compared with that of other fishes, based on Pauly et al. (1998). Note that coelacanths have the smallest brains compared with other fishes of similar size, and much smaller than those of electrogenic fishes. This is, however, also true of Petromyzontiformes (open dots with arrows).

Figure 5. Growth in length of *Latimeria chalumnae*, based on data in Hureau & Ozouf (1977) assuming deposition of 1 scale ring per year. Open dots are females, filled dots are males. The outlier was excluded from the calculation. $L_m = 150$ cm refers to length at first maturity and $L_\infty = 218$ cm is the asymptotic length.

Figure 6. Total weight of *Latimeria chalumnae* per 20 cm year class, used to estimate L_{opt} and natural mortality.