

PRETENDING THEY ARE

D. PAULY*

Size is the single most important biological attribute of organisms, and it is the interplay of body mass and some limiting surface which determines the maximum size organisms can reach. In animals, the limiting surface depends, among other things, on whether they are terrestrial or aquatic, so breathing in air or water. In squid, fish and other water breathers, the limiting surface is that controlling respiration, i.e. gill surface area. A theory constructed from this is then presented along with six of its major corollaries, which are shown to be corroborated by available evidence. The key implication of the theory so articulated is that comparative approaches, such as used to infer or check the values of vital statistics in fish, should also work in squid. Also, current, very low estimates of longevity in large squid should be revised upwards.

This contribution follows an earlier attempt to show that many observed differences among fish groups are minor, relative to the profound similarities of the processes shaping their growth, mortality, etc. (Pauly 1994). Here, a theory developed earlier from what may be called “first principles” is adapted to explain features of growth and related phenomena in fish (Pauly 1981, 1984), a vertebrate group, compared to squid, an invertebrate group.

GROWTH AS AN INTERPLAY OF SURFACE AND VOLUME

The size of an organism is at any phase of its life cycle its most important feature (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Goolish 1991). Thus, the amount by which an organism can grow is, at any time, a function of the size it has already reached. A copepod can grow by only a few mg per day, whereas a whale can grow by dozens of kg in a day.

Similarly, the predation animals experience is largely a function of body size. Therefore, arrow-worms are innocuous to carcharhinid sharks not because the latter have evolved particular adaptation to escape predation by *Sagitta* spp., but because they are, throughout their life cycle, too large to be bothered by arrow-worms. Conversely, carcharhinid sharks are perfectly innocuous to copepods, which must instead avoid arrow-worms.

The question is: what is it that ultimately determines the size of an organism? The correct general answers could be their “genes”, their physiology (Atkinson

and Sibly 1997) or their ecology (Colinvaux 1978). The problem with such answers is that they do not necessarily allow for predictions. Moreover, a good predictive answer should not be biological, because most organisms would tend to evolve beyond a purely biological constraint to their size.

To be truly effective, constraint must be non-biological. Thus, geometry itself provides the constraint on organismic size (Pauly 1997). This manifests itself through the “tension” (or “contradiction” as defined by Hegel or Engels) between volumes, usually growing in proportion to the 3rd power of a linear dimension of organisms, and surfaces, always growing in proportion to a lesser power of the same linear dimension (though not necessarily with length squared; see below). This dimensional problem manifests itself differently in different organisms (Fig. 1).

In terrestrial mammals and birds, the tension occurs between the volume of the body wherein heat is produced, and the body surface through which heat is lost. One of the results of this is Bergmann’s Rule, stating that mammals and birds of high latitudes will tend to be larger (and have relatively shorter extremities) than their low-latitude congeners (Bergmann 1847). In very large mammals, so much internal heat may be generated that surfaces have evolved to dump excess heat (ears in elephants, flukes in whales), a minor variation on this theme.

There is another volume-to-surface problem in terrestrial organisms, where masses growing in proportion to length-cubed must be accommodated by legs or trunks whose resistance is proportional to their cross-sectional area, i.e. to πr^2 . Hence, gravity dictates the thin legs of passerine birds, the ostrich-like

* Fisheries Centre, 2204 Main Mall, University of British Columbia, Vancouver, B.C., Canada V6T 1Z4. Email: pauly@fisheries.com

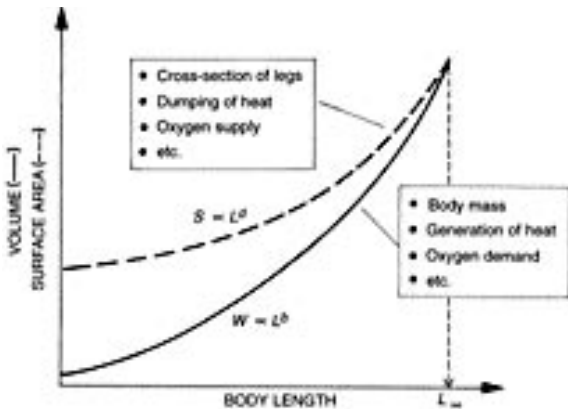


Fig. 1: In organisms, the increase of mass and related features is in proportion to a power (b) of length, usually near 3. Growth of surfaces is always proportional to a power $d < b$, so making some surface limiting for growth and maximum length, which must remain smaller than asymptotic length (L_{∞}). The specific surface varies among organisms, and may be limiting locomotion, heat generation, respiration, etc.

legs of ostriches, and the elephant-like legs of (extinct) moas (Thompson 1942). Similar comparisons are possible among arachnids, daddy longlegs and tarantulas, or among plants, grasses and sequoia trees.

In insects, respiration takes place through trachea, thin tubes which divide up into finer and finer tubelets, which bring oxygen to, and take CO_2 from, individual body cells. This surface-limited system is so inefficient that it almost entirely fills larger insects, so providing a built-in constraint against there ever being monster ants!

GILLS AS LIMITING SURFACE FOR GROWTH

For fish, squid and other animals breathing in water through gills, gravity is not a problem. That is why the largest invertebrates (giant squid) and vertebrates (whales) live in the sea and not on land (Angel 1976). On the other hand, water is a difficult medium from which to extract oxygen: there is typically 30 times less O_2 in water than in air, water is 55 times more viscous than air, and the diffusion of O_2 in water is a staggering 300 000 times slower than in air (Schumann and Piiper 1966). Therefore, fish for example may spend up to 40% of their resting metabolism on breathing itself, a figure much higher than, for example, in

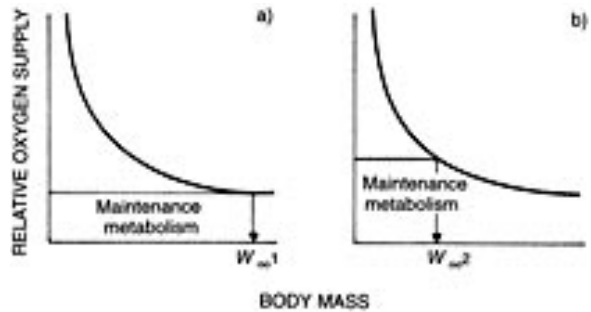


Fig. 2: Relationship between oxygen supply per unit of body mass (i.e. gill surface area per unit body mass) and the body mass of growing squid. Note that, in (a), growth in mass must cease when, at $W_{\infty,1}$, O_2 supply is equal to routine requirements (including capture and processing of prey). (b) shows that any factor increasing routine requirements (elevated ambient temperature, reduced food availability, stress, etc.) will tend to reduce the mass at which O_2 supply becomes limiting to further growth and hence reduces W_{∞} (adapted from Pauly 1984)

humans, where only 2% of resting metabolism is used for breathing itself (Schumann and Piiper 1966).

In gill-breathers, oxygen uptake is proportional to surface area of the gills (Pauly 1981). Thus, large squid will have greater oxygen uptake than small squid of the same species. However, the mass-specific or "relative" oxygen uptake of larger squid is bound to be less than that of their small congeners, given that their respiratory surfaces (gills and body) cannot grow as fast as their volume, and hence their demand for oxygen (see below). There must therefore be, for any species of water-breathing animals, a level of oxygen supply that is just sufficient to meet the routine metabolism appropriate to a certain habitat. This defines for a given species the maximum size that can be reached in a given environment (Fig. 2).

There is no reason why the mechanism illustrated in Figure 2 should not apply to squid, notwithstanding their hollow bodies. Therefore, it is necessary to follow up on some corollaries of a theory articulated about this graph.

FIRST COROLLARY: MAXIMUM SIZE DECREASES WITH INCREASING TEMPERATURE

The first obvious corollary that may be deduced from assigning a size-limiting role to gills is that the

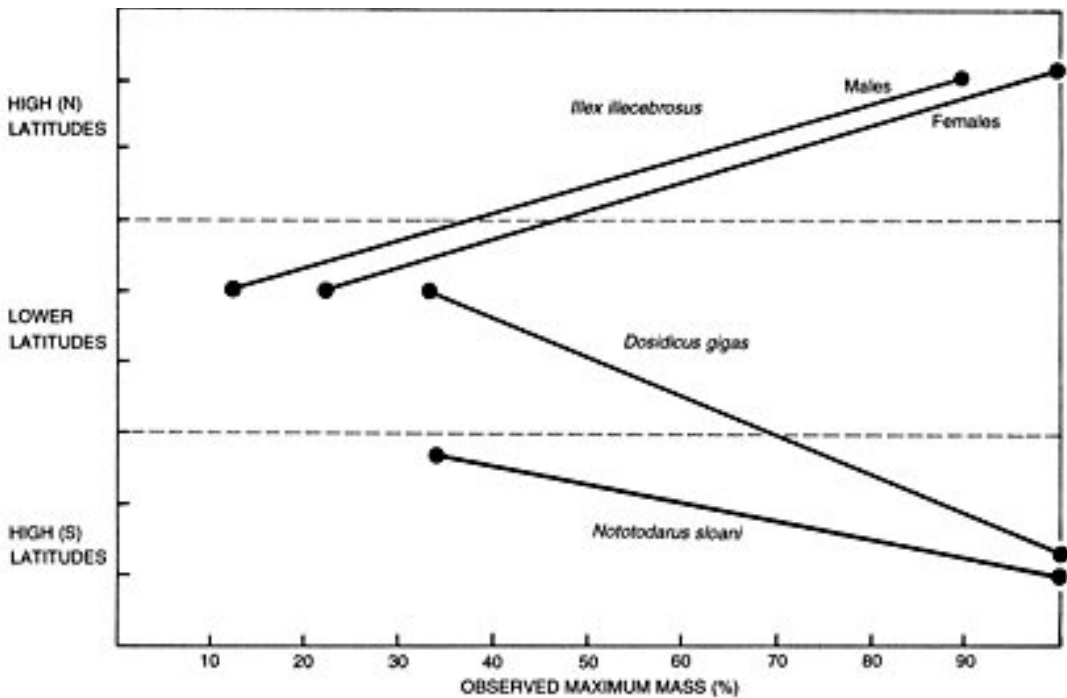


Fig. 3: Maximum size in three species of squid in relation to sea temperature as indicated by latitude (based on maximum mass in Ehrhardt *et al.* 1983, Roper *et al.* 1984)

maximum size squid can reach should decrease with increasing environmental temperature. As water surface temperature tends to decline with increasing latitude, an increase of observed maximum size with latitude would be expected in squid species that are neritic for at least some of their lives. Figure 3 shows an example for three species; Roper *et al.* (1984) may be consulted for other cases.

As size increases, so must longevity, because the factor (low temperature) associated with large maximum size also reduces metabolic rate. Hence, large (e.g. Antarctic) species should have much greater longevity than (smaller) temperate and tropical species (see below).

SECOND COROLLARY: pH CHANGES GENERATE STATOLITH RINGS

If oxygen supply ultimately determines the maximum size of squid, then it is also likely to affect squid growth before maximum size is reached. Strong

evidence exists to show that squid growth is oxygen-limited, although this evidence is often not perceived as such. Here is meant the daily rings shown to occur on the statoliths of all squid species so far examined for such structures.

Linking the processes relevant here (oxygen limitation during daily bouts of activity, and the formation of daily rings on statoliths) is straightforward in principle, and several physiological/chemical mechanisms have been proposed which provide this link. Lutz and Rhoads (1977) have proposed a comprehensive theory from which such mechanisms can be derived for molluscs in general, and bivalves in particular. The key point of their theory is that bouts of daytime activity (or of night-time activity in nocturnal species) increase oxygen requirements to a level that cannot be met by supply through the gills. The animal must revert to anaerobiosis, which lowers tissue pH and which causes, in bivalves, daily "etching" of the shells. The theory also accommodates stressful events, such as low tides, which induce non-daily rings (see e.g. Vakily 1992, who showed this and the other key tenets of the theory presented here to apply to bivalves). Similar

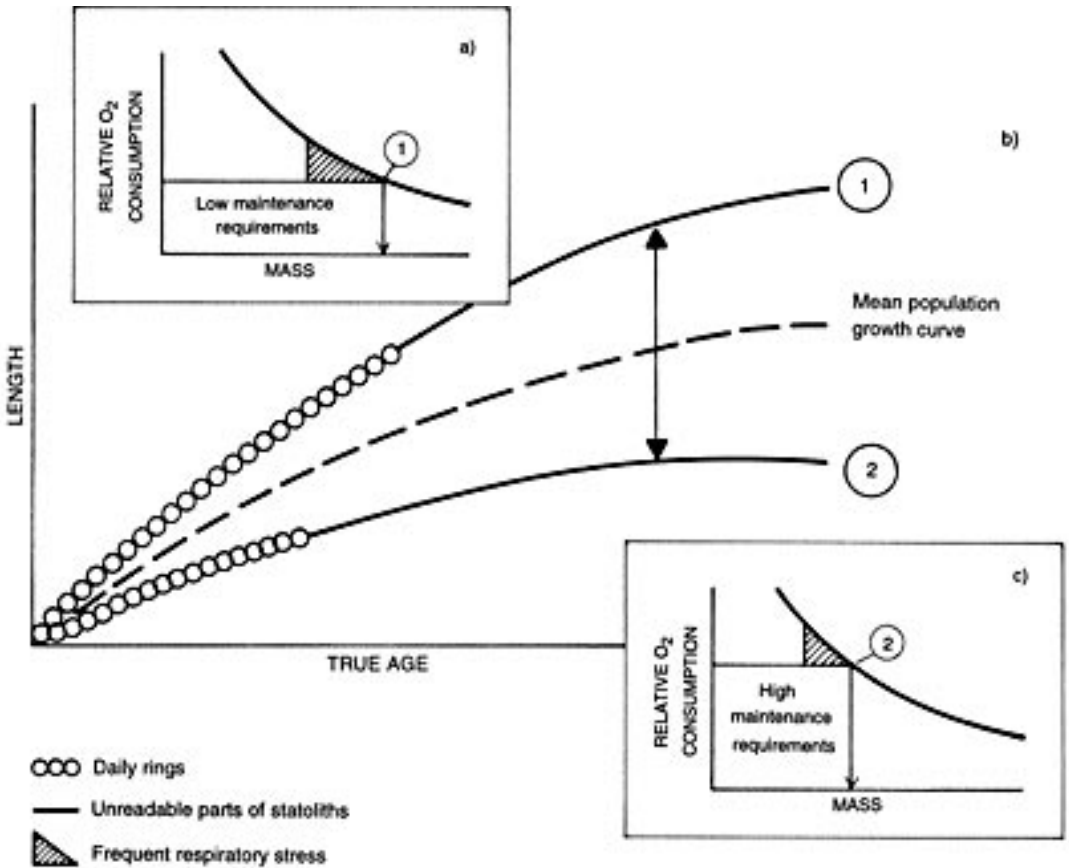


Fig. 4: Schematic representation of the process by which the mean growth rates of large squid tend to be overestimated, owing to non-consideration of slow-growing squid with unreadable statoliths (see text)

non-daily, stress-induced structures are also reported from fish: tidal rings, storms passing through reefs, spawning checks, etc. (see, e.g., Panella 1971, 1974, Longhurst and Pauly 1987, Gauldie and Nelson 1990).

Morris (1991), without citing the theory of Lutz and Rhoads (1977), proposed a similar mechanism for daily rings in squid statoliths. Interestingly, he noted that experimental stress, which keeps activity and hence O_2 consumption at elevated levels, suppressed the occurrence of a daily pH cycle, as required for the formation of daily rings. Lipiński (1993), also without reference to Lutz and Rhoads (1977), proposed a mechanism for changes in the pH of the endolymph surrounding statoliths that differs from that of Morris (1991). However, he retained the diurnal cycle of activity, and the diurnal cycle of periodic undersupply

of O_2 to their tissue as ultimate cause for the formation of daily statolith rings in squid.

Lipiński (1993) considered his and Morris' hypotheses of statolith formation incomplete because they "do not provide satisfactory explanations for a plethora [of phenomena such as] strong definition of some checks, variable number of growth layers per increment, variable increment width [...], etc.] which remain to be explained and investigated in detail". This statement is true if the key "role" assigned to statolith rings is to enable squid age to be determined. However, the scientifically interesting role of statolith rings is that their formation contributes crucial evidence to understanding the key factor limiting squid growth, so indirectly influencing other aspects of their biology.

THIRD COROLLARY: RESPIRATORY STRESS CAUSES AGEING BIAS

Figure 2 implies that respiratory stress is stronger and more frequent in adult gill-breathers than in the juvenile forms. On the other hand, different individuals of a given population will differ in their maintenance requirements for O_2 (even if they do not differ in their relative gill area), which leads to their having different growth curves (see Inserts a and c and Curves 1 and 2 in Fig. 4). This generates the observed variance in length about age in fish and squid populations (arrow in Fig. 4b).

Given its slower metabolic rate, the squid in Figure 4a will experience the size-associated respiratory stress at a larger size than the squid in Figure 4c. Such stress prevents daily rings (circles in Fig. 4b) from being formed, leading to blurred zones in otoliths and presumably also in statoliths. Otoliths (and statoliths) with such blurred zones (solid lines in Fig. 4b) must be discarded when daily age readings are performed, leading to only the fast-growing fish (and squid) being considered in age analyses (see Morales-Nin 1988). This is bound to cause considerable underestimation of mean age in adult squid. Indeed, this may be the very reason why "linear" or "exponential" growth curves often emerge from size-at-age data based on age readings presumed to be daily. Morales-Nin (1988) described this problem as follows:

"When the otolith increments in adult fishes are studied with light microscopy, areas with unclear increments are found. Ralston (1985) attributed these areas to imperfect sample preparations, and proposed the use of a method based on increment thickness to determine growth rate and interpolate age based on increment measurements. However, in *Lutjanus kasmira* from Hawaii, it has been shown that these areas are composed of very thin increments and are below the detection power of the light microscope. Thus, if growth is determined by Ralston's method, only the clearer and thicker increments, will be employed. Consequently, the growth parameters obtained were clearly overestimated."

This biasing effect (which is independent of any growth model being fitted to size-at-age data) has seemingly not been considered in statolith age studies involving adult squid. Indeed, the only serious discussion so far of the often large differences between age- and length-based studies in squid is that of Caddy (1991), who assumed, in spite of the admonitions

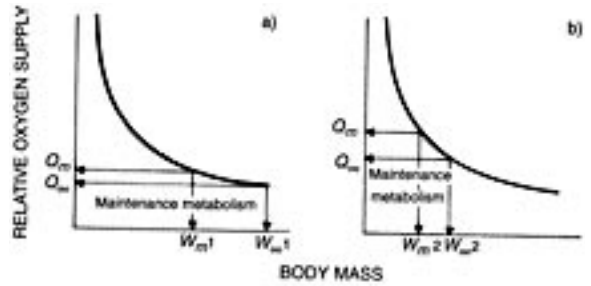


Fig. 5: Interrelationships between oxygen supply at maintenance level (Q_m), oxygen supply near first maturity (Q_{∞}), and the mass of fish. Note that the Q_m/Q_{∞} ratio is constant for two different habitats, one of which (a) is linked with large asymptotic size and a large size at first maturity, the other (b) associated with the opposite situation (modified from Pauly 1984). A similar mechanism can be assumed to trigger reproduction in squid as well (see text)

of Beamish and McFarlane (1983), that it is the length-based analyses which are inherently biased.

Performing the test implied by Figure 4 should be straightforward, because it implies the hypothesis of an increase with length of the unreadable fraction of statoliths. Such a test seems acutely needed for studies that involve adult squid from which "subdaily" rings are reported (and perhaps ignored, by lowering the magnification of one's microscope) without objective criteria for the distinction between daily and subdaily rings being presented. Thus, in a telling example, Jackson (1990) writes that "when using high magnification, or a very sharp focus, numerous subdaily rings could be discerned which often made counting of daily rings difficult. This was especially true in areas of the statoliths where rings were quite thick (wide). Using a lower magnification, or changing the plane of focus helped to delineate the true daily rings that were superimposed on the numerous subdaily rings."

FOURTH COROLLARY: RESPIRATORY STRESS INDUCES MATURATION

It is generally accepted among fish biologists that the growth of fish slows down after first spawning "because energy previously allocated to somatic growth" is allocated to gonad growth. This belief, although widespread, should be treated as the hypothesis that it is, i.e. the "reproductive drain hypothesis".

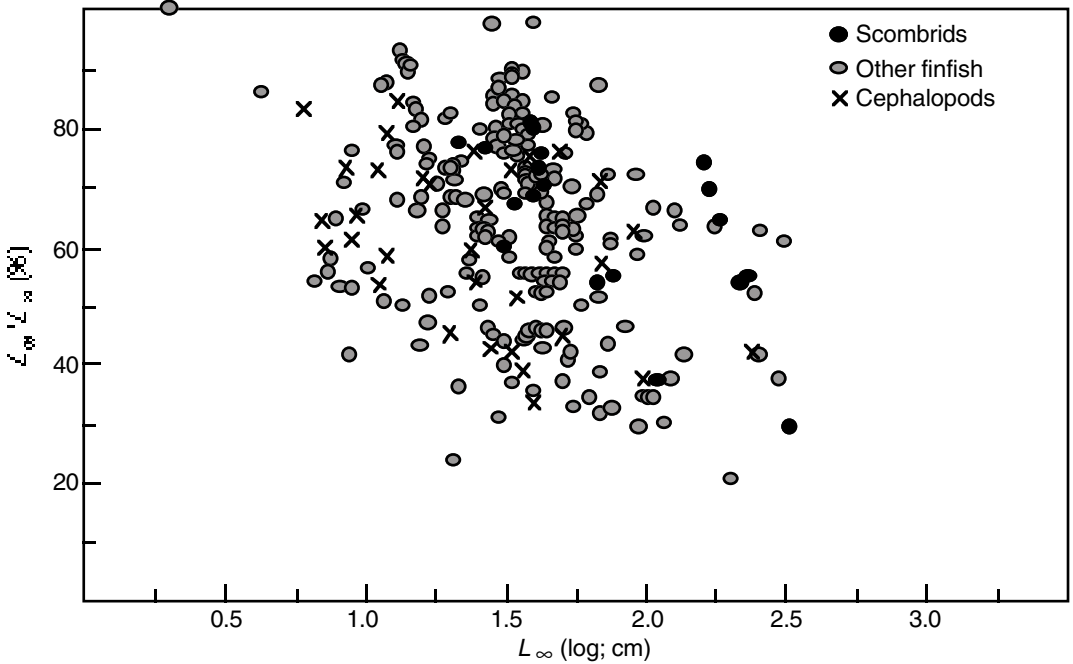


Fig. 6: Relation between L_m/L_∞ in 13 species of scombrid (22 cases), and 133 other species of fish (208 cases), and L_m/L_{max} in 32 species (and cases) of squid. Fish data from FishBase 97 (Froese and Pauly 1997); squid data from Roper *et al.* (1984)

In all species with anisogamy, i.e. throughout virtually the entire animal and plant kingdoms, it is the females which (by definition) make the bigger investment when they reproduce. Therefore, if the reproductive drain hypothesis holds, mature females should tend to be smaller than males of the same age, given their higher reproductive investment.

In about 80% of all fish species, the females become larger, or much larger, than the males, which is incompatible with the reproductive drain hypothesis (Pauly 1994). In Roper *et al.* (1984), information on which of the two sexes reaches larger maximum sizes, or reproduces at larger size (these two measures are equivalent here), is available for 50 species of cephalopod. Females were larger than males in 35 of 50, i.e. 70% of all cases, a value similar to that estimated for fish (Pauly 1994). This implies that the reproductive drain hypothesis does not apply for cephalopods any more than it does for fish.

The biological alternative to fish and squid ceasing to grow because they allocate energy to spawning is that the signal(s) which trigger(s) maturation is (are) set off when growth starts to decline, because relative gill area approaches the size at which all of the oxygen

passing through the gills must be devoted to routine metabolism, including capture and processing of prey (Pauly 1984). This is illustrated in Figure 5.

The energy required for elaboration of gametes is obtained by a slight reduction of activity, which in most fish (and most probably in squid as well) requires far more energy than growth, both somatic and gonadal (Koch and Wieser 1983). Relating maximum size and size at first maturity led in fish to the estimation of 1.4 as the ratio of metabolic rate at first maturity to that at W_{max} (Pauly 1984, 1994). Given that, in squid, the fraction L_m/L_{max} behaves approximately as in fish (Fig. 6), a similar ratio of about 1.4 may also be expected in squid.

Mangold (1987, p. 189), in her review of cephalopod reproduction, identified the following factors as related to "late spawning and large size": (1) long day length and high light intensity, (2) *ad libitum* feeding, (3) low temperature. Of these three factors, (2) and (3) can be directly derived from the theory proposed here, which is, at least in its present form, neutral to (1). Conversely, the factors which Mangold (1987) identifies as "leading to early spawning and small sizes" are: (4) short day length and low light

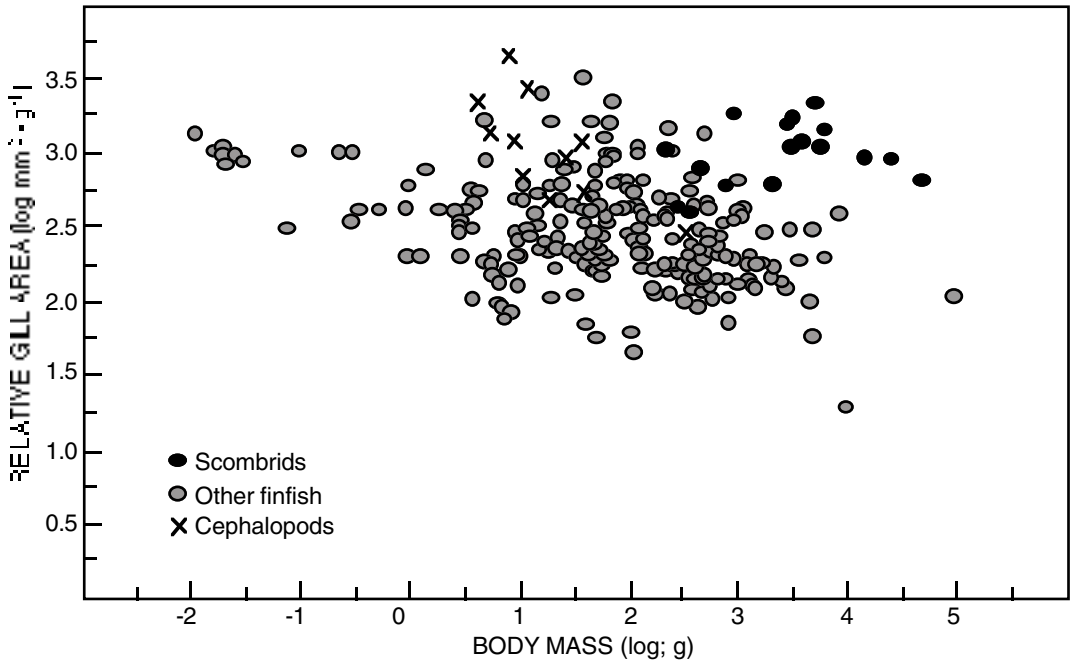


Fig. 7: Relative gill area (= gill area/body mass) of fish and squid v. their body masses. The data referring to 7 species of scombrid (18 cases) and 110 other fish species (245 cases) are from FishBase 97 (Froese and Pauly 1997); those for the 11 species of squid are from Madan and Wells (1996)

intensity, (5) restricted feeding, (6) high temperature. Again, the effects of factors (5) and (6) were predictable (Fig. 2).

FIFTH COROLLARY: GROWTH RATES INCREASE WITH GILL AREA

One obvious corollary of a theory linking gill area and growth is that species with large gills should exhibit rapid growth and *vice versa*. Figure 7 shows the gill area measurements for 11 species of squid, superimposed on gill area measurements for 117 species of fish, including 7 species of scombrid (mackerels and tunas), which have both fast growth and large gills (Pauly 1981, 1994). As may be seen, the 11 species of squid considered tend to have large gills, although not as large as those of tuna, as alleged by Madan and Wells (1996). This discrepancy stems from their comparison of relative gill area (mm²·g⁻¹) irrespective of body size, notwithstanding that relative gill area always declines with size (see above).

Growth parameters are not available for the entire

set of fish and squid species in Figure 7. However, Figure 8 still confirms that squid tend to have fast growth rates when compared with fish. (Whether or not one believes in asymptotic growth or not, it remains true that the product of W_{∞} and K has the dimension of a rate, e.g. g·day⁻¹, and so can be used to compare growth among species.) Indeed, squid display growth performances similar to those of small to medium-sized scombrids (but again, smaller than tuna).

SIXTH COROLLARY: ASYMPTOTIC GROWTH DOES OCCUR

The use of the von Bertalanffy growth curves in conjunction with cephalopods in general and squid in particular is fraught with controversy, as it was earlier concerning fish, and it would be better if this theme could be avoided. However, it cannot, because asymptotic growth is an inescapable prediction of growth as the net result of a difference between two rates, one related to a volume, the other to a surface (von Bertalanffy 1938, 1951, and see above). There-

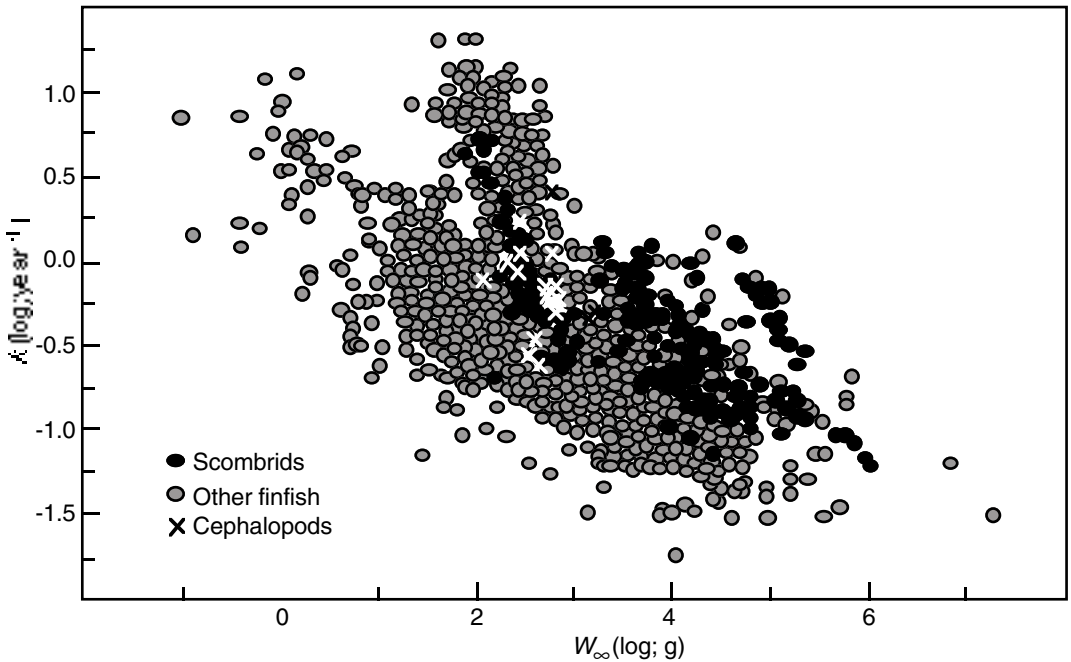


Fig. 8: Auximetric plot of 219 sets of mass growth parameters, representing 23 species of scombrid, 2 288 sets representing 1 121 other fish species, and 18 sets of cephalopod mass growth parameters, representing 15 species. (Fish data from FishBase 97, Froese and Pauly 1997; cephalopod data from Table 3 in Jarre *et al.* 1991.) Note position of cephalopods, corresponding to that of small scombrids (i.e. mackerels)

fore, if oxygen supply limits the growth of squid and other cephalopods, then their growth should conform to an asymptotic curve, i.e. either to the familiar von Bertalanffy model or to one of its variants (see below). That this is a necessary, but not a sufficient condition, for the theory to be correct goes almost without saying, as also noted by Lipiński and Roeleveld (1990). Many of those working with cephalopods have argued, on the other hand, that the von Bertalanffy growth model cannot accommodate the variety of growth patterns observed in cephalopods.

Figure 9 shows the variety of growth curves that can be generated with a von Bertalanffy growth curve incorporating seasonal growth oscillations (Pauly 1985). Clearly, such a version of the von Bertalanffy model is versatile enough to accommodate many observed cephalopod growth shapes, especially if the bias discussed in the third corollary is considered (recall Fig. 4). It is shown below that an even more versatile curve exists, the generalized von Bertalanffy growth function (Pauly 1981), one which can be used to describe the “exponential” growth of squid.

The ancestors of today’s cephalopods had shells

(Roper *et al.* 1984). The only surviving nautiloid genus *Nautilus* has only four species, with growth rates much slower than those of squid, and longevities ranging from 10 to 20 years (Kanie *et al.* 1979, Saunders 1983, Cochran and Landman 1984, Landman *et al.* 1988, 1989). Rodhouse (1998) suggests that squid evolved from shelled cephalopods through a process involving neoteny, or more precisely paedomorphosis (Gould 1977). This, among other things, would explain their rapid growth, akin to that occurring among the juveniles of most animals.

In many squid and other cephalopods, moreover, a strong spawning mortality eliminates many of the older specimens, leaving the initial “linear” or “log-linear” segments of growth curves, to which almost any function can be fitted, whether this makes physiological sense or not (see e.g. Bigelow 1994), and whether or not adult ages are underestimated (see the third corollary above). The disadvantage of such an eclectic approach is that when empirical observations (e.g. age-length pairs), are fitted to empirical curves, all that increases (instead of insight) is the amount of information available for later generalizations. No

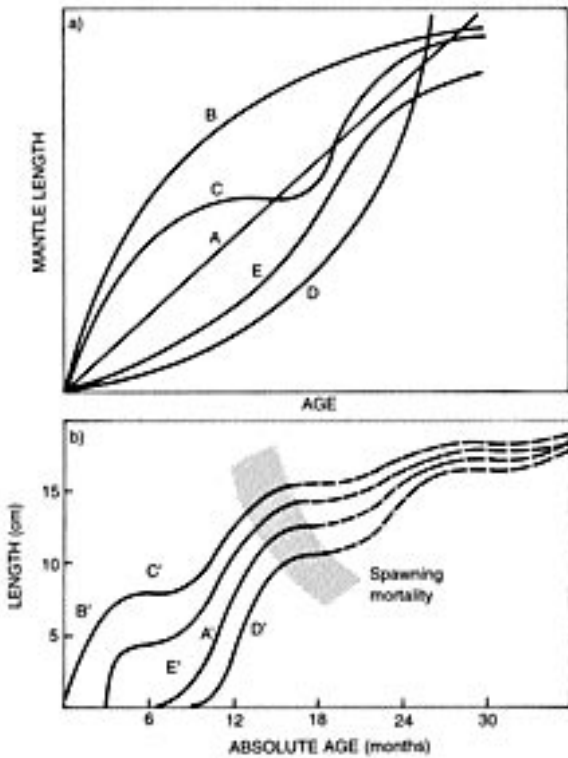


Fig. 9: Empirical v. von Bertalanffy growth curves for cephalopods. (a) Empirical curves for five loliginid species (after Hixon 1980). A, linear growth of *Loligo opalescens* (Fields 1965); B, asymptotic growth of *L. pealei* (Verrill 1881); C, cyclic growth of *L. vulgaris* (Tinbergen and Verwey 1945); D, exponential growth of *L. vulgaris* (Mangold 1963) and *L. pealei* (Summers 1971); E, sigmoid growth of *L. pealei*, *L. plei* and *Lolliguncula brevis* (Hixon 1980). (b) Curves generated by a seasonally oscillating version of the von Bertalanffy growth function (see Longhurst and Pauly 1987) using the same set of parameters ($L_{\infty} = 20$ cm, $K = 1 \cdot \text{year}^{-1}$), and the same amplitude of seasonal oscillations, but different birthdates. (Note that these curves largely duplicate the shapes above, assumed representative of squid growth, i.e. $A \approx A'$, $B \approx B'$, etc.)

theory is being tested and enriched which could be used to tell, for example that some of the empirical approaches are misguided. Thus, the growth estimates of Clarke (1980) for *Kondakovia longimana* of two years to spawning stood unchallenged for years. Even since then there has been a widespread belief that squid (including monstrously large ones) have annual life cycles, although such lifespan and the corresponding growth rates strain credulity given the large size reached by some species.

Clarke later prompted a re-examination on a statistical basis of the evidence which had led to his estimate (Jarre *et al.* 1991). Longevity, based on the pattern in Figures 8 and 9, was 8–10 years, a figure independently confirmed by Bizikov (1991) on the basis of age-related structures on cross-sections of *K. longimana* gladii.

Lipiński and Roeleveld (1990) showed that *Growing Sealife*TM plastic squid, when placed in water, display asymptotic growth; this shows, indeed, that “if a fit to growth data by the von Bertalanffy curve looks satisfactory, it does not therefore follow that this is evidence for anabolic and catabolic changes”. As it turns out, *Growing Sealife*TM plastic squid exhibit, however, as much “anabolism” and “catabolism” as can be expected from dead pieces of plastic.

Plastic squid do not grow “logarithmically” as fish larvae do, or as real squid seem to, especially when the age of the older specimens is underestimated. This would have implied that growth was limited only by food intake (i.e. water intake in the case of plastic squid), and that absolute growth rate (e.g. $\text{g} \cdot \text{day}^{-1}$) increased until an external limit was reached (metamorphosis in the case of fish larvae). Rather, the plastic squid displayed a form of asymptotic growth well represented by the standard von Bertalanffy model, with growth rates that declined linearly with length (see Fig. 2 in Lipiński and Roeleveld 1990), proof that something was working, from the onset, against water diffusing into the plastic.

This something is the cohesive force of the plastic itself, whose magnitude (k) should be proportional to the volume (W) of plastic that may absorb the water. Thus, the force acting against expansion of the plastic squid is a negative term, $-kW$. The force which pulls water into the plastic body of the squid is probably capillarity, which is by definition proportional to a surface, i.e., $HW^{2/3}$ (Thompson 1942). Therefore, the growth in mass (plastic + water) of a *Growing Sealife*TM plastic squid should conform to

$$dW/dt = HW^{2/3} - kW \quad (1)$$

Assuming $W = aL^3$ and integrating leads to

$$L_t = L_{\infty} (1 - e^{K(t-t_0)}) \quad (2)$$

i.e. the standard von Bertalanffy growth equation, which goes to show that there may be something to the surface v. volume story presented above.

Perhaps more importantly, this account provides a lead to the introduction of the generalized von Bertalanffy model. Throughout, it has been tacitly assumed that the limiting surface for growth itself grows in proportion of a linear dimension squared (as in Equation 1). As noted by von Bertalanffy (1951) this needs not be the case, however, and a generalized model can be derived from

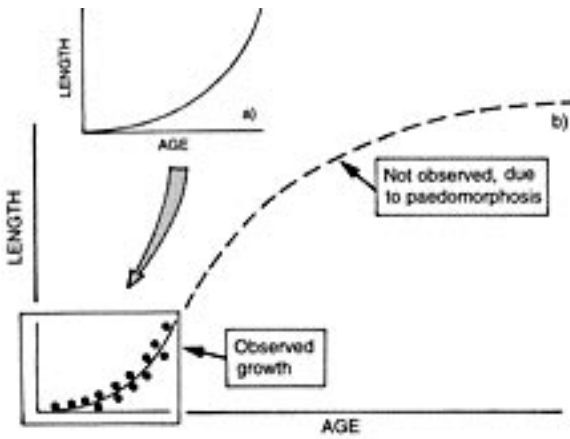


Fig. 10: Schematic representation of how the apparent "logarithmic growth" of cephalopods can be reinterpreted as the first phase of a generalized von Bertalanffy model sporting an inflexion point (Equation 6). (a) Curve describing apparent logarithmic growth. (b) Asymptotic model, describing juvenile and early adult growth (solid line) and the projected growth of the late adults (dashed line), usually not observable owing to spawning mortality and senescence

$$dW/dt = HW^d - kW \quad (3)$$

as long as $d < 1$.

In water breathers, gill area (G) can be straightforwardly linked to body mass using

$$G = aW^{d_g} \quad (4)$$

whereas metabolic rate (O_2) can be linked to body mass through

$$O_2 = a' W^{d_{O_2}} \quad (5)$$

Assuming that $d = d_g = d_{O_2}$ (see above), the exponent of the metabolism-mass relationships in a given species of squid can be used to parameterize the version of Equation (3) suitable for that species. (Note that the multiplicative terms of Equations 4 and 5 are irrelevant to this argument, as is therefore the observation that squid may use part of their body area to augment their gill area; only the exponents of the relationship matter here.) This leads to the appropriate value of D in a generalized von Bertalanffy model, of the form

$$L_t = L_\infty (1 - e^{-KD(t-t_0)})^{1/D} \quad (6)$$

where $D = 3(1 - d)$; Pauly (1981).

O'Dor and Wells (1987) pointed out that, for squid, d_{O_2} is generally ≈ 0.75 (implying $D \approx 0.75$), but with some very high values in some species, e.g. 0.96 for *Illex illecebrosus*, implying $D = 0.12$. Such

values of $D \ll 1$ lead to growth curves that may be interpreted as having two phases:

- (i) increasing growth rates in the juvenile phase, mimicking "logarithmic" growth;
- (ii) declining growth rates as the (relatively high) asymptote is approached (see Fig. 10b).

Owing to mortality (and possibly to paedomorphosis and the ageing bias mentioned earlier), the second phase, however, is often not visible in field-sampled specimens, although it is apparent in the growth curves of cephalopods raised in captivity, e.g. those compiled by Forsythe and Van Heukelem (1977, their Fig. 8.2).

Asymptotic growth is therefore not incompatible with accelerating growth in the juvenile stage. Indeed, the generalized von Bertalanffy growth model, which incorporates this feature, whose additional parameter (D) links growth with metabolic studies, and which can readily accommodate seasonal growth oscillations, may well be a good candidate for the generic squid growth model called for by Jackson (1994). It may even be speculated that one of its uses would be to allow assessing the "degree of paedomorphosis" displayed by various squid species, by establishing a relationship between the observed and non-observed parts of the curve (see Fig. 10, Curve b, whose latter part is exaggerated for emphasis, in analogy to the graphical "clock model" used by Gould (1977) to describe different forms of heterochrony).

DISCUSSION

More corollaries than the six presented above can be derived from the first principles in Figures 1 and 2. For example, it may be shown that fish growth increases, other things being equal, when the amount of dissolved O_2 in the water is increased (see e.g. Bedja *et al.* 1992); the same should apply to squid, etc.

However, expanding computations and evidence of this sort are useless if the intended audience assumes that generalities derived from another group of organisms do not apply to the group they study, just because it is "different". The point here is: in what manner is it different? It is evident that squid are different (e.g. in their bauplan, in the manner they feed, swim, capture prey, or communicate) from mackerel, or from fish in general. However, squid are affected, as fish are, by the physical constraints that shape the universe. Therefore, constraints to biological expression that are framed in terms of geometry, physics or elementary chemistry cannot be brushed

Table I: Evidence for applicability to *Loligo pealei* of a theory which gives a limiting role to O₂ supply, and hence to gill surface area

Observation*	Interpretation
Largest specimens in coldest parts of range	See Fig. 3 and Roper <i>et al.</i> (1984) for other squid, and Fig. 2 for explanation
Maturation occurs at smaller sizes in warmer parts of range	As occurs in fish, see Fig. 5, Pauly (1984, 1994), Mangold (1987)
Gill filaments grow relatively faster in warm parts of range	As required to elevate routine metabolism in warm, low O ₂ water
Males have more gill filaments than females	Males reach 50 cm mantle length, females only 40 cm, off New England (Roper <i>et al.</i> 1984)
<i>L. pealei</i> has relatively larger gills than <i>L. roperi</i>	<i>L. pealei</i> is the larger species where both occur in same area

* All observations are from Cohen (1976)

aside as irrelevant to a group of organisms because they were originally identified in another group. Rather, to the extent that an argument exists that links a biological phenomenon to an underlying physical phenomenon, and supportive data can be presented (see Table I for a last example), then it would be necessary to show from "first principles" why a favourite organism should be the exception. Therefore, for example, Bergmann's Rule does not apply to fish not because it was first found to apply in mammals, but because its very logic implies that it can only apply to terrestrial endotherms, whereas fish are ectotherms.

Similarly, the fact that squid absorb oxygen though their body surface does not overcome the gill-based argument presented here: body surface cannot keep up with body mass any more (and in fact even less) than gills can, as shown by the estimates of squid d_{O_2} tabulated by O'Dor and Wells (1987), which have a mean of 0.75, as in fish (Winberg 1960).

Therefore, in a sense, the point in the title of this paper, obviously meant to be provocative, is in reality moot. The theory presented should apply, with minor modification, to account for differences in bauplan to all aquatic, water-breathing ectotherms, whether fish, crustaceans, polychaetes or molluscs, anywhere. Indeed, as shown in Pauly (1989, 1994), it even applies to Arde, a two-dimensional world.

ACKNOWLEDGEMENTS

I thank several colleagues at ICLARM for their inputs: Dr M. L. Palomares for her crucial help with the graphs derived from FishBase 97; Ms A. Atanacio for redrawing the figures; Dr V. Christensen for encouraging me to think more deeply about plastic squid; and Ms S. Gayosa for the timely emergence of a complete manuscript. Two anonymous reviewers are thanked for their well meant advice.

LITERATURE CITED

- ANGEL, H. 1976 — *Monsters of the Deep. Sharks, Giant Squid, Whales and Dolphins*. London; Octopus Books: 128 pp.
- ATKINSON, D. and R. M. SIBLY 1997 — Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* **12**(6): 235–239.
- BEAMISH, R. J. and G. A. McFARLANE 1983 — The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112**(6): 735–743.
- BEJDA, A. J., PHELAN, B. A. and A. L. STUDHOLME 1992 — The effect of dissolved oxygen on the growth of young-of-the-year winter flounder, *Pseudopleuronectes americanus*. *Environ. Biol. Fishes* **34**(3): 321–327.
- BERGMANN, C. 1847 — Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gött. Stud.* **1**: 595–708.
- BIGELOW, K. A. 1994 — Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific. *Fishery Bull., Wash.* **92**(1): 13–25.
- BIZIKOV, V. A. 1991 — A new method of squid age determination using the gladius. In *Squid Age Determination using Statoliths. Proceedings of an International Workshop, Mazara del Vallo, Italy, October 1989*. Jereb, P., Ragonese, S. and S. von Boletzky (Eds). *Spec. Publ. NTR-ITPP* **1**: 39–51.
- CADDY, J. F. 1991 — Daily rings on squid statoliths: an opportunity to test standard population models? In *Squid Age Determination using Statoliths. Proceedings of an International Workshop, Mazara del Vallo, Italy, October 1989*. Jereb, P., Ragonese, S. and S. von Boletzky (Eds). *Spec. Publ. NTR-ITPP* **1**: 53–66.
- CALDER, W. A. 1984 — *Size, Function and Life History*. Cambridge, Mass.; Harvard University Press: 431 pp.
- CLARKE, M. R. 1980 — Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Rep.* **37**: 1–324.
- COCHRAN, J. K. and N. H. LANDMAN 1984 — Radiometric determination of the growth rate of *Nautilus* in nature. *Nature, Lond.* **308**(5961): 725–727.
- COHEN, A. C. 1976 — The systematics and distribution of *Loligo* (Cephalopoda, Myopsida) in the western North Atlantic, with descriptions of two new species. *Malacologia* **15**(2): 299–367.
- COLINVAUX, P. 1978 — *Why Big Fierce Animals are Rare: an Ecologist's Perspective*. Princeton, New Jersey; University Press: 256 pp.
- EHRHARDT, N. M., JACQUEMIN, P. S., GARCÍA B. F., GONZALEZ D. G., LOPEZ B. J. M., ORTIZ C. J. and A. SOLÍS N. 1983 — On the fishery and biology of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico. In

- Advances in Assessment of World Cephalopod Resources*. Caddy, J. F. (Ed.). *F.A.O. Fish. tech. Pap.* **231**: 306–340.
- FIELDS, W. G. 1965 — The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. *Fish Bull. Calif.* **131**: 108 pp.
- FROESE, R. and D. PAULY 1997 — *FishBase 97: Concepts, Design and Data Sources*. Manila; ICLARM: 256 pp.
- FORSYTHE, J. W. and W. F. VAN HEUKELEM 1987 — Growth. In *Cephalopod Life Cycles. 2. Comparative Reviews*. Boyle, P. R. (Ed.). London; Academic Press: 135–156.
- GAULDIE, R. W. and D. G. A. NELSON 1990 — Otolith growth in fishes. *Comp. Biochem. Physiol.* **97A**(2): 119–135.
- GOOLISH, E. M. 1991 — Aerobic and anaerobic scaling in fish. *Biol. Rev.* **66**(1): 33–56.
- GOULD, S. J. 1977 — *Ontogeny and Phylogeny*. Cambridge, Mass.; Harvard University Press: 501 pp.
- HIXON, R. F. 1980 — Growth, reproductive biology, distribution and abundance of three species of loliginid squid (Myopsida, Cephalopoda) in the northwestern Gulf of Mexico. Ph.D. thesis, University of Miami: 234 pp.
- JACKSON, G. D. 1990 — Age and growth of the tropical nearshore loliginid squid *Septoteuthis lessoniana* determined from statolith growth-ring analysis. *Fishery Bull., Wash.* **88**(1): 113–118.
- JACKSON, G. D. 1994 — Application and future potential of statolith increment analysis in squids and sepioids. *Can. J. Fish. Aquat. Sci.* **51**(11): 2612–2625.
- JARRE, A., CLARKE, M. R. and D. PAULY 1991 — Re-examination of growth estimates in oceanic squids: the case of *Kondakovia longimana* (Onychoteuthidae). *ICES J. mar. Sci.* **48**(2): 195–200.
- KANIE, Y., MIKAMI, S., YAMADA, T., HIRANO, H. and T. HAMADA 1979 — Shell growth of *Nautilus macromphalus* in captivity. *Venus* **38**(2): 129–134.
- KOCH, F. and W. WIESER 1983 — Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? *J. expl Biol.* **107**: 141–146.
- LANDMAN, N. H., DRUFFEL, E. R. M., COCHRAN, J. K., DONAHUE, D. J. and A. J. T. JULL 1988 — Bomb-produced radiocarbon in the shell of the chambered nautilus: rate of growth and age at maturity. *Earth planet. Sci. Letts* **89**(1): 28–34.
- LANDMAN, N. H., COCHRAN, J. K., CHAMBERLAIN, J. A. and D. J. HIRSCHBERG 1989 — Timing of septal formation in two species of *Nautilus* based on radiometric and aquarium data. *Mar. Biol.* **102**(1): 65–72.
- LIPINSKI, M. R. 1993 — The deposition of statoliths: a working hypothesis. In *Recent Advances in Cephalopod Fisheries Biology*. Okutani, T., O'Dor, R. K. and T. Kubodera (Eds). Tokyo; Tokai University Press: 241–262.
- LIPINSKI, M. R. and M. A. ROELEVELD 1990 — Minor extension of the von Bertalanffy growth theory. *Fish. Res.* **9**(4): 367–371.
- LONGHURST, A. R. and D. PAULY 1987 — *Ecology of Tropical Oceans*. San Diego; Academic Press: xi + 407 pp.
- LUTZ, R. A. and D. C. RHOADS 1977 — Anaerobiosis and a theory of growth line formation. Micro- and ultrastructural growth patterns within the molluscan shell reflect periodic respiratory changes. *Science* **198**(4323): 1222–1227.
- MADAN, J. J. and M. J. WELLS 1996 — Why squid can breathe easy. *Nature, Lond.* **380**(6575): p. 590.
- MANGOLD, K. 1963 — Biologie des céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu Suppl.* **13**: 285 pp. + 4 Plates + 2 Charts.
- MANGOLD, K. 1987 — Reproduction. In *Cephalopod Life Cycles. 2. Comparative Reviews*. Boyle, P. R. (Ed.). London; Academic Press: 157–200.
- MORALES-NIN, B. [A.] 1988 — Caution in the use of daily increments for ageing tropical fishes. *Fishbyte* **6**(2): 5–6.
- MORRIS, C. C. 1991 — Statocyst fluid composition and its effects on calcium carbonate precipitation in the squid *Alloteuthis subulata* (Lamarck, 1798): towards a model for biomineralization. *Bull. mar. Sci.* **49**(1–2): 379–388.
- O'DOR, R. K. and M. J. WELLS 1987 — Energy and nutrient flow (cephalopods). In *Cephalopod Life Cycles. 2. Comparative Reviews*. Boyle, P. R. (Ed.). London; Academic Press: 109–133.
- PANELLA, G. 1971 — Fish otoliths: daily growth layers and periodic patterns. *Science* **173**: 1124–1127.
- PANELLA, G. 1974 — Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In *Ageing of Fish*. Baginal, T. B. (Ed.). Old Woking, Surrey; Unwin Bros: 28–39.
- PAULY, D. 1981 — The relationships between gill surface area and growth performance in fish: a generalization of Von Bertalanffy's theory of growth. *Meeresforsch.* **28**(4): 251–282.
- PAULY, D. 1984 — A mechanism for the juvenile-to-adult transition in fishes. *J. Cons. perm. int. Explor. Mer* **41**: 280–284.
- PAULY, D. 1985 — Population dynamics of short-lived species, with emphasis on squids. *NAFO scient. Coun. Stud.* **9**: 143–154.
- PAULY, D. 1989 — A theory of fishing for a two-dimensional world. *Fishbyte* **7**(3): 28–31.
- PAULY, D. 1994 — *On the Sex of Fish and the Gender of Scientists. Collected Essays in Fisheries Science*. London; Chapman & Hall: 250 pp.
- PAULY, D. 1997 — Geometric constraints on body size. *Trends Ecol. Evol.* **12**(11): p. 442.
- PETERS, R. H. 1983 — *The Ecological Implications of Body Size*. Cambridge; University Press: 329 pp.
- RALSTON, S. 1985 — A novel approach to aging tropical fish. *ICLARM Newsl.* **8**(1): 14–15.
- RODHOUSE, P. G. 1998 — Physiological progenesis in cephalopod molluscs. *Biol. Bull., mar. biol. Lab., Woods Hole* **195**: 17–20.
- ROPER, C. F. E., SWEENEY, M. J. and C. E. NAUEN 1984 — F.A.O. species catalogue. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. *F.A.O. Fish. Synop.* **125**(3): 277 pp.
- SAUNDERS, W. B. 1983 — Natural rates of growth and longevity of *Nautilus belauensis*. *Paleobiol.* **9**(3): 280–288.
- SCHMIDT-NIELSEN, K. 1984 — *Scaling: why is Animal Size so Important?* Cambridge; University Press: 241 pp.
- SCHUMANN, D. and J. PIIPER 1966 — Der Sauerstoffbedarf der Atmung bei Fischen nach Messungen an der narkotisierten Schleie (*Tinca tinca*). *Pflügers Arch. Ges. Physiol.* **288**: 15–26.
- SUMMERS, W. C. 1971 — Age and growth of *Loligo pealei*, a population study of the common Atlantic Coast squid. *Biol. Bull. mar. biol. Lab., Woods Hole* **141**: 189–201.
- THOMPSON, D'A. 1942 — *Growth and Form, Volumes 1 and 2*. Cambridge; University Press: 1116 pp.
- TINBERGEN, L. and J. VERWEY 1945 — Zur Biologie von *Loligo vulgaris* Lam. *Archs neérl. Zool.* **7**(1–2): 213–286.
- VAKILY, J. M. 1992 — Determination and comparison of bivalve growth, with emphasis on Thailand and other tropical areas. *Tech. Rep. ICLARM* **36**: 125 pp.
- VERRILL, A. E. 1881 — The cephalopods of the north-eastern coast of America. 2. The smaller cephalopods, including the squids and the octopi, with other allied forms. *Trans. Conn. Acad. Sci.* **5**: 260–446.
- VON BERTALANFFY, L. 1938 — A quantitative theory of organic growth (inquiries on growth laws II). *Human Biol.* **10**(2): 181–213.
- VON BERTALANFFY, L. 1951 — *Theoretische Biologie*. Zweiter Band: Stoffwechsel, Wachstum. Bern; A. Francke: 418 pp.
- WINBERG, G. G. 1960 — Rate of metabolism and food requirements of fishes. *Fish. Res. Bd Can. Transl. Ser.* **194**: 239 pp.