Growth of Cephalopods:
Conceptual Model

Marek R. Lipinski*)

5 Text-Figures

Cephalopods
Growth
Paralarvae

Contents

Modellvorstellungen zum Cephalopodenwachstum

Zusammenfassung

In Übereinstimmung mit dem Lebenszyklus und der Physiologie wird das Wachstum der Cephalopoden mit Hilfe von drei linearen Funktionen beschrieben. Die erste Funktion gilt für das langsame Wachstum während der paralarvalen Phase und die zweite beschreibt das schnelle Wachstum der juvenilen Tiere bis zum adulten Stadium. Die dritte Funktion repräsentiert das Wachstum wahrend des reproduktiven Lebensabschnittes. Die erste Funktion kann modifiziert werden, um Temperatur- und Nahrungsbedingungen zu berücksichtigen. Die dritte Funktion erlaubt, unterschiedliche Energiereserven während der reproduktiven Phase zu verwenden. Die Vielzahl von Literaturdaten von allen größeren systematischen Gruppen passt sich dem vorgestellten Modell sehr gut an. Das Modell berücksichtigt ebenfalls die intraspezifische Variabilität der sozialen Struktur bei vielen Cephalopodenarten. Die Steigungen und Längen von jeder der drei Regressionsabschnitte sowie deren Kombination sind typisch z.B. für die groß- und kleinwüchsigen Männchen sowie alle Weibchen von *Loligo vulgaris reynaudii*. Die zweite Funktion beschreibt das sehr unterschiedliche Wachstum der großwüchsigen Männchen und die dritte Funktion das Wachstum der Weibchen dieser Art.

Abstract

Following the life cycle approach and physiological analysis of cephalopod growth, it is proposed that this growth be described by three linear equations: the first representing slower paralarval growth, the second representing fast juvenile-adult growth, and the third representing reproductive growth. The first and the third equation can, if necessary, be modified to account for paralarval temperature and food constraints, and effect of energy storage during reproduction, respectively. Accumulated literature data fit well the proposed model in all major systematic groups of cephalopods. The proposed model also accounts for the intra-specific variability in the social structure of many cephalopod species. Slope and length of each of the three lines comprising the model, and their combination are, for example, specific for large males, small males (sneakers) and females of *Loligo vulgaris reynaudii*. In addition, the second equation describes the variable growth most prevalent in large males, while the third equation is most appropriate for adult females of this species.

1. Introduction

In their classical review of molluscan growth, Wilbur & Owen (1964) provided very little information about cephalopods.

However, a specific cephalopod growth review, 23 years later (Forsythe & Van Heukelem, 1987), was based both on aquarium maintenance experiments and population studies in the field. Forsythe & Van Heukelem (1987) noted problems, which authors had in fitting cephalopod growth data to any of the existing growth models available, which had been mainly developed and used for fish (e.g. Guerra, 1979). Ever since the powerful and influential formula of Packard (1972, p. 243:

*) Author's address: Specialist Scientist Marek R. Lipinski PhD, Marine and Coastal Management, Private Bag X2, Roggebaai 8012, South Africa.

"cephalopods functionally are fish"), it was only natural to attempt to use these concepts and models, especially in fisheries-related applications (for a review of this concept, see LONGHURST & PAULY [1987 p. 322]). This usage however, led to a controversy. It was soon found that the modal progression (or Petersen's) method could not be used for cephalopods without the risk of serious error (e.g. CADDY, 1991). The aquarium evidence indicated that even large cephalopods such as *Sepioteuthis lessoniana* or *Octopus apollyon* grew very quickly, much quicker than predicted by traditional, fisheries-related data and the models associated with them. The von Bertalanffy growth curve in its original or generalized form was usually found to be too simple and too general an approximation of cephalopod growth to be of any use (see FORSYTHE & VAN HEUKELEM, 1987; JACKSON, 1994; ARKHIPKIN & PEREZ, 1998). Nevertheless, the traditional approach is still being used (e.g. JARRE et al., 1991; MOHAMED, 1996). Most recently, PAULY (1998a,b) has defended this approach on theoretical grounds, arguing that large squids cannot grow fast as they are limited in their oxygen supply (as determined by the gill area).

In this contribution, a simple cephalopod growth model is proposed which may help to resolve this controversy by providing a useful tool for modeling growth, especially when some parts of a life cycle of a given cephalopod species are unlikely to be known in detail.

2. Conceptual Model of the Cephalopod Life Cycle

It was assumed on the basis of available evidence, that the cephalopod life cycle has three basic phases: paralarval, juvenile-adult, and mature. The paralarval phase is relatively long, with a high mortality risk and trial-and-error learning process, during which food is usually abundant but difficult to catch, and where temperature of the surrounding water profoundly affects development. The duration of the juvenile-adult phase is largely determined by food availability, behavioural relations between individuals and, to a lesser degree, by temperature and other environmental factors. This is a phase of intense feeding and growth which is often associated with energy accumulation (e.g. in the digestive gland). The last phase, that of the mature cephalopod, is mainly determined by behavioural factors, and is not
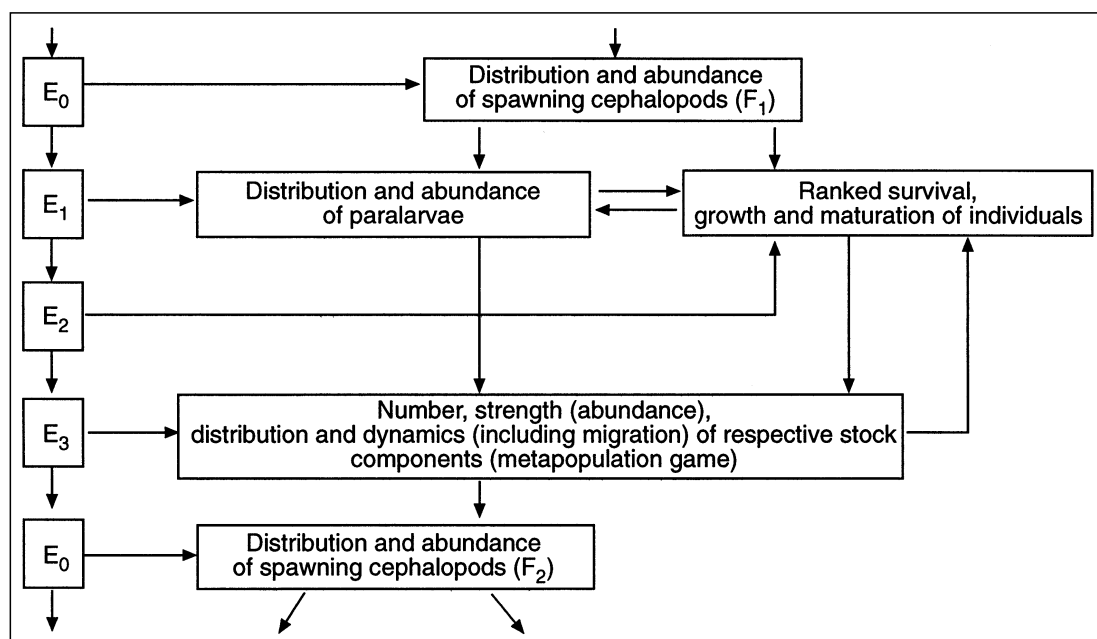
strongly influenced by food availability. Environmental factors are important in so much as they enhance, or inhibit, the behavioural reactions of individuals (e.g. turbidity of, and visibility in, the water).
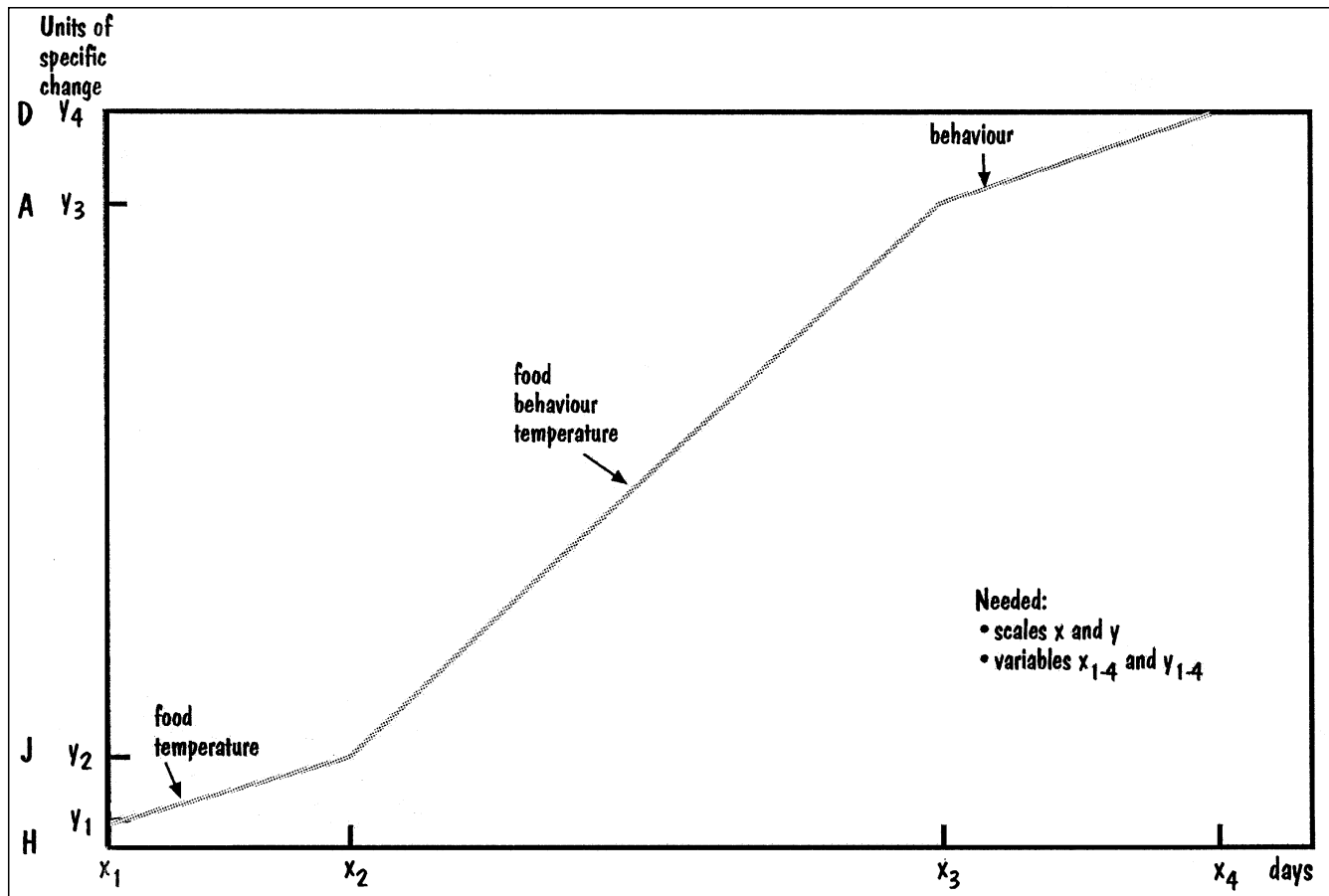
In the first phase, cephalopods learn to survive, in the second phase essentially they feed and grow, and in the third they reproduce. Their chances of completing their life cycle in large numbers depend upon the environmental holon (= combination of factors), spatial distribution of the previous generation, and on interactions with other species of marine organisms (e.g. prey, competitors, predators).

Cephalopod life cycle models are difficult to quantify because of the very large individual variability typical within the group. In addition, data pertaining to some of the life cycle parameters are hard to obtain. The models require spatial- and time-scale strength of metapopulation components (in numbers), and quantification of their dynamics (see LIPINSKI [1998] for the use of metapopulation concept in cephalopods). A schematic introduction to such a model is given in Text-Fig. 1. It is strongly felt that even the very basic ideas inherent in such a model are necessary for the construction of an adequate growth model.

3. Conceptual Model of Cephalopod Growth

The concept rests on the assumption that a Basic General Growth Model (BGM) of cephalopods should be found first, from which Specific or derived Models (SM) can be developed for different species, or even groups within a species.

Under the BGM it is assumed that physiological processes in cephalopods lead to a three-phase linear growth process (Text-Fig. 2). The first phase involves a relatively long and slow paralarval growth, limited mainly by temperature, food availability and the ability to learn how to capture prey. The second phase is typified by fast growth during the juvenile-adult life. Limiting factors include food availability and behavioural constraints (such as intra-specific competition). The third phase is triggered by the onset of the final stages of sexual maturation (variable between species), resulting in copulation and/or spawning,

Text-Fig. 1.
Flow diagram of a cephalopod life cycle. E0–E3 represent environmental modifiers, which have an impact on the processes marked in the other consecutive blocks (after LIPINSKI, 1998).

134

Text-Fig. 2.
Graphic representation of the proposed basic general growth model (BGM) of cephalopods.
Water temperature, food availability and behaviour determine the length and slope of each of the three stages of the model.
Scales x (number of days) and y (units of specific change) and variables x_{1-4} and y_{1-4} are needed to describe growth of any cephalopod.

in which growth may be relatively slow (or absent) and determined mainly by behavioural constraints. Growth may not slow down during this step in some species whilst in others (e.g. octopods) it may assume a negative sign when expressed in terms of weight.

In order to construct a BGM, the life cycle of a given species needs to be relatively well known; in particular, maximum age (x scale) should have been determined and a specific unit of change (y scale) chosen carefully. Points $x_1 y_1$, $x_2 y_2$, $x_3 y_3$ and $x_4 y_4$ of the model (Text-Fig. 2) should be estimated experimentally, preferably through a combination of fieldwork and aquarium studies.
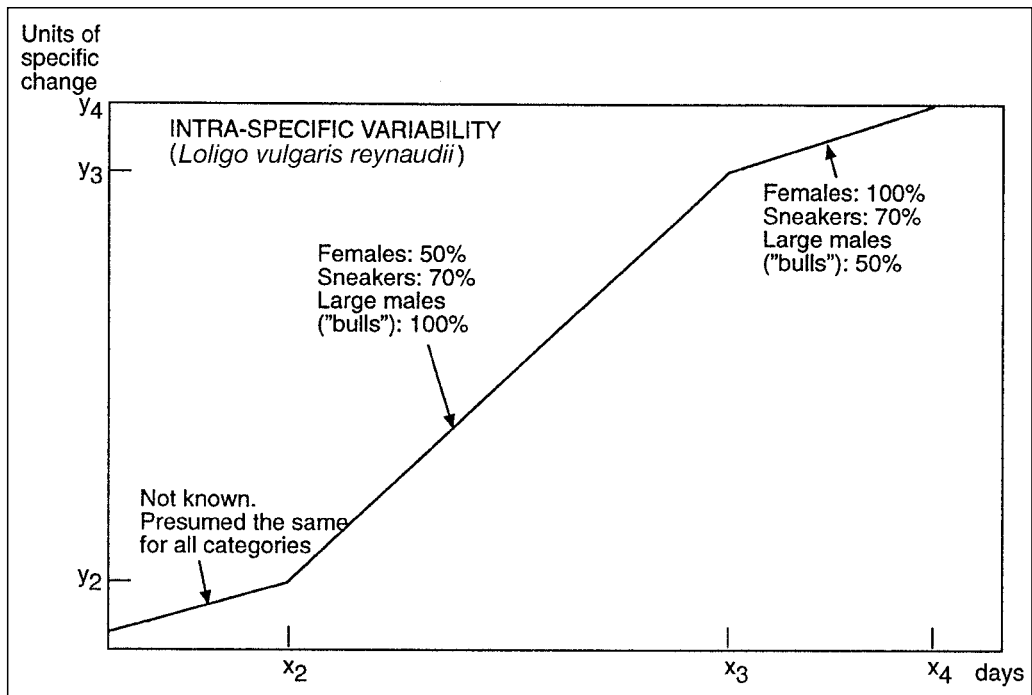
The BGM will vary considerably, not only between various species of cephalopods, but also between various social categories within a single species (Text-Fig. 3), excluding the paralarval growth phase, which is assumed to be the same for all social categories. These differences are based on average growth for the species (broken lines in Text-Fig. 3) and average growth for social categories (solid lines on Text-Fig. 3). Also, the degree (range) of intra-specific variability may be different in second and third stage of growth between social categories (Text-Fig. 4). During fast growth, large males may account for the whole range of observed variability; during the maturity growth phase, the same is true for females.

Text-Fig. 3.
BGM differences between females, small mature males ("sneakers") and large mature males ("bulls") in the loliginid squid *Loligo vulgaris reynaudii*.
The differences are not quantified, but are derived by analysis of the life cycle of chokka.

135
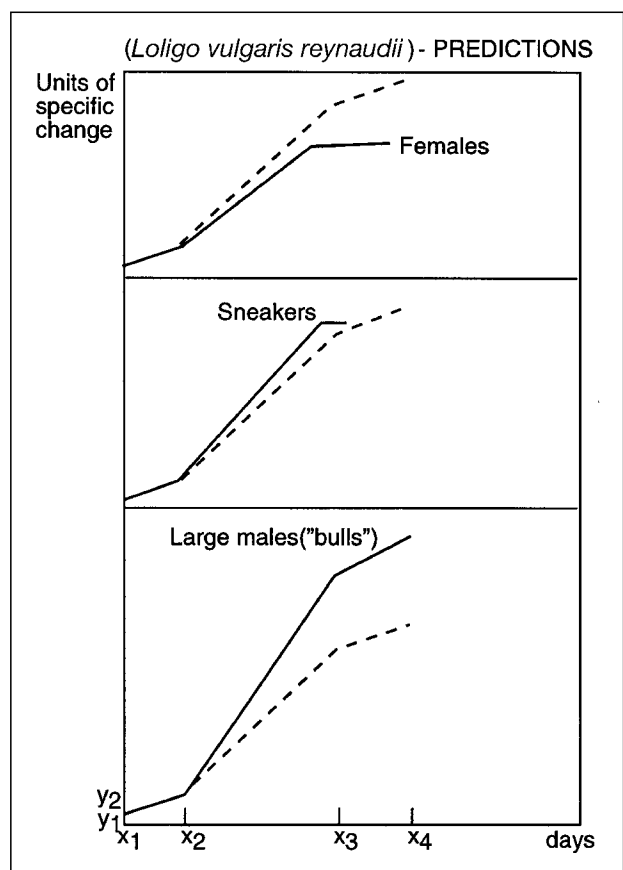
Text-Fig. 4.
Intra-specific variability in each step of the BGM except the first (paralarval) phase for *Loligo vulgaris reynaudii.*
The length of each phase, as well as the amplitude of its slope, are the measures of this variability. Numbers given are approximate and based on the life-cycle oriented research. Numbers for the last phase (maturing and mature squids) are highly hypothetical as there is very little information about growth in this stage.

INTRA-SPECIFIC VARIABILITY
(*Loligo vulgaris reynaudii*)

Females: 50%
Sneakers: 70%
Large males
("bulls"): 100%

Females: 100%
Sneakers: 70%
Large males
("bulls"): 50%

Not known.
Presumed the same for all categories

The BGM, however, seldom remains in its purely "physiological" form because of the influence of environmental and biological modifiers. These may act as constrainers, which slow down the paralarval growth, or enhancers, which accelerate the growth rate (Text-Fig. 5). The result may resemble a logistic curve, which may not, however, be approximated by the generalized von Bertalanffy growth equation.

4. Discussion

The eighteenth century mathematician, engineer and philosopher, J.M. HOENE-WRONSKI dreamt (and wrote hundreds of pages) about his quest for a single all-encompassing mathematical formula of the Universe. After some XXth century developments in physics (e.g. Heisenberg rule, quantum mechanics, lack of progress in the field theory, etc.), this ideal has proven to be somewhat elusive and has been abandoned for the time being However it is alive and well in the fisheries science, albeit in a slightly less-ambitious form. The ultimate goal in fisheries science is to efficiently manage, and make accurate predictions of responses within complex biological scenarios, a task impossible at the present level of knowledge. Typically, fisheries science has to deal with enormous amounts of data which are continually at risk of not being representative of the whole populations being investigated. Therefore, there is a quest for an all-encompassing formula for management and prediction, and for the integral components of these: mortality, abundance, recruitment, growth and others. Recently, PAULY (1998a,b) has claimed to have found such a formula for growth. He has revived a deductive approach to biological reasoning and has applied extreme reductionism in the interpretation of biological data. However, biology cannot easily/convincingly be reduced to simple physical and chemical components, and in my view, this approach

Text-Fig. 5.
Examples of possible modifications of the BGM, which will transform it into a specific (derived) model (SM) of cephalopod growth.
Left side of the drawing represents BGM (linear). First example of departure from BGM concerns the first, i.e. paralarval phase in the model (lower right of the drawing). To calculate this modification, α and a should be known, then the curve representing the departure from the linear growth due to underfeeding of paralarvae can be drawn.
The second example (upper right part of the drawing) describes maturing or mature cephalopods in the model. To calculate this modification, β and b should be known. The resulting curve represents a dampening effect of feeding on depletion of the body resources due to the gamete production.
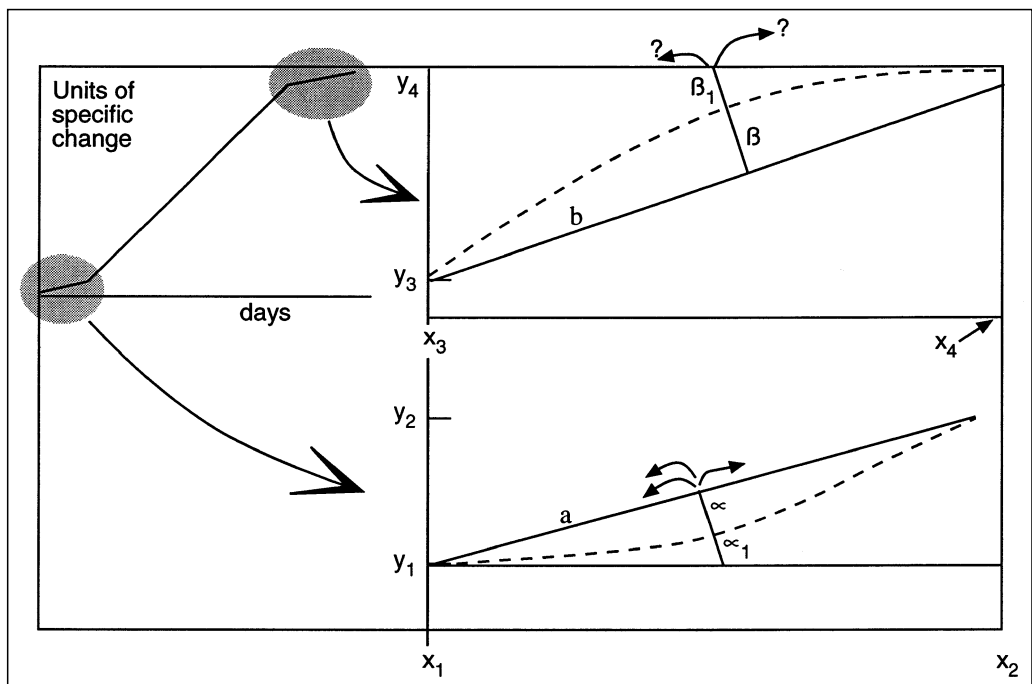
fails. The inductive approach (of Francis Bacon) should not for the moment, be abandoned in favour of deductive approach. Data, even if incompatible, must stand their ground while theory must be regarded as ephemeral. Growth in any group of organisms, is better understood, and more frequently investigated, in the bottom-up (inductive), rather than in the top-down (deductive) approach. More importantly, it follows that in natural sciences, our deductions are, and should be judged by our "inductions" and not vice versa.

The cephalopod growth model presented here is based on accounts from the literature relating to various octopod, cuttlefish and squid research, as well as on South African collaborative work on the life cycle of the squid *Loligo vulgaris reynaudii* (AUGUSTYN et al., 1992, 1994; SAUER, 1993; DURHOLTZ, 1999). According to NEEDHAM ([1964], quoted by FORSYTHE & VAN HEUKELEM [1987]), growth is defined as increase in size, while differentiation in conjunction with growth should be termed growth development. While this definition may not hold on a molecular level, it may be useful on the morphological level. Studies of PECL & MOLTSCHANIWSKYJ (1997, 1999) and MARTINEZ & MOLTSCHANIWSKYJ (1999) suggest that continuous hyperplasia and hypertrophy in cephalopods may lead to continuous linear growth in these animals. A massive body of evidence, mainly from aquarium maintenance, statolith and life-cycle studies (e.g. BOYLE, 1983; FORSYTHE & VAN HEUKELEM, 1987; LEE et al., 1994; ARKHIPKIN & SILVANOVICH, 1997; ARKHIPKIN et al., 1998; GONZALEZ et al., 1998) suggest that there are three main elements to cephalopod growth, and that the first and last (if any) part consist of a slower growth, and the middle part of fast growth as represented on Text-Fig. 3. On a more general note, DAY & TAYLOR (1997) pointed out that the period of sexual maturity in any organism is physiologically and energetically a very special one and should not be subject to unitary modeling attempts (such as indiscriminate application of the von Bertalanffy equation). DOI & KAWAKAMI (1979) and LIPINSKI et al. (in prep.) suggested that the paralarval phase is equally important when considering growth in cephalopods. In conclusion, available evidence supports a tri-partite growth model, with a simple linear approach (see RODHOUSE, 1998 p. 19). This model has several advantages. First of all, it may easily account for inter- and intra-specific variability, facilitating comparisons (Text-Figs. 3–4). Data about *Loligo vulgaris reynaudii* (LIPINSKI & DURHOLTZ, 1994; LIPINSKI, 1994; LIPINSKI et al., 1998a; DURHOLTZ, 1999) were used to illustrate gross differences in growth and in variabilities about that growth, in various social categories. There are still many gaps in these data and the results presented should be regarded as specific predictions of BGM rather than firmly established facts. The same evidence suggests further that in *Loligo vulgaris reynaudii* there are various deviations from the basic linear growth approach, namely slow growth during the paralarval stage and less of a decline in growth rate than predicted during the final phase (maturity) (Text-Fig. 5). These modifications may be modeled and $\alpha-x_0$ and $\beta-x_0$ as well as the distance of α and β from the $\beta-x_0$ point may be determined.

This short paper does not attempt to review all available evidence on cephalopod growth. Several comments however, may be made to facilitate further discussion on the subject.

1) There is a need for a simple, basic and general conceptual model of cephalopod growth, which may act as a firm basis for detailed experimental investigations and design (JACKSON, 1994; PAULY, 1998a). It is hoped that the BGM may fulfill this role.

2) Cephalopod physiology and life cycles are unique and profoundly different to that of fish and other organisms (including other molluscs), and these differences have an impact on our understanding, and plotting of growth curves (PÖRTNER, 1994; PÖRTNER et al., 1993; PÖRTNER & ZIELIINSKI, 1998; LIPINSKI et al., 1998b). In particular, their growth during the paralarval phase and after approaching maturity, cannot be ignored or approximated by the classic or generalized von Bertalanffy model (as postulated by PAULY, 1998a; see RODHOUSE, 1998). The asymptote in the third equation of the BGM model is not due to oxygen-related limitations in large squid (as implied by PAULY [1998a]), but the result of approaching sexual maturity.

3) The fast growth phase is the longest and most important one on the population scale.

4) Some large cephalopods grow very quickly in aquaria. This evidence should not be regarded as biased or irrelevant in the discussion of cephalopod growth (WELLS & CLARKE, 1996).

5) Growth of cephalopods should be investigated in a bottom-up approach. Aside from the important theoretical grounds for this, there are also practical reasons why pooled or averaged data lead to erroneous conclusions (ALFORD & JACKSON, 1993).

6) The forced use of the von Bertalanffy growth equation in cephalopods leads to extreme anti-biological reductionism and should be abandoned. The physiological concept behind this equation may be interpreted as energetic saturation, or loss, at the end of the life of most organisms (just as it is the case of plastic squid, which grow when placed in water; LIPINSKI & ROELEVELD [1990]). This level of generalization may well be interesting to a physicist. Unfortunately, most biologists are interested in the processes between birth and reproduction of the organism, and therefore this interpretation contributes little understanding to any life-cycle investigation, at least where asymptotic growth occupies an insignificant part.

References

ALFORD, R.A. & JACKSON, G.D.: Do cephalopods and larvae of other taxa grow asymptotically? – Am. Nat., **141**, 717–728, Lancaster 1993.

ARKHIPKIN, A.I., LAPTIKHOVSKY, NIGMATULLIN, CH.M., BESPYATYKH, A.V. & MURZOV, S.A.: Growth, reproduction and deeding of the tropical squid *Ornithoteuthis antillarum* (Cephalopoda, Ommastrephidae) from the central-east Atlantic. – Sci. Mar., **62/3**, 273–288, Barcelona 1998.

ARKHIPKIN, A. & PEREZ, J.A.A.: Life-history reconstruction. – In: RODHOUSE, P.G, DAWE, E.G. & O'DOR, R.K. (Eds.): Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability, FAO Fisheries Technical Paper, **376**, 157–180, XII+273 pp., Rome 1998.

ARKHIPKIN, A.I. & SILVANOVICH, N.V.: Age, growth and maturation of the squid *Martialia hyadesi* (Cephalopoda, Ommastrephidae) in the south-west Atlantic. – Antarct. Sci. **9/4**, 373–380, Cambridge 1997.

AUGUSTYN, C.J., LIPINSKI, M.R. & SAUER, W.H.H.: Can the Loligo squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. – In: PAYNE, A.I.L., BRINK, K.H., MANN, K.H. & HILBORN, R. (Eds.): Benguela Trophic Functioning, S. Afr. J. mar. Sci., **12**, 903–918, 1108 pp., Cape Town 1992.

AUGUSTYN, C.J., LIPINSKI, M.R., SAUER, W.H.H., ROBERTS, M.J. & MITCHELL-INNES, B.A.: Chokka squid on the Agulhas Bank: life history and ecology. – S. Afr. J. Sci., **90**, 143–154, Pretoria 1994.

BOYLE, P.R. (Ed.): Cephalopod Life Cycles. Vol. I Species Accounts. – XVII+475   pp., London (Academic Press) 1983.

CADDY, J.F.: Daily rings on squid statoliths: an opportunity to test standard population models? – In: JEREB, P., RAGONESE, S. & VON BOLETZKY, S. (Eds.): Squid Age Determination Using Statoliths, NTR-ITPP Special Publication, **1**, 53–66, 127 pp., Palermo 1991.

DAY, T. & TAYLOR, P.D.: Von Bertalanffy's growth equation should not be used to model age and size at maturity. – Am. Nat., **149**, 381–393, Lancaster 1997.

DOI, T. & KAWAKAMI, T.: Biomass of Japanese common squid *Todarodes pacificus* STEENSTRUP and the management of its fishery. – Bull. Tokai Reg. Fish. Res. Lab., **99**, 65–83, Shimizu, 1979.

DURHOLTZ, M.D.: Biomineralization in Loliginid Squid Statocysts and the Use of Statoliths to Estimate Age. – Ph.D. Thesis, 191 pp., Cape Town (University of Cape Town) 1999.

FORSYTHE, J.W. & VAN HEUKELEM, W.F.: Growth. – In: BOYLE, P.R. (Ed.): Cephalopod Life Cycles Vol. II Comparative Reviews, 135–156, XXI+441 pp., London (Academic Press) 1987.

GONZALEZ, A.F., MACY III, W.K. & GUERRA, A.: Validation of a semi-automatic image analysis system to age squids and its application to age *Illex coindetii* statoliths. – ICES J. mar. Sci., **55**, 535–544, London 1998.

GUERRA, A.: Fitting a von Bertalanffy expression to *Octopus vulgaris* growth. – Inv. Pesq., **43/1**, 319–326, Barcelona 1979.

JACKSON, G.D.: Application and future potential of statolith increment analysis in squids and sepioids. – Can. J. Fish. Aquat. Sci., **51**, 2612–2625, Ottawa 1994.

JARRE, A., CLARKE, M.R. & PAULY, D.: Re-examination of growth estimates in oceanic squids: the case of *Kondakovia longimana* (Onychoteuthidae). – ICES J. mar. Sci., **48**, 195–200, London 1991.

LEE, P.G., TURK, P.E., YANG, W.T. & HANLON, R.T.: Biological characteristics and biomedical applications of the squid *Sepioteuthis lessoniana* cultured through multiple generations. – Biol. Bull., **186**, 328–341, Woods Hole 1994.

LIPINSKI, M.R.: Differences among basic biological parameters in a population of chokka squid (*Loligo vulgaris reynaudii*, Cephalopoda: Loliginidae) sampled by three methods. – S. Afr. J. mar. Sci., **14**, 281–286, Cape Town 1994.

LIPINSKI, M.R.: Cephalopod life cycle: patterns and exceptions. – 439–447. – In: PAYNE, A.I.L., LIPINSKI, M.R., CLARKE, M.R. & ROELEVELD, M.A.C. (Eds.): Cephalopod Biodiversity, Ecology and Evolution. – S. Afr. J. mar. Sci., **20**, 469 pp, Cape Town 1998.

LIPINSKI, M.R., BUTTERWORTH, D.S., AUGUSTYN, C.J., BRODZIAK, J.K.T., CHRISTY, G., DES CLERS, S., JACKSON, G.D., O'DOR, R.K., PAULY, D., PURCHASE, L.V., ROBERTS, M.J., ROEL, B.A., SAKURAI, Y. & SAUER, W.H.H.: Cephalopod fisheries: a future global upside to past overexploitation of living marine resources? Results of an international workshop, 31 August – 2 September 1997, Cape Town, South Africa. – In: PAYNE, A.I.L., LIPINSKI, M.R., CLARKE, M.R. & ROELEVELD, M.A.C. (Eds.): Cephalopod Biodiversity, Ecology and Evolution, S. Afr. J. mar. Sci., **20**, 463–469, 469 pp., Cape Town 1998a.

LIPINSKI, M.R. & DURHOLTZ, M.D.: Problems associated with ageing squid from their statoliths: towards a more structured approach. – Antarct. Sci., **6/2**, 215–222, Cambridge 1994.

LIPINSKI, M.R., DURHOLTZ, M.D. & UNDERHILL, L.G.: Field validation of age readings from the statoliths of chokka squid (*Loligo vulgaris reynaudii* D'ORBIGNY, 1845) and an assessment of associated errors. – ICES J. Mar. Sci., **55**, 240–257, London 1998b.

LIPINSKI, M.R. & ROELEVELD, M.A.: Minor extension of the von Bertalanffy growth theory. – Fish. Res., **9/4**, 367–371, Amsterdam 1990.

LIPINSKI, M.R., WISSEL, C. & NAVARRO, R.: A model of loliginid squid survival (Cephalopoda: Loliginidae) [in preparation].

LONGHURST, A.R. & PAULY, D.: Ecology of Tropical Oceans. – XI+407 pp., London (Academic Press) 1987.

MARTINEZ, P. & MOLTSCHANIWSKYJ, N.A.: Description of growth in the tropical cuttlefish *Sepia elliptica* using muscle tissue. – J. Mar. Biol. Assoc. U.K., **79**, 317–321, London 1999.

MOHAMED, K.S.: Estimates of growth, mortality and stock of the Indian squid *Loligo duvauceli* ORBIGNY, exploited off Mangalore, Southwest coast of India. – Bull. Mar. Sci., **58/2**, 393–403, Miami 1996.

NEEDHAM, A.E.: The Growth Process in Animals. – 522 pp., London (Pitman) 1964.

PACKARD, A.: Cephalopods and fish: the limits of convergence. – Biol. Rev., **47**, 241–307, London 1972.

PAULY, D.: Why squid, though not fish, may be better understood by pretending they are. – In: PAYNE, A.I.L., LIPINSKI, M.R., CLARKE, M.R. & ROELEVELD, M.A.C. (Eds.): Cephalopod Biodiversity, Ecology and Evolution, S. Afr. J. mar. Sci., **20**, 47–58, 469 pp., Cape Town 1998a.

PAULY, D.: Tropical fishes: patterns and propensities. – J. Fish Biol., **53** (Supplement A), 1–17, London 1998b.

PECL, G.T. & MOLTSCHANIWSKYJ, N.A.: Changes in muscle structure associated with somatic growth in *Idiosepius pygmaeus*, a small tropical cephalopod. – J. Zool., Lond., **242**, 751–764, London 1997.

PECL, G.T. & MOLTSCHANIWSKYJ, N.A.: Somatic growth processes: how are they altered in captivity? – Proc. R. Soc. Lond. B, **266**, 1133–1139, London 1999.

PÖRTNER, H.O.: Coordination of metabolism, acid-base regulation and haemocyanin function in cephalopods. – Mar. Fresh. Behav. Physiol., **25**, 131–148, Amsterdam 1994.

PÖRTNER, H.O., WEBBER, D.M., O'DOR, R.K. & BOUTILIER, R.G.: Metabolism and energetics in squid (*Illex illecebrosus, Loligo pealei*) during muscular fatigue and recovery. – Am. J. Physiol., **265**, R157–R165, Boston 1993.

PÖRTNER, H.O. & ZIELIINSKI, S.: Environmental constraints and the physiology of performance in squids. – In: PAYNE, A.I.L., LIPINSKI, M.R., CLARKE, M.R. & ROELEVELD, M.A.C. (Eds.): Cephalopod Biodiversity, Ecology and Evolution, S. Afr. J. mar. Sci., **20**, 207–221, 469 pp., Cape Town 1998.

RODHOUSE, P.G.: Physiological progenesis in cephalopod molluscs. – Biol. Bull., **195**, 17–20, Woods Hole 1998.

SAUER, W.H.H.: The ecology of spawning squid, *Loligo vulgaris reynaudii*, in the inshore areas of the Eastern Cape, South Africa. – Ph.D. Thesis, 122 pp., Port Elizabeth (University of Port Elizabeth) 1993.

WELLS, M.J. & CLARKE, A.: Energetics: the costs of living and reproducing for an individual cephalopod. – Phil. Trans. R. Soc. Lond. B, **351**, 1083–1104, London 1996.

WILBUR, K.M. & OWEN, G.: Growth. – In: WILBUR, K.M. & YONGE, C.M. (Eds.): Physiology of Mollusca, Vol. I., 211–242. , London (Academic Press) 1964.