

## Introduction

# Cephalopod growth: historical context and future directions

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Research into the biology and management of cephalopods continues to accelerate rapidly. This has been especially so in the past decade. The discovery of new and bizarre species (Vecchione *et al.* 2001), the advancement of large-scale studies based on geographic information systems (GIS; Waluda *et al.* 2001), the use of new technology to track individuals and study activity *in situ* (O'Dor *et al.* 2002), the challenges of managing growing cephalopod fisheries (Lipinski *et al.* 1998), the patterns of growth at a cellular level (Semmens and Moltschaniwskyj 2000), the physiological constraints on life spans (Zielinski and Pörtner 2000) and the potential use of individuals as ecosystem indicators (Jackson and Domeier 2003) are all examples of advances in this field in recent years. Furthermore, understanding and describing cephalopod growth continues to pose challenges and difficulties. While ageing structures in squid, such as, statoliths and gladii to some extent, have proven to be valuable tools for deciphering and describing growth, we are still facing challenges with other groups, such as, cuttlefish and octopus. Even when ageing data are available and we can construct size-at-age plots, this does not necessarily reveal the form of growth. Individual growth rates can be so plastic that attempting to fit curves to such scatter plots is not straightforward or helpful.

In the context of these challenges, a workshop was convened on cephalopod growth and held in association with the 2003 Cephalopod International Advisory Council (CIAC) symposium on the island of Phuket in Thailand. The purpose of this workshop was to bring together experts from around the world, to review and evaluate the current state of knowledge, to work on techniques to advance the field and to provide direction for the future. This special issue is a direct, but independently derived, result of that workshop and attempts to provide a synthesis of our current knowledge and to provide stimulus for future work.

Why attempt to understand the growth of cephalopods? Is it really that important? The significance of cephalopods in the world's oceans can be appreciated by the trend of increasing cephalopod catches worldwide, which is in marked contrast to traditional finfish fisheries (Caddy and Rodhouse

1998). Perhaps a more satisfying rationale for studying the dynamics of cephalopod populations has been given by Clarke (1983) who has estimated that sperm whales alone consume > 100 million tonnes of squid annually and that this figure probably exceeds half of the biomass of humanity. If this is the estimate of just squids eaten by all individuals of only one predator, the total biomass of cephalopods in the world's oceans must greatly exceed that of humans. Thus, a better knowledge of their growth and dynamics will help to assist us in understanding an important component of the world marine ecosystem.

This special issue provides broad-scale review and discussion papers as well as specific data papers, all related to issues of cephalopod growth. The majority of work in cephalopod age and growth has been focused on both the near-shore myopsid and offshore oegopsid squid. Hence, Jackson (2004, myopsid squid) and Arkhipkin (2004, oegopsid squid) present timely reviews in this issue. These reviews argue that there is considerable scope for further research on statolith ageing techniques, as many species have not yet been studied in any detail. They also suggest that stringency in statolith ageing techniques needs to be maintained and call for an expansion of increment periodicity studies. There are greater challenges studying age and growth of octopus because there are no standard ageing techniques. Semmens *et al.* (2004) review the history and challenges in studying octopus growth, and highlight the need to develop and expand novel techniques for ageing octopus. Cuttlefish are also an important, widespread and challenging group to study in terms of age and growth, and deserve further attention.

Moltschaniwskyj (2004) takes a novel approach in reference to the history and overview of cephalopod growth at a variety of biological scales, including relative growth of organs, muscle fibres, proximal composition and protein synthesis. Examining these processes has helped explain how cephalopods fuel their rapid growth and life histories, although different measurements will provide information on different time scales. Moltschaniwskyj (2004) points out that protein synthesis can provide information on the

immediate nutritional or environmental history while size-at-age provides a more integrated measure of lifetime growth.

Forsythe (1993) published an initial working hypothesis on how cephalopod growth can be dramatically accelerated, even with a minor increase in temperature. In this special issue, Forsythe (2004) provides a synopsis of research undertaken in the 10 years since the publication of his original 'Forsythe Hypothesis'. The body of work reviewed by Forsythe (2004), and Pecl (2004) in this issue outlines the evidence and historical context of how our understanding of the influence of temperature on cephalopod growth has changed from a working hypothesis to a physiological understanding. This developing awareness of how cephalopod growth rate can alter radically even after small changes in temperature has been one of the more exciting developments in the field during the past decade. As a result, when referring to the influence of temperature on cephalopod growth, the term 'Forsythe Effect' (FE) should now replace the term 'Forsythe Hypothesis' — as suggested by both Pecl (2004) and Forsythe (2004).

Two papers in this special issue tackle the modelling of cephalopod growth, and thereby provide a unique understanding of the processes governing size and growth. These papers provide a basis for the examination of existing and future field and laboratory datasets. Grist and Jackson (2004) provide a physiologically based model for two-phase growth in cephalopods, first described by Forsythe (1993). The model suggests that there are biological constraints that result in a shift from exponential growth after reaching a critical size, to growth that is slower and often described by a power function. Further, Pecl *et al.* (2004) provide a model that suggests that hatchling size can have a marked influence on individual size: a large hatchling could be double the size of a small hatchling growing at the same constant rate after 3 months, even given equal, and constant growth rates. Life at the start of the race can be important down the track. The Pecl *et al.* (2004) model provides a much needed and useful basis for future work and may provide another mechanism for understanding the marked plasticity seen in size-at-age of individuals within a cohort.

Several original data papers again emphasise the progress made by focused field or laboratory-based studies. Sakai *et al.* (2004) provide useful and fresh insight into statolith increment periodicity and formation for *Illex argentinus* hatchlings grown under different temperatures. This paper is exciting because the researchers used a combination of cutting-edge techniques/technologies (artificial fertilisation, ship-board incubation at different temperatures, and staining of statoliths with alizarine complexone) to reveal patterns of increment periodicity. These data can be vital for interpreting statolith increments from field-captured individuals. Minton (2004) investigated differences in growth data from individual-based models compared to group cultures of cuttlefish. This study provides a means for ground-truthing how different types of datasets can provide us with different

perspectives on growth. This work again reveals how such information can only be obtained with high-quality culture facilities, such as those developed at Galveston Texas, USA.

Three studies focus on the dynamics of growth of the myopsid squid *Sepioteuthis australis*. Triantafillos (2004) documents the spatial variability in growth due to environmental and genetic differences across southern Australia and New Zealand. This study is significant as it is the first to clearly show that variation in growth may have a strong genetic (not just environmental) basis. Therefore, the presence of cryptic species may be a factor in the observed marked plasticity in growth shown in other studies. Pecl (2004) also examines a substantial database for *S. australis* in relation to seasonal growth at one location in Tasmania, Australia. This comprehensive study on a single species again forcefully shows how growth, condition and possibly life span are all dependent on changing environmental conditions. Ho *et al.* (2004) show, for example, that for *S. australis*, females may not be allocating the same level of energy to somatic growth due to a greater requirement to re-allocate energy for reproductive growth. That is, patterns in the allocation of energy for growth and reproduction were gender-specific, and this held for the hierarchical levels of the whole-body, muscle fibre and proximal composition.

This special issue reveals that our knowledge of cephalopod growth is far from complete. The success of this issue, I believe, is embodied in the many instances in which more questions have been raised, than have been answered. All those involved hope that this set of work encourages and stimulates further investigations into cephalopod growth. Clearly, there is greater scope for statolith-based studies, especially those that incorporate validation in unstudied species. We also need to make more progress in developing techniques to accurately age octopus and cuttlefish. The early life history of many species remains unknown and the factors responsible for marked plasticity in size-at-age need more attention. Finally, there is a need for appropriate techniques to describe the form of growth. I would like to take this opportunity to thank colleagues in Thailand and members of CIAC for organising the 2003 CIAC symposium and growth workshop that provided the stimulus for this important issue. I am also indebted to Ron O'Dor who was instrumental in organising the growth workshop and Alexander Arkhipkin who undertook a lot of the groundwork to make this special issue a success. The production of this issue was supported by the Falkland Islands organisations listed on the title page; their assistance is very much appreciated.

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