

Review**Understanding octopus growth: patterns, variability and physiology**

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Abstract. Octopuses are generally characterised by rapid non-asymptotic growth, with high individual variability. However, *in situ* octopus growth is not well understood. The lack of an ageing method has resulted in the majority of our understanding of octopus growth coming from laboratory studies. Despite not being applicable to cephalopods, Modal Progression Analysis (MPA) of length–frequency data is the most common method for examining *in situ* octopus growth. Recently, counting growth increments in beaks and vestigial shells, and quantifying lipofuscin in brain tissue, have all shown promise for the ageing octopus. Octopuses generally demonstrate two-phase growth in the laboratory, with physiological changes possibly associated with the switch between an initial rapid exponential phase and a slower power growth phase. Temperature and food ration and quality are key factors influencing the initial growth phase. Temperature, however, does not appear to affect the second phase in any consistent way, perhaps because maturity stage can influence the growth response. There may be basic differences in the mechanisms of octopus muscle growth compared with that of other cephalopods. Furthermore, higher relative maintenance energy expenditure, along with the low energy content of their prey, may account for the relatively slow growth of deep-sea octopuses compared to littoral species.

Extra keywords: ageing, cephalopod, growth, growth modelling, octopus.

Introduction

It has been 17 years since Forsythe and Van Heukelem's 1987 comprehensive review of cephalopod growth, and we have made great advances since then, particularly in the area of understanding squid growth. This has largely been a function of statolith ageing becoming a standard technique, allowing the generation of reliable squid growth models. An accurate ageing tool for the octopus comparable with the statoliths of squid, unfortunately still eludes us, although there are several promising new methods for ageing octopuses currently being trialled. However, it is now possible to raise octopuses with planktonic hatchlings in captivity and examine growth over a significant portion of their lifespan. As for all cephalopods, there has been a distinct lack of research

on deep-sea and pelagic species. This is far from trivial and needs to be addressed, given that ~40% of octopus species live in the deep-sea alone (Voss 1988). There have, however, been recent advances in our knowledge of life-history traits and growth rates of deep-sea octopuses. In addition, small but significant advances have been reached in understanding the mechanisms of octopus growth, such as defining energy budgets for deep-sea octopuses, and determining the mechanisms of muscle growth. This study seeks to update our understanding of octopus growth and determine where future challenges lie. We appraise methods for measuring and modelling octopus growth; describe the general pattern of octopus growth and compare early and sub-adult/adult growth, including the affect of abiotic and biotic factors on each phase; and finally,

Table 1. A comparison of various indirect and direct growth assessments for octopus

Method	Advantages	Disadvantages
Indirect: Modal Progression Analysis using field-based length–frequency data Growth examined at population level, with cohorts followed through time	Allows quick, low-cost fisheries assessments, e.g. <i>Octopus maya</i> in Mexico (Solis-Ramirez 1997); <i>Octopus mimus</i> in Chile (Cortez <i>et al.</i> 1999b)	Generally not considered applicable for cephalopods. The age of cohorts have not been independently validated, i.e. using tag–recapture studies
Indirect: Biochemical indices of instantaneous growth rate Usually expressed as RNA and/or RNA/DNA or RNA/protein ratios of muscle tissue	Indices related to growth rate of octopus in the laboratory e.g. RNA/protein ratio in <i>Eledone cirrhosa</i> (Houlihan <i>et al.</i> 1998) and <i>Octopus vulgaris</i> (Houlihan <i>et al.</i> 1990)	No consistent relationship between indices and laboratory growth of octopus, with RNA concentration and RNA/protein ratio of <i>Octopus vulgaris</i> not related to growth rate in Pierce <i>et al.</i> (1999) study. Have not been applied to field caught octopus
Direct: Laboratory studies Growth of cultured or laboratory-maintained animals followed during captivity	Growth can be followed for the entire lifespan e.g. cultured <i>Octopus vulgaris</i> (Iglesias <i>et al.</i> in press) or parts of the lifespan, e.g. <i>Octopus mimus</i> (Cortez <i>et al.</i> 1999a)	Laboratory studies do not replicate the natural environment
Direct: Mark–recapture studies Growth of marked octopus directly followed in the field	Natural field growth examined using external tags, e.g. sub-adult/adult <i>Octopus vulgaris</i> (Domain <i>et al.</i> 2000) or chemical tags, e.g. marking statoliths of sub-adult (Sakaguchi <i>et al.</i> 2000) and hatchling (Fuentes <i>et al.</i> 2000) <i>Octopus vulgaris</i> with alizarin complexone solution	Mark–recapture studies of octopus rare due to the low retention rate for traditional tags. Difficult to traditionally tag juveniles and thus follow the entire life cycle. Tagged animals have to be recaptured
Direct: Growth increments in hard structures visualised, counted and the periodicity of these increments validated so animals can be individually aged	Field captured animals at any stage of development can be aged and growth examined at the population level, e.g. vestigial shells in <i>Octopus vulgaris</i> (Sousa Reis and Fernández 2002) and beaks in <i>Octopus vulgaris</i> (Raya and Hernández-González 1998; Hernandez-López <i>et al.</i> 2001)	Weak relationship between the number of increments in the vestigial shells of <i>Octopus vulgaris</i> and octopus length or weight. The rings in beaks are worn away with age. The assumption of one ring = 1 day, still remains to be validated for both structures
Direct: Histological quantification of lipofuscin in nervous tissue Proportional to physiological age and proxy for chronological age in many crustaceans e.g. <i>Marsupenaeus japonicus</i> (Vila <i>et al.</i> 2000) and the clam <i>Eurhomalea exalbida</i> (Lomovasky <i>et al.</i> 2002)	As for growth increments, e.g. Sobrino and Real (2003) quantified the lipofuscin levels in the optic gland of the brains of wild-caught <i>Octopus vulgaris</i> , which suggested that lipofuscin may be a reliable marker of age for octopus	Lipofuscin ageing in the octopus has yet to be validated using known-aged animals

examine the energetics and cellular mechanisms of octopus growth.

Measuring and modelling growth

In general, the methods for measuring and modelling growth can be classified as either indirect, such as Modal Progression Analysis (MPA), or direct, for example laboratory studies of known-age individuals. Both types of study have been used to examine octopus growth, with each having its own set of inherent advantages and disadvantages (Table 1).

Indirect methods

Modal Progression Analysis on length–frequency data of wild-caught animals is currently the most common indirect method used for examining octopus growth, primarily as it provides a quick, low-cost technique for fisheries assessments

(see Table 1 for examples). However, despite its common use in octopus growth studies, Domain *et al.* (2000) suggests octopus studies using MPA need to be reassessed, as this methodology is not applicable for the study of cephalopod growth. There are two major problems with applying this technique to cephalopods: (i) length is not a good measure of size in a soft-bodied animal (Forsythe 1984) and is dependent on the state of contraction of the muscles in cephalopods (Cortez *et al.* 1999a; Domain *et al.* 2000); (ii) variability in growth rates is a prominent feature of cephalopods (Forsythe and Van Heukelem 1987), and so size is not a good indicator of age. It should be noted that the majority of studies agree that MPA is inappropriate for cephalopods, due to these and other aspects of their biology being incompatible with the requirements of the model (Mangold 1983a; Alford and Jackson 1993; Hatfield and Rodhouse 1994; Pierce *et al.* 1994; Boyle *et al.* 1995; Boyle and Boletzky 1996; Collins *et al.* 1997;

Jackson *et al.* 1997; Pierce *et al.* 1999; Jackson *et al.* 2000). An additional problem associated with the octopus is that the age of the cohorts derived from MPA cannot be independently validated. However, until an ageing method is established for the octopus (see below), it is suggested that a concerted effort is made to replace or at least complement MPA with direct monitoring by mark–recapture techniques (Table 1), as used successfully for *Octopus vulgaris* in Senegal (Domain *et al.* 2000).

An emerging indirect method for examining growth of the octopus is the use of biochemical techniques to establish indices of instantaneous growth (Moltschaniwskyj 2004), usually expressed as RNA concentrations and ratios (with protein and DNA) of muscle tissue (see Table 1 for examples). These indices have been related to growth in laboratory-maintained octopuses, although not consistently (e.g. *O. vulgaris*, Table 1), however, they have not been validated for wild-caught individuals. RNA concentration and ratios were not related to growth rate in statolith-aged squid *Sepioteuthis australis* (Ho *et al.* 2004) and *Moroteuthis ingens* (Semmens and Jackson, unpublished data), suggesting that these biochemical indices may not be a good measure of relative growth for wild-caught cephalopods. This may be a function of the increased complexity of growth in the field, where a suite of factors may be affecting growth synergistically, unlike the laboratory where factors are isolated and controlled. These techniques therefore need refining before they are applicable to field studies.

Direct methods

The most common direct method for examining octopus growth is laboratory studies of cultured known-age individuals or laboratory-maintained field-caught animals (see Table 1 for examples). Mark–recapture programmes using external, and more recently chemical tags, have also been used to directly follow the growth of sub-adult/adult octopuses in the field. In the future, chemical tagging may provide information about early octopus growth in the field (Table 1).

Apart from monitoring growth through time, another means of ‘directly’ examining growth is to age individuals by validating and counting increments in hard structures such as statoliths. In squid, increments in the statoliths of many species have been shown to be laid-down daily (Jackson 1994). This may also be the case for some octopuses, but as yet their use as ageing tools has not been successful (Young 1960; Morris 1988; Raya 2001). Recently, two other structures with growth increments (beaks and vestigial shells) have shown promise for the ageing octopus. However, the assumption of one ring equalling 1 day remains to be validated for both structures (Table 1). Another new potential technique for determining the age of individual octopuses is the quantification of the metabolic waste product lipofuscin, which accumulates in nervous tissue. Lipofuscin concentration is proportional to physiological age

(Lomovasky *et al.* 2002) and has been used successfully as a proxy for chronological age, particularly in crustaceans (Table 1). It is important that these and other new direct techniques for determining the growth of field-caught animals be pursued, as laboratory studies may not replicate the natural environment.

General growth form

The majority of octopuses whose growth has been studied are in the family Octopodidae and are characterised by rapid growth, with large individual variability (e.g. *Octopus vulgaris*; Domain *et al.* 2000). Various mathematical equations have been used to model octopus growth, with the most common being based on the exponential and power models (Van Heukelem 1973; Forsythe 1984; DeRusha *et al.* 1987; Forsythe and Hanlon 1988; Hartwick *et al.* 1988; Forsythe and Toll 1991; Cortez *et al.* 1999a; Domain *et al.* 2000), although linear (Iribarne 1991a) and logarithmic (Cortez *et al.* 1999a) models have also been used. It should be noted that Forsythe and Van Heukelem (1987) referred to power growth (i.e. $y = a x^b$) as logarithmic because it forms a straight line on log–log paper, and this trend has continued in the literature. However, as it is not true log growth (i.e. $y = a + b \ln x$), this form of growth will be referred to as power in this study. Most literature agree that cephalopod growth is non-asymptotic (Alford and Jackson 1993; Jackson *et al.* 2000) and the use of asymptotic equations to model cephalopod growth has been discouraged (Forsythe and Van Heukelem 1987). Despite this, asymptotic models are still used to model octopus growth (e.g. *Octopus maya* and *O. vulgaris*, Arreguin-Sanchez 1992; *Octopus mimus*, Wolff and Perez 1992; *O. maya*, Nepita Villanueva and Defeo 2001).

The diversity of the mathematical models used to describe cephalopod growth is due, at least partly, to the inability of any single model to account for the large variability in growth at the individual level. Numerous biotic and abiotic factors are able to dramatically modify the growth of cephalopods (Forsythe and Van Heukelem 1987). As a result of this growth plasticity, several different models may be used to describe the growth of a single octopus species (e.g. *O. vulgaris* in the north-west African and Mediterranean region; Fig. 1). In addition, what adequately describes the growth of a population may be a very poor descriptor of growth at an individual level (Alford and Jackson 1993). Model fits are chosen that reduce the variation around the population average, although with cephalopods this individual variation may be what is of interest.

Forsythe and Van Heukelem (1987) highlighted a trend of two-phase growth in cephalopod laboratory studies, including in the octopus. This involves an initial rapid exponential phase, followed by a slower power growth phase. During the exponential phase instantaneous relative growth rates remain constant, whereas in the power phase growth rate gradually

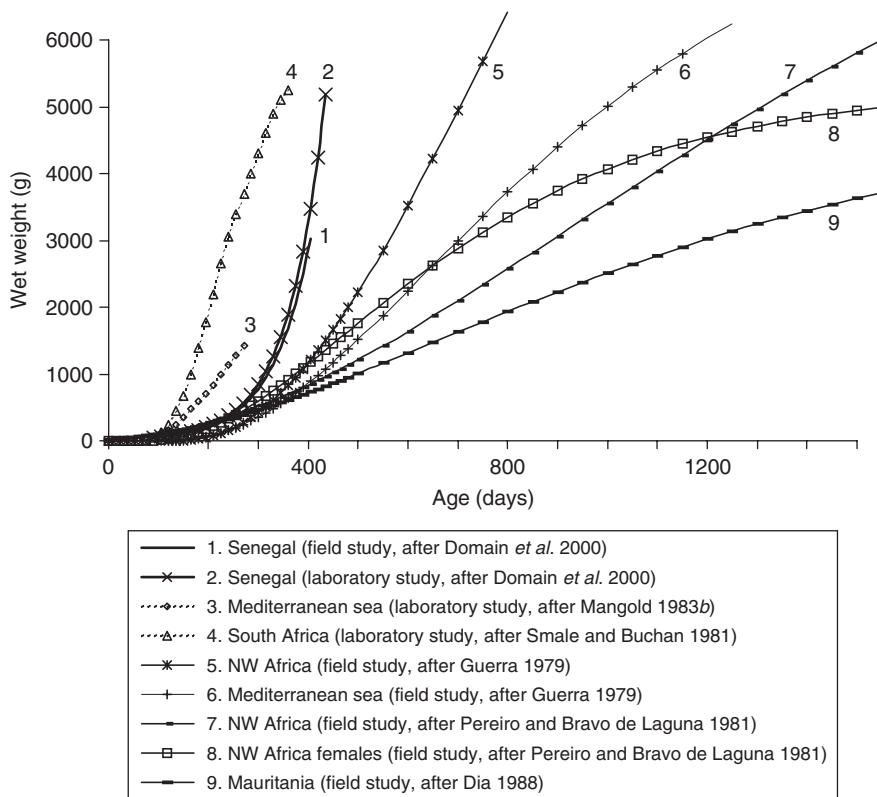


Fig. 1. Comparison of growth curves calculated for *Octopus vulgaris* in the north-west African and Mediterranean region using data from various studies (adapted from Jouffre *et al.* (2002)). Curves 1 and 2 exponential model; 3 and 4 undetermined; 5–9 asymptotic model (von Bertalanffy function). Note: As an asymptotic model was used, curves 5–9 should be compared separately to 1–4.

declines with age (Forsythe 1993a). This two-phase growth can be masked however, if only length data is examined (Forsythe 1984).

Since the Forsythe and Van Heukelem (1987) review, several octopus species have been shown to demonstrate this two-phase growth in the laboratory (e.g. *Octopus digueti*, DeRusha *et al.* 1987; *Octopus bimaculoides*, Forsythe and Hanlon 1988; *Octopus briareus*, Hanlon and Wolterding 1989; *Octopus joubini*, Forsythe and Toll 1991; *Octopus ocellatus*, Segawa and Nomoto 2002). Interestingly, laboratory-maintained *O. mimus* and *Enteroctopus dofleini* demonstrate two-phase growth (Cortez *et al.* 1999a; Rigby and Sakurai in press), however, the second phase is true logarithmic growth and not the typical power growth. In such a model where two mathematical functions are combined, the determination of the inflexion point between the two growth forms is often uncertain due to highly variable individual growth rates (Cortez *et al.* 1999a).

Early growth

It is crucial that we examine the rapid early-growth phase of cephalopods, as a non-asymptotic growth form means that even very small changes in the growth parameters are magnified over time. To date, our understanding of early octopus growth has come entirely from laboratory studies. One critical dichotomy between laboratory and field studies is that there is little selective mortality in the laboratory, whereas

in the field we are looking only at the survivors of what must have been originally a larger group with more diversity in their growth and other life-history characteristics. Small changes in the mortality rates of juveniles will change the characteristics of the resultant adult population. This is an important factor that is usually ignored when comparing the results of laboratory and field work, or applying the results of laboratory work to field situations.

Temperature

If food is not limiting, temperature is a key factor influencing cephalopod growth rates, particularly during the early growth phase (Forsythe 1993b). Benthic *Octopus bimaculoides* hatchlings reared at temperatures of 18 and 23°C produced respective growth rates of 3.6 and 4.5% BW day⁻¹ (Forsythe and Hanlon 1988). Similarly, growth rates for the first 25 days were higher in *Octopus ocellatus* hatchlings grown at 25°C, 8.3 ± 2.3% BW day⁻¹ than at 20°C, 5.6 ± 2.5% BW day⁻¹ (Segawa and Nomoto 2002). The faster growth rates at the higher temperatures resulted in a shorter exponential phase for both *O. bimaculoides* and *O. ocellatus* (Forsythe and Hanlon 1988; Segawa and Nomoto 2002). *Octopus vulgaris* paralarvae reared from hatching to settlement grew at 11.5% BW day⁻¹ at 24.7°C (Itami *et al.* 1963) compared to 8.2% BW day⁻¹ at 21.2°C (Villanueva 1995).

Since Forsythe and Van Heukelem's (1987) review, growth rates for octopuses growing at temperatures below 10°C

have been published, with hatchlings of the deep-sea octopus *Bathypolypus arcticus* fed *ad libitum* growing at rates of 0.12, 0.22 and 0.78% BW day⁻¹ at 2, 6 and 10°C, respectively, although individual variation was quite high (Wood 2000). These growth rates are very low compared with most octopuses, even when the physiological time measure of degree-days (average daily temperature in degrees Celsius × time in days) is applied (Wood 2000). This may be due, however, to the diet of deep-sea octopuses differing from that of littoral octopuses (see sub-adult/adult growth, nutrition section).

Nutrition

Availability of food, together with temperature, is the main modulator of cephalopod growth, however, Castro and Lee (1994) suggested that temperature should affect all individuals of a population more homogeneously than either the availability or nutritional quality of food. Wood and O'Dor (2000) state that the availability of food in the field is probably not limiting for the octopus, however, this may not be the case for paralarval octopuses, with starvation a common cause of mortality in larval fish (Ferron and Leggett 1994). Food ration (Villanueva *et al.* 2002) and food quality (Hamazaki *et al.* 1991; Villanueva 1994; Iglesias *et al.* 2000) are critical factors that influence the growth of paralarval and juvenile octopuses in the laboratory. Examinations of the nutritional requirements of the young octopus indicate that phospholipids, cholesterol, and especially polyunsaturated fatty acids, particularly docosahexaenoic acid (DHA), are important for the maintenance of the structural and functional properties of cell membranes during the rapid early growth phase (Navarro and Villanueva 2000, 2003).

Sub-adult/adult growth

In addition to temperature and nutrition, sub-adult/adult growth is affected by gender, maturation and reproductive investment, further adding to the individual variation in octopus growth.

Temperature

Laboratory studies suggest that temperature does not appear to affect the power or sub-adult/adult growth phase of the octopus in any consistent way (Forsythe and Hanlon 1988; Forsythe 1993a), perhaps because the stage of maturity may influence the growth response (Rigby and Sakurai in press). However, Forsythe (1993a, 1993b, 2004) noted that a major shortcoming of laboratory studies was the routine use of artificial constant temperature regimes throughout experiments, and suggested that experiments simulating natural temperature regimes were required. Hoyle (2002) grew laboratory-raised sub-adult *Octopus pallidus* (grown under identical conditions for 5 months previously) under three different temperature regimes for 3 months. Individuals were

grown under simulated seasonally increasing temperatures (14–18°C), simulated seasonally decreasing temperatures (18–14°C), and a constant temperature mid-way between seasonal peaks (16°C). *Octopus pallidus* grew exponentially over the experimental period, with no detectable effect of temperature on growth rates, suggesting that the sub-adult/adult growth phase, in this species at least, is not influenced by temperature. However, more laboratory studies simulating the natural environment are needed to determine whether this is the case for other octopus species, and to better examine octopus growth in general.

Despite it being unclear how elevated temperatures affect the power phase of growth, temperature will only increase growth within the physiological limits of a species. Growth rate of a species may either increase or decrease with increases in temperature, depending on the nature of the food × metabolism × temperature relationship (Brett 1979). In laboratory-maintained *Octopus vulgaris*, the optimum temperature for growth (17.5°C), food intake (20°C) and maximum conversion rates (16.5°C) do not coincide (Aguado Giménez and García García 2002). Domain *et al.* (2000) found that faster growth was exhibited in the colder season by *O. vulgaris* in Senegalese waters compared to the warmer season. Temperatures above 23°C resulted in weight loss and negative feeding efficiency in captive *O. vulgaris* (Aguado Giménez and García García 2002), suggesting that the high summer temperatures of 28–29°C are potentially a limiting factor for *O. vulgaris* growth in Senegal. Faster growth under cooler temperature regimes can also occur in squid, and has been linked to increased productivity (Villanueva 1992a; Jackson and Domeier 2003). This remains to be examined in the octopus.

Nutrition

Despite increases in our understanding of the nutritional requirements of the fast-growing juvenile octopus (Navarro and Villanueva 2000, 2003), there has been virtually no study of these requirements for sub-adult/adult growth (Lee 1994), and yet these requirements are likely to change with reproductive maturation. Although the exact dietary requirements are unknown, it appears that, as is the case with squid (O'Dor and Webber 1986), *O. vulgaris* and *Enteroctopus dofleini* grow poorly on diets high in lipid and low in protein (García García and Aguado Giménez 2002; Rigby and Sakurai in press). Growth and food intake of *O. vulgaris* were higher on a crab diet compared with a fish diet, with individuals fed on fish more sensitive to temperature increases above optimum (Aguado Giménez and García García 2002). A mixed low-lipid diet fed in moderation to captive immature *E. dofleini* maintained between 7 and 9.5°C, resulted in the largest amount of energy being available for growth and activity (Rigby and Sakurai in press). Conversely, captive *E. dofleini* fed on single-food diets appeared to suppress their metabolism, perhaps as a result of a lack of essential

Table 2. Octopus reproductive/growth strategies

Octopus	Strategy	References
Family Octopodidae in general (e.g. <i>Octopus vulgaris</i>)	Terminal spawners. Feeding and growth slows at maturity then ceases with egg spawning/brooding	Mangold <i>et al.</i> 1993
<i>Octopus chierchiaie</i> (family Octopodidae)	Feeds and grows between laying multiple egg batches	Rodaniche 1984
Deep-water cirrate octopus genus <i>Opisthoteuthis</i>	Spawn and grow continuously throughout most of their adult size range	Villanueva 1992b; Boyle and Daly 2000
Pelagic octopus of the genus <i>Argonauta</i> and <i>Ocythoe</i>	Spawn over a prolonged period at the end of the life cycle, while continuing to feed and grow	Mangold <i>et al.</i> 1993; Laptikhovskiy and Salman 2003

nutrients in their diet. It may be this mechanism that allows brooding females to suffer weight loss and muscle degradation at a relatively slow rate, following cessation of feeding (Rigby and Sakurai in press).

From stomach content analysis we know that brittle stars are one of the primary food sources for at least some species of deep-sea octopus such as *Bathypolypus arcticus* (O'Dor and Macalaster 1983) and *Bathypolypus sponsalis* (Quetglas *et al.* 2001), with the low energy content of this prey (Wood 2000) perhaps contributing to their relatively slow growth. It is clear from the paucity of information in this area that the nutritional requirements of sub-adult and adult octopuses need to be further examined.

Maturation and reproduction

As a function of non-asymptotic growth, reproduction and growth in cephalopods proceed together for much of the 'adult' lifespan. However, there is a point where energy becomes limiting and the amount of energy available for growth may be reduced, as reproduction becomes the dominant process. Several different reproductive strategies coexist within the octopus group, with the mode of reproduction influencing the growth pattern (Table 2).

The trade-off between reproduction and growth may also be different between the sexes, with Forsythe and Van Heukelem (1987), suggesting that the differential growth of males and females is only seen during the slower growth phase, with the approach of sexual maturity. Males in the family Octopodidae start maturing at the end of the rapid phase of growth (e.g. cultured *Octopus bimaculoides*, Forsythe and Hanlon 1988; *Eledone massyae*, Perez and Haimovici 1991; *O. vulgaris*, Sánchez and Obarti 1993). Conversely, females in this family attain sexual maturity late in their lifecycle towards the end of the slower growth phase (Forsythe 1993a). This could explain why females can have faster 'adult' growth rates and may achieve larger sizes (e.g. cultured *Octopus digueti*, DeRusha *et al.* 1987; *Eledone cirrhosa*, Boyle *et al.* 1988; *Octopus tehuelchus*, Iribarne 1991a,b; *O. vulgaris*, Domain *et al.* 2000), although males commit

at most only 5% BW to reproductive mass compared to 20–50% for females (Forsythe 1993a). Males may also expend more energy on reproduction behaviourally, through searching for females to mate with (Hanlon and Messenger 1996). Further study into the reproductive strategies of the octopus is still required, as are examinations of the trade-off between reproduction and growth for the various strategies.

Mechanisms of octopus growth

Muscle growth

Although growth is usually determined by measuring the increase in whole-animal size (weight or length), the actual process of growth takes place by cell multiplication, an increase in cell size, and the formation of intercellular substances (Weatherley and Gill 1987). As muscle comprises ~75–90% of the live weight of a cephalopod, growth will depend at least partly on that of their muscle tissue. For squid and cuttlefish, the bulk of the musculature is contained within the mantle; thus, this is the region where most somatic growth occurs. Although the mantle is obviously still a major component of their muscle mass, octopuses have a much heavier somatic investment in the arms and arm crown, although the growth mechanisms of octopus arms have not been examined.

In general, muscle growth may occur by one, or a combination of the following two processes: (i) hyperplasia, the generation of new muscle fibres; (ii) hypertrophy, the increase in size of those fibres already in existence (Weatherley 1990). The mantle muscle tissue of cephalopods grows by a combination of hyperplasia and hypertrophy throughout the entire lifespan (Moltschaniwskyj 2004). However, recent work by Hoyle (2002) examining the littoral octopus *Octopus pallidus*, suggests there may be some basic differences in the mechanisms of octopus muscle growth compared with that of other cephalopods. Those differences are:

- (1) Hyperplasia appears to be more important in the growth mechanism of *O. pallidus*, compared to squid and cuttlefish. In these cephalopods, as body size increases the relative importance of hyperplasia either decreases

(e.g. the squid *Photololigo* sp., Moltshaniwskyj 1994; the sepoid *Idiosepius pygmaeus*, Pecl and Moltshaniwskyj 1997) or remains constant (e.g. the cuttlefish *Sepia elliptica*, Martínez and Moltshaniwskyj 1999; the squid *Sepioteuthis lessoniana*, Semmens and Moltshaniwskyj 2000). Conversely, it appears that as *O. pallidus* grows, new fibre production is not only sustained, but can become the dominant process of muscle growth.

- (2) Narrower muscle blocks in the posterior region of the mantle of *O. pallidus* suggests that this region is the main proliferation zone for muscle blocks, whereas growth in the anterior and mid-mantle region is predominantly directed to mantle thickness. The opposite has been found in *I. pygmaeus* (Pecl and Moltshaniwskyj 1997) and *S. elliptica* (Martínez and Moltshaniwskyj 1999; Martínez *et al.* 2000), where the rate of new muscle block formation is more rapid anteriorly.

The different mantle growth mechanics of littoral octopuses compared with actively swimming squid and cuttlefish may be a reflection of their less active lifestyle. The cephalopod mantle is crucial to locomotion, ventilation, respiration, subcutaneous oxygen extraction and, in many species, fuel storage. With the different lifestyles of the various octopods (e.g. littoral *cf* pelagic *cf* deep-sea species), the structure of octopus muscle may also vary within the group, as well as showing differences from that of other cephalopods. The dominance of hyperplasia in the growth process of the octopus may have a large influence on the growth efficiency. Small muscle fibres are more efficient in terms of metabolic processes because of their high surface to volume ratio, and the minimal fibre size facilitated by the dominance of hyperplasia may allow the octopus an advantage in terms of energetic efficiency. This may in part compensate for the lower metabolism of the octopus compared with squid and cuttlefish (O'Dor and Wells 1987).

There are two factors of crucial importance here: (i) the plasticity observed in cephalopod growth is facilitated by the flexible mechanisms of cephalopod muscle growth; and (ii) we have only a very superficial understanding of the mechanisms of growth of cephalopods in general and even less for the octopus. The relative contributions of hyperplasia and hypertrophy, and the structure and distribution of fibres are modified by external factors (e.g. captivity, Pecl and Moltshaniwskyj 1999; temperature, Hoyle 2002), and changes in the hyperplasia/hypertrophy balance may change the rate and possibly form of the growth curve as it does in fish (Weatherley and Gill 1987). As such, more research into the mechanisms of octopus muscle growth, including that of the arms, is needed.

Energetics

An energy budget at the individual level conveys the way energy is held, used, packaged and passed on, and is crucial

to understanding the physiology of growth. There has been little recent work completed on octopus energetics since O'Dor and Wells (1987) published their review of energy and nutrient flow in cephalopods, and is an area of research that needs greater attention. Despite this, recent research on octopus energetics suggests that there might be physiological changes associated with the switch from exponential to power growth commonly seen in the laboratory. Oxygen consumption rate and ammonia excretion rate per unit bodyweight in *Octopus ocellatus* became relatively constant near the inflection point of the two growth forms, after previously decreasing steadily (Segawa and Nomoto 2002). Oxygen consumption rate was also sensitive to temperature in *O. ocellatus*, particularly during the rapid exponential growth phase. In *Enteroctopus dofleini* there was a significant drop in respiration rates in animals above 100 g BW, suggesting that this is the point where growth changes from the initial rapid phase to a slower phase (Rigby and Sakurai in press). There was also another decrease in respiration rates in *E. dofleini* individuals greater than 1000 g, which may relate to the beginning of maturation in this species.

An important advance in our understanding of octopus energetics has been with deep-sea octopuses. Recent work on energy balance equations for these cephalopods may explain why they appear to grow very slowly, with the metabolic rate of *Pareledone charcoti* demonstrated to be very low (2.45 mg O₂ h⁻¹ at 0°C; Daly and Peck 2000). This low level is consistent with the Q₁₀ (measure of the change in energy use with temperature) of the shelf-dwelling octopus *Eledone cirrhosa* (Daly and Peck 2000). In a preliminary comparison with the littoral octopus *Octopus cyanea*, diet assimilation efficiency was similar but respiration costs, as a percentage of energy consumption, were higher in *E. cirrhosa* (Daly and Peck 2000). With higher relative maintenance expenditure, there is less energy available for growth in *P. charcoti*. This difference in the amount of energy available for growth, along with the low energy content of the prey of some deep-sea species (O'Dor and Macalaster 1983; Quetglas *et al.* 2001), may account for the relatively slow growth of the deep-sea octopus compared to littoral species (Daly and Peck 2000; Wood 2000).

In summary, the last 17 years have seen many exciting developments in terms of understanding the growth of the octopus, but still many challenges lie ahead and it is hoped that this review can spark some interest in tackling the key questions that remain. Much time and energy is spent in acquiring individual-level data for the octopus (and other cephalopods) only to, in general, place all data into a single model that generates one population descriptor and seeks to statistically minimise differences between individuals. Given that a high degree of individual variation is a major characteristic of cephalopod growth, perhaps it is time to move away from treating this variation as a source of error, and instead utilise the differences between individuals to further

our understanding of the impacts of various factors on growth. Even siblings reared under identical conditions display a high level of variation in their size-at-age and we do not yet understand if this is due to diversity in the paternal genetics, small differences at the start of growth (e.g. hatchling size (Pecl *et al.* 2004)), or other unidentified factors.

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