Somatic growth processes: how are they altered in captivity?

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The cellular growth mechanisms of captive cephalopods were examined to determine whether the growth processes in aquaria are the same as those of wild individuals. Mantle muscle tissue growth in cephalopods is a function of both the production of muscle fibres and the growth of existing fibres. After seven days, captive animals had thicker mantles, a greater proportion of mitochondria-rich tissue, muscle fibres with smaller mitochondrial cores and fewer small muscle fibres. This suggests a reduced rate of new fibre generation, indicating an alteration to the cellular growth mechanisms and not simply a change in the physiological rate of growth. Smaller individuals were affected to a greater extent. Such modifications to the actual mechanisms of growth may have the potential to alter the shape of an individual's growth curve and can also affect final body size. Alterations to the proportion and structure of mantle components may impact upon many critical aspects of an individual's biology, as the muscular mantle is central to locomotion, ventilation of gills, energy storage and possibly subcutaneous oxygen extraction.

Keywords: captivity; growth; muscle fibre; cephalopod; mantle

1. INTRODUCTION

Although easily measured, growth is a complex process representing the net outcome of a series of behavioural and physiological processes (Forsythe & Van Heukelem 1987). Growth takes place as a cellular process by cell multiplication, an increase in cell size and the formation of intercellular substances (Hafez 1969). As such, growth is essentially changes in the relative number or size of different cell types and any response in growth is a reflection of changes in either cellular growth rates or cellular mechanisms of growth (Weatherley & Gill 1987). However, the study of animal growth at the cellular level of organization has received little attention for many taxa (Martinez 1996).

Descriptions of cephalopod growth have been obtained from field surveys of commercially important species and laboratory-based studies. Growth patterns in aquaria may not and, indeed, for cephalopods generally do not reflect those in nature. Comparisons of cultured and wild populations of *Loligo opalescens* have indicated that field individuals grow faster than cultured individuals (Jackson 1994). The growth rates obtained by Forsythe & Hanlon (1989) for captive *Loligo forbesi* during the logarithmic phase were considerably lower than those estimated by Collins *et al.* (1995) for wild animals. Reduced growth rates occur in molluscs when they are in captivity (Joll 1977) and it has been suggested that the logarithmic growth phase sometimes observed for cephalopods may be due to culture conditions (Alford & Jackson 1993). We need to determine how accurately laboratory studies

reflect the growth of wild individuals because information about food conversion efficiencies, excretion rates, costs of locomotion (Wells & Clarke 1996) and some life-history parameters (Boletzky & Hanlon 1983) can only be collected from captive animals.

Describing how muscle tissue increases in bulk during somatic growth has the potential of leading to a clearer understanding of growth patterns observed at the whole animal level (Hoyle *et al.* 1986). In turn this allows us to assess the application of laboratory-based growth research to wild populations. Growth of muscle tissue occurs by two processes: enlargement of existing fibres (hypertrophy) and production of new fibres (hyperplasia) (Heath 1993). Recruitment of new fibres stops shortly after birth in higher vertebrates and hypertrophy alone is responsible for postnatal muscle growth (Koumans *et al.* 1993). The number of fibres present when hyperplasia ceases determines the maximum somatic size attained by an individual (Weatherley & Gill 1987), because the physiological constraint of surface area to volume ratio determines the maximum size of individual fibres. In contrast to vertebrate teleost (Weatherley *et al.* 1988) and invertebrate crustacean muscle growth (Bittner & Traut 1978), hyperplastic growth continues throughout the life cycle in cephalopods. Growth in cephalopods is a function of both hypertrophy of existing fibres and continuous recruitment of new fibres throughout the life cycle (Moltschaniwskyj 1994; Preuss *et al.* 1997).

Idiosepius pygmaeus is a small tropical sepoid which undergoes growth by hyperplasia and hypertrophy (Pecl & Moltschaniwskyj 1997), resulting in continuous growth (Jackson & Choat 1992). This species has a very short life span (<80 days) (Jackson 1989) and is easily kept in captivity making it an ideal cephalopod for growth investigations. The aim of this paper is to describe the effect of

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Figure 1. Schematic diagram of sepoid mantle muscle showing the orientation of muscle fibres within the mantle (reproduced from Pecl & Moltschaniwskyj (1997), after Ward & Wainwright (1972)).

captivity on the growth processes of cephalopods by comparing the muscle fibre organization, structure and size distribution in captive and wild *I. pygmaeus*.

2. MATERIAL AND METHODS

Adult *I. pygmaeus* (62–148 mg) were collected between May and September 1994 from surface waters adjacent to rocky breakwaters and mangroves near Townsville, North Queensland, Australia (19°15' S, 146°50' E). Animals were maintained individually in 30 cm³ glass aquaria, attached to a 120 000 l recirculating seawater system situated outdoors to maintain natural diel periodicity. Individuals had *ad libitum* access to live freshly caught *Acetes sibogae australis* (glass shrimp) and were observed eating six to ten *Acetes* a day each. *Idiosepius pygmaeus* were maintained for seven days, which represents approximately 20% of the adult life span. This was considered sufficient time to detect changes in somatic growth due to captivity. Captive animals were compared to individuals of similar size from the wild (Pecl & Moltschaniwskyj 1997).

Individuals were killed by chilling them, fixed whole in Marine Bouin's and then washed in 70% ethanol. Specimens were dehydrated through an ascending isopropanol series, cleared in choloform and infiltrated with paraffin wax (Paramat). Specimens were mounted whole and sectioned longitudinally from the dorsal side midway through the animal. Sections were cut at 6 µm, stained with Mayer's haematoxylin and Young's eosin and mounted on slides with dibutylphthalate-polystyrene-xylene (DPX).

Cephalopod mantle muscle is predominantly made up of circular smooth muscle fibres separated into blocks by thin regions of radial muscle tissue (figure 1) (Ward & Wainwright 1972). Circular muscle fibres are present in two structural states: mitochondria-rich fibres that line the inner and outer surfaces of the mantle and mitochondria-poor fibres in a central zone occupying the bulk of the mantle musculature (Gosline & DeMont 1985). Mantle muscle tissue was sectioned along the long axis so that circular fibres, i.e. those muscle fibres that encircle the muscle mass, were cut transversely (figure 1). Measurements of muscle block widths and circular fibre diameters were taken from three positions along the mantle: anteriorly near the lip of

Table 1. *Analysis of covariance table for the analysis of overall mantle thickness, using total body weight as a covariate*

(SS, sum of squares; d.f., degrees of freedom; MS, mean squares; *F*, *F*-value; *p*, *p*-value, significant if *p* < 0.05; *n* = 10 wild and 8 captive *Idiosepius*.)

source of variation	SS	d.f.	MS	<i>F</i>	<i>p</i>
state (captive or wild)	3783	1	3783	5.44	0.034
covariate (weight)	21 170	1	21 170	30.42	<0.001
residual	10 438	15	696	—	—

Table 2. *Width of mitochondria-rich mantle zones (± s.e.) expressed as a percentage of total mantle width in captive and wild individuals*

(Average width refers to an average of measurements taken over the entire mantle and is not an average of anterior and posterior measurements only.)

animal status and size	anterior mantle (<i>n</i> = 3)	posterior mantle (<i>n</i> = 3)	average over all mantle positions (<i>n</i> = 10)
small wild (<i>n</i> = 5)	19.13 ± 1.34%	19.88 ± 0.98%	19.08 ± 0.90%
small captive (<i>n</i> = 5)	29.19 ± 2.64%	19.51 ± 1.75%	24.87 ± 0.83%
large wild (<i>n</i> = 5)	22.71 ± 0.91%	22.70 ± 3.70%	20.72 ± 1.31%
large captive (<i>n</i> = 3)	28.21 ± 1.59%	17.93 ± 2.34%	21.53 ± 1.2%

the mantle, exactly halfway along the long axis of the mantle (mid-mantle) and posteriorly near the fins.

The width of the mitochondria-rich inner and outer zones and the maximum mantle thickness (excluding the tunics) were measured and the width of the central mitochondria-poor zone calculated for each individual. Changes in the relative thickness of these zones at anterior and posterior positions of the mantle were compared between captive and wild animals.

The widths of five circular muscle blocks were measured at each mantle position for each individual. Block width was taken as the distance between but not including radial muscle partitions.

Both mitochondria-poor and mitochondria-rich circular muscle fibres at each mantle position were measured. As fibres are oval in cross-section, the maximum diameters of the muscle fibres were measured. To obtain an adequate number of muscle fibre diameters for size frequency analysis, 50 randomly selected mitochondria-poor fibres from each mantle position of each individual were measured. Twenty mitochondria-rich fibres were measured at each zone (inner and outer) of the mantle at each position. Fibres were randomly selected using an eyepiece micrometer and random number table. The sandwich structure of the mantle tissue, with fibres containing large mitochondrial cores (mitochondria-rich fibres) lining the inside and outside surfaces of the mantle and mitochondria-poor fibres in the centre, suggests that a considerable fraction of the oxygen requirements of decapods may enter via the skin, particularly over the mantle (Pörtner 1994). The diameter of the central mitochondrial core and the total fibre diameter were measured to calculate the

Figure 2. Frequency distribution of muscle blocks at the anterior, mid- and posterior positions of the mantle in (a) captive ($n=8$), and (b) wild ($n=10$) animals. Values in brackets are the means and standard deviations of the distribution, respectively.

Figure 3. Frequency distribution of mitochondria-poor circular muscle fibres at the anterior, mid- and posterior positions of the mantle in (a) captive ($n=8$), and (b) wild ($n=10$) animals. Values in brackets are the means and standard deviations of the distribution, respectively.

mitochondrial core area for 20 fibres from each mantle zone at each position. The relative diameter of the core in each fibre is directly related to mitochondrial volume (Johnston & Maitland 1980).

(a) Statistical analyses

To examine the effect of size on captive growth, individuals were separated into two size classes at the end of the seven-day captive period: <100 mg (five individuals) and 100–199 mg (three individuals). Muscle block and muscle fibre size frequency distributions were analysed using multiway frequency analysis.

This allowed a test of the hypothesis that the observed size frequency of fibres was independent of mantle position (anterior, mid-mantle or posterior), zone (outer, central or inner), individual size and treatment (wild or captive). An analysis of covariance was used to analyse the summed total fibre core area of the fibres measured from each individual, where total fibre area was used as a covariate. Differences in core area between size classes of *I. pygmaeus*, treatments and position within the mantle at each mantle zone were examined. An analysis of covariance was also used to examine the effect of treatment on total mantle thickness, using weight as a covariate. Residuals were examined

Figure 4. Frequency distribution of mitochondria-rich circular muscle fibres at the anterior, mid- and posterior positions of the mantle in (a) captive ($n=8$), and (b) wild ($n=10$) animals. Values in brackets are the means and standard deviations of the distribution, respectively.

Table 3. *Analysis of covariance table for the analysis of core area using fibre area as a covariate*

(The italicized terms are significant and were of interest in examining the effects of captivity. SS, sum of squares; d.f., degrees of freedom; MS, mean squares; F , F -value; p , p -value, significant if $p < 0.05$.)

source of variation	SS	d.f.	MS	F	p
position	14.86	2	7.43	66.44	<0.001
zone	1.86	2	0.94	8.36	<0.001
state (captive/wild)	9.32	1	9.32	83.34	<0.001
size	0.26	1	0.26	2.33	0.130
position $\times$ zone	1.63	4	0.41	3.64	0.008
state $\times$ position	3.06	2	1.53	13.70	<0.001
state $\times$ zone	0.68	2	0.34	3.06	0.050
state $\times$ size	0.80	1	0.80	7.18	0.008
position $\times$ size	0.19	2	0.10	0.86	0.425
zone $\times$ size	0.18	2	0.09	0.82	0.442
state $\times$ position $\times$ zone	0.65	4	0.16	1.46	0.218
state $\times$ position $\times$ size	0.14	2	0.07	0.62	0.540
state $\times$ zone $\times$ size	0.08	2	0.04	0.36	0.696
position $\times$ size $\times$ zone	0.45	4	0.11	1.00	0.411
state $\times$ position $\times$ size $\times$ zone	0.22	4	0.05	0.48	0.749
covariate (fibre size)	52.71	1	52.71	471.33	<0.001
residual	13.98	125	0.11	—	—

to check for equal variances and data were log transformed to homogenize variances. All values quoted as $\pm$ in the text refer to standard errors.

3. RESULTS

(a) Mantle regions

Mantle muscle tissue was 17% thicker in captive ($199.05 \pm 9.42 \mu\text{m}$) than in wild ($169.35 \pm 8.41 \mu\text{m}$) individuals

when adjusted for total body mass (table 1). The spatial distribution of the muscle fibre types within an individual also differed between captive and wild individuals. Wild animals did not differ in their relative proportions of mitochondria-rich and mitochondria-poor zones in the anterior and posterior mantle positions. In contrast, the anterior muscle tissue of captive animals had proportionally more mitochondria-rich tissue (table 2). When averaged over the entire body, larger captive individuals had comparable amounts of mitochondria-rich tissue to wild individuals of similar size. However, small captive individuals had proportionally more mitochondria-rich tissue throughout the entire mantle compared with small wild animals (table 2).

(b) Muscle block widths

The muscle block size distribution changed as a function of position (figure 2), but not treatment ($\chi^2=17.04$, d.f.=12 and $p=0.148$). Muscle block size was therefore not affected by captivity.

(c) Mitochondria-poor fibre diameters

Overall mitochondria-poor fibres in captive animals were larger, but the nature of the difference depended on the mantle position (anterior, mid or posterior) (figure 3). In both groups of animals the fibres in the mid- and posterior positions were larger than in the anterior, as previously described for wild individuals (Pecl & Moltschaniwskyj 1997). However, captive animals had fewer small fibres ($<1 \mu\text{m}$) and more larger fibres ($>3 \mu\text{m}$) in all mantle positions when compared with wild animals. This suggests that fewer new fibres are being generated in captive individuals; however, hypertrophy of existing fibres is occurring to a greater extent. This effect was more pronounced in smaller captive animals, resulting in the size dependence of the analysis.

Figure 5. Mitochondrial core area of muscle fibres, adjusted for total fibre size, in captive and wild animals at each mantle position.

(d) Mitochondria-rich fibre diameters

Mitochondria-rich fibres were also larger in captive animals; however, the effect depended upon the mantle position. The terms in the multiway frequency analysis that best described the observed size frequency distribution of fibres were treatment $\times$ position and position $\times$ zone ($\chi^2 = 11.03$, d.f. = 9 and $p = 0.27$). The second term in the model, a fibre size difference between inner and outer zones at the different mantle positions, was described in a previous study (Pecl & Moltschaniwskyj 1997) and these patterns were consistent between captive and wild animals. The difference between captive and wild animals for the mantle positions was due to captive animals having fewer small fibres (<3 mm) and more larger fibres than wild individuals (figure 4). This pattern was evident anteriorly and posteriorly, but not in the mid-mantle, although fibres in the mid-mantle were on average larger in captive animals. It appeared that, overall, proportionally more new mitochondria-rich fibres were being generated in wild than in captive animals. However, proportionally greater growth of existing fibres in captive animals was occurring, as shown by the relatively large numbers of fibres greater than 7 μm at the anterior and posterior mantle (figure 4).

(e) Mitochondrial core

Mitochondrial core size, adjusted for fibre size, was affected by captivity, but this effect was modified by fibre type, the position of the fibre in the mantle and animal size (table 3). Overall, mitochondrial core areas in captive animals were smaller than in wild animals (figures 5–7). Among the three mantle positions, captive animals had cores up to 31% smaller (figure 5). Furthermore, the increase in mitochondrial core size posteriorly in wild animals was not evident in captive individuals, as shown by the significant position by state interaction (table 3). Much of this difference was largely a function of the mitochondria-rich fibres (figure 6). Captive animals had mitochondria-poor fibres with core sizes comparable to wild animals; however, the captive animals had mitochondria-rich fibres with cores up to 21% smaller. A

Figure 6. Mitochondrial core area of muscle fibres, adjusted for total fibre size, in captive and wild animals at each mantle zone.

Figure 7. Mitochondrial core area of muscle fibres, adjusted for total fibre size, in small and large captive and wild animals.

further significant term not involving the effect of captivity was the position by zone interaction (table 3).

Body size also affected the mitochondrial core size, but this was not consistent between wild and captive individuals. Wild animals showed a decrease in mitochondrial core size with increasing body size (figure 7). In contrast, captive animals showed an increase in mitochondrial core size with increasing body size. As a result, the reduction in core size between wild and captive individuals went from 18% in large animals to 33% in small animals.

4. DISCUSSION

Aquarium maintenance of *I. pygmaeus* substantially modifies the processes of somatic growth at the cellular level and not simply the baseline physiological rate of growth. Wild-caught animals which were held in aquaria for seven days had fewer small muscle fibres, muscle fibres with smaller mitochondrial cores, a greater proportion of

mitochondria-rich tissue and a thicker mantle, when compared with wild-caught animals of similar size. Fewer small muscle fibres suggests that the relative rate of new fibre generation for both muscle fibre types was reduced by captivity. The growth of existing fibres would be more important in the overall growth pattern, suggesting a shift towards a more hypertrophic-driven growth process in captive individuals.

The effect of captivity was very much dependent on animal size. The greater changes in small captive animals may be partly because they contained fewer muscle fibres within the mantle by virtue of their smaller body size. Changes in the relative contributions of hyperplasia and hypertrophy to the growth pattern would, therefore, be more obvious in the smallest animals. Although captive individuals of both sizes had muscle fibres with proportionally smaller cores, the difference in smaller animals was greater. While wild animals demonstrated a decrease in core size with increasing body size, captive animals showed an increase in core size with increasing body size, resulting in a dramatic reduction in average fibre core size for smaller captive animals.

The anterior mantle muscle of captive individuals showed the most dramatic changes in mitochondria-poor fibre size frequency and the increase in width of the mitochondria-rich zone was also evident at the anterior region of the mantle. This appears to be the region where the growth processes have been most altered, supporting a previous suggestion that the anterior mantle is the primary growth region of *I. pygmaeus* (Pecl & Moltschaniwskyj 1997), a possible equivalent to the proliferation zones found in teleost myotome muscles (Rowlerson *et al.* 1995). Mitochondria-rich fibres have a greater capacity for hypertrophic increase as they attain a larger maximum size than mitochondria-poor fibres. A shift towards growth by hypertrophy may then lead to an increase in the thickness of the mitochondria-rich region and the mantle as a whole.

Although continuous growth in *I. pygmaeus* occurs by a combination of muscle hyperplasia and hypertrophy throughout the life span, hyperplasia is the most important growth mechanism because of the small maximum size (11 µm) that fibres may attain. A shift towards a more hypertrophic-dominated growth process in captive *I. pygmaeus* may well have the capacity to alter the shape of the growth curve and affect final body size. These are critical factors to consider, particularly for laboratory studies concentrating on life-history parameters, as the form of the growth curve has important implications for both longevity and fecundity (Sebens 1987).

From this study, it is evident that the growth of *I. pygmaeus* mantle muscle, with respect to the relative contributions of hyperplasia and hypertrophy and the structure and distribution of the fibres, is a plastic process that can be modified to a degree to meet local requirements or as a consequence of extrinsic factors. It is interesting that *I. pygmaeus* is capable of such flexibility and plasticity in its cellular mechanisms of growth. Fibre size in teleost muscle remains similar under the influence of different conditions (Weatherley & Gill 1984; McCormick & Molony 1995). Weatherley & Gill (1987) stated that this is not surprising given that a fish will have much the same functional and metabolic requirements of

various major tissues as any other of the same length and species, no matter how rapidly or slowly it has grown to 20 cm. The cephalopod mantle is critical to locomotion, respiration and ventilation and possibly subcutaneous oxygen extraction (Hochachka *et al.* 1975; O'Dor & Webber 1986; O'Dor & Shadwick 1989). Muscle structure must be adapted to meet these functional requirements, with major changes to this complex system demanding coordinated adjustments of many biological processes.

While an obvious alteration to the processes of growth was evident in captive animals, this study did not address which aspects of captivity are responsible for such changes. However, activity levels are usually substantially reduced in captive animals. Skeletal muscle of vertebrates undergoes morphological, biochemical and physiological changes due to increased contractile activity (Antonio & Gonyea 1993). Hypertrophy, the dominant growth mechanism in mature fish, is enhanced by sustained exercise (Greer Walker & Emerson 1978). As hyperplasia is the dominant growth mechanism in cephalopods this may be reduced under circumstances of decreased activity as experienced in aquaria.

Nutrition is a fundamental factor influencing growth; however, in this study we are confident that neither food quality nor quantity was responsible for the observed alterations to growth in captivity. Despite being offered a wide range of larval fish and crustaceans, *I. pygmaeus* would only consume *Acetes* and field observations of feeding have seen only *Acetes* taken (G. Pecl, personal observation). Captive individuals are likely to be stressed to some degree; however, our knowledge of the physiological effects of handling stress on cephalopods is very limited.

Until we understand the relationship between the observed changes to the growth processes and captive maintenance, caution should be used in the extrapolation of laboratory-based growth research to wild populations and the size-dependent effect of captivity needs to be considered. Future work needs to determine why captivity induces changes in the growth processes, addressing factors such as activity levels, oxygen availability, density of individuals, diet and handling stress. In addition to examining the relationship between cause and effect, experiments of this nature would also allow critical assessment of the factors responsible for the plasticity in growth that is typical of cephalopods.

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