Growth and tissue composition as a function of feeding history in juvenile cephalopods

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Abstract

We present the results of a series of experiments that examined the effect of feeding history on the growth and tissue composition of juveniles of two tropical cephalopods; the squid Sepioteuthis lessoniana and the cuttlefish Sepia elliptica. Juveniles were reared in individual containers for between 35 and 42 days at different ration levels, three ration levels for the squid and two levels for the cuttlefish. Although differences in ration were sufficient to cause different growth rates, both in body length and mass, the effects on tissue composition were less definitive. Sepioteuthis juveniles on the highest rations had higher concentrations of water, but no difference in lipid, carbohydrate or protein when compared with their lower ration siblings. In the case of juvenile cuttlefish no difference in tissue composition was detected between the two ration levels.

RNA:protein ratios were also determined for the juveniles to provide an estimate of instantaneous growth. A significant correlation was found between body size and RNA:protein ratio in the squid; those juveniles that ate more had higher RNA:protein ratios than lower ration individuals. Significantly, the juvenile cuttlefish showed no relationship between growth rate and RNA:protein ratios, which means that we are unable to use this measure to estimate the growth rates of wild individuals. In conclusion, ration level did affect growth rates and food availability is an important factor in modifying growth rates of wild individuals. However, we could not find, at the individual level, an index or measure that could be used to explain the variability of observed differences in growth rates as a function of nutritional history. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Cuttlefish; Growth; Feeding experiment; Juvenile cephalopods; Tissue composition; RNA:protein; Squid

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1. Introduction

The variability of growth displayed by many cephalopods is an important part of the equation in the life history of these complex invertebrates. The non-asymptotic growth of these animals adds a further complexity to the life history characteristics of these animals (Jackson and Choat, 1992). Variability in growth rates will not determine the age at which an individual reaches maximum size, because of continuous growth. However, it will determine how quickly an individual reaches reproductive maturity, and the reproductive output and longevity of an individual. Part of the reason that variability in growth rates has the potential to have dramatic effects on the population structure is that young cephalopods typically grow exponentially (Jackson, 1994). Hence, very small differences in the daily proportional increase in body size have a considerable effect several months later, and have the potential to be responsible for the variability in size-at-age that has been recorded in adult wild populations (Forsythe, 1993).

The processes influencing the growth and survival of wild juveniles are poorly understood and estimates of growth and survival during the juvenile phase are limited (Vecchione, 1987). Natural mortality estimates during the paralarval phase of Abralia trigonura were estimated at 7% per day (Bigelow, 1992), which is relatively low compared with estimates for fish species (Houde, 1989). However, it is likely that starvation may be a major cause of mortality of planktonic juvenile cephalopods (Vecchione, 1987). Therefore, there is a need to not only generate size-at-age relationships, but also to be able to determine and assess processes responsible for growth and survival during the juvenile phase.

Temperature has been clearly identified as a factor that has an immediate effect on growth and is likely to be important in determining size-at-age. Seasonal differences in adult growth rates have been identified in most squid species for which good growth data is available (Jackson, 1993, 1995; Coelho et al., 1994; Jackson et al., 1997). Temperature is also an important parameter incorporated into population dynamic models for short-lived animals (Grist and des Clers, 1999). This is not surprising since laboratory experiments and modelling of juvenile growth have shown that changes in temperature as little as 1°C have the potential to increase specific growth rates by 0.5% body weight/day (Forsythe, 1993). The only other factor that has the potential to modify growth rates and population structures to the same degree is food. The importance of food to juvenile survival has been proposed in the past (Vecchione, 1987), and it is expected that animals given more food will grow faster, than those animals fed less. However, regardless of water temperature wild juveniles must obtain sufficient food to be able to maintain maximum growth rates. Water masses that will influence coastal systems will differ in both temperature and nutrients. Therefore warmer water will not always be richer in nutrients and may not always support faster growth rates. The role of feeding rates in determining growth rates of wild individuals needs to be assessed.

Many juvenile cephalopods, particularly squid and octopus, have an immediate post-hatching phase that is planktonic (Boletzky, 1977). Typically, cephalopod species undergo direct development, with a long embryonic phase, resulting in a hatchling that is structurally and developmentally advanced (Boletzky, 1987; Okutani, 1987). Their sensory systems are well developed and therefore these juveniles are probably better equipped for prey capture and predator avoidance than their teleost counterparts.
However, in an environment in which mobility is limited and where food is temporally and spatially patchy (Kingsford and Choat, 1986) it is unlikely that juveniles will consistently have access to sufficient food levels to constantly feed to satiation. Variability in the quality and quantity of food is likely to affect both growth rates and survival of pelagic juveniles. However, direct measurement of these parameters is difficult. Size-at-age information provides average lifetime growth rates for individuals, but it will be necessary to use indirect measures to determine the vulnerability to mortality of an individual as a result of starvation. Where mortality is caused by starvation, condition indices have been used to provide an indication of growth, nutritional status and vulnerability to mortality as a function of limited food in fish (Ferron and Leggett, 1994; Theilacker et al., 1996) and bivalve molluscs (Crosby and Gale, 1990). This has been explored in the temperate cuttlefish, Sepia officinalis (Clarke et al., 1989; Koueta and Boucaud-Camou, 1999), but not in any of the tropical species which are faster growing and short lived.

In recent years biologists working with larval and juvenile fish have suggested that body size alone may not confer an advantage or ensure success in surviving the early stages of life, but the growth rate and/or condition of the individual will (Suthers, 1998). Instead the ability to store reserves and be in good condition, as measured by levels of lipid and carbohydrate, may be important in surviving periods of low food availability. Feeding experiments using reef and estuarine teleosts have shown that increased access to food does not just manifest itself as an increase in body size, but also in an array of complex biochemical interactions (McCormick and Molony, 1992; Molony, 1993). Biochemical indices of condition provide a measure of the energy reserves available to an individual. Concentrations of constituents such as protein, lipid, carbohydrate, and water provide information about the build-up or mobilisation of resources that are dependent upon the nutritional status of the individual (Ferron and Leggett, 1994). RNA concentration in the muscle tissue, either as a ratio to tissue wet weight or protein concentration, has the potential to be used as a measure of instantaneous growth that could be used to determine growth rates of individuals from wild populations. This index is of particular value in studies of those cephalopods, such as octopus and cuttlefish, which cannot be aged using structural features of the statoliths or gladii (Pierce et al., 1999) and for which we have no measure of growth rates for wild individuals. This tool also has the potential to be used when population-based estimates of growth are not providing sufficient resolution about growth at the individual level.

This paper presents the results of two experiments in which we reared juvenile squid at three different feeding levels and cuttlefish under two different feeding regimes for approximately 35–42 days to determine if the constituents of the muscle tissue would provide a record of feeding history. The aim of this research was to determine if we could provide a measure of condition that is a record of feeding or nutritional history of wild juveniles. Such a tool would aid our understanding of the processes affecting the early life history and variability in growth in wild populations of cephalopods.

2. Materials and methods

Juvenile individuals of Sepioteuthis lessoniana and Sepia elliptica were hatched in
captivity from eggs collected in the field. In the first experiment *S. lessoniana* eggs were collected from inter-tidal flats on Palleranda Beach in the Townsville region of north Queensland on 3 July 1996. The *S. elliptica* eggs were collected by otter trawl in Cleveland Bay, off the north Queensland coast during July. Both these batches of eggs hatched between 15 July and 24 July. For the second run of the experiment the RV James Kirby obtained *S. lessoniana* eggs during trawling in Princess Charlotte Bay, off the far north Queensland coast in September 1997. Three rearing experiments were conducted using these two cephalopods species over 2 years (Table 1). During 1996 and 1997 *S. lessoniana* hatchlings were reared for 41 and 35 days, respectively at two ration levels. In 1996 *S. elliptica* hatchlings were reared for 41 days at two ration levels.

Each individual squid or cuttlefish was reared in a 2.6-l plastic container (18 cm long, 13 cm wide and 11 cm high) with mesh bottom and lid, floating within a 300-l tank, attached to a 12 000-l recirculating, natural seawater system. Individuals were held separately so that food intake could be monitored, but also to prevent competition and cannibalism. At the start of each experiment 10–12 hatchlings were allocated to each treatment and placed randomly within four (1996 experiment) or three (1997 experiment) 300-l tanks. All tanks were located inside with a 12:12 h light–dark cycle and with air conditioning to assist in controlling water temperature. Water temperature was recorded daily (±0.05°C) with maximum–minimum thermometers. Temperatures ranged from 24.5 to 27.5°C in 1996 and from 26.5 to 28.0°C in 1997.

Each individual was fed live prey a maximum of three times per day, at approximately 0800 h, 1200 h and 1700 h. From past experience we knew that it was not possible to feed all the prey to the squid and cuttlefish at one time because when provided with an abundance of food they will often only eat half of each prey item making it difficult to quantify how much was eaten. We also found that very young individuals, despite being hungry, will refuse to eat a prey item that had been present in the tank for an extended period. Therefore, at each feeding time, the containers were checked for the presence of dead and live food, both were removed and recorded and a fresh quantity of food added. The major prey items for *S. lessoniana* were juvenile fish (mullet, *Mugil* sp. and glassfish, *Ambassis* sp.), and occasionally the glass-shrimp *Asces sibogae australis*. The juvenile *S. elliptica* were predominantly fed live glass-shrimps, and occasionally juvenile fish. Details of the squid feeding protocols for each day are outlined in Jackson and Moltschaniwskyj, in press, and the cuttlefish were held under the same feeding regime.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Age at start</th>
<th>Age at end</th>
<th>Length of experiment</th>
<th>Started</th>
<th>Finished</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sepioteuthis</td>
<td>21 days</td>
<td>62 days</td>
<td>41 days</td>
<td>30/8/96</td>
<td>9/10/96</td>
</tr>
<tr>
<td>Sepioteuthis</td>
<td>16–24 days</td>
<td>50 days</td>
<td>35–44 days</td>
<td>29/9–7/10/97</td>
<td>11/11/97</td>
</tr>
<tr>
<td>Sepia</td>
<td>21 days</td>
<td>62 days</td>
<td>41 days</td>
<td>31/8/96</td>
<td>9/10/96</td>
</tr>
</tbody>
</table>
During 1997, high mortalities in the first 8 days of the experiment resulted in the experiment being restarted, with four individuals carried over; three individuals from the high rations and one individual on low rations. The ration provided to the *S. lessoniana* juveniles was doubled from the start of the experiment because high mortality rates in 1996 were thought to be a result of underfeeding. Details of the feeding regime are outlined in Jackson and Moltschaniwskyj, in press. Ration levels were lowest in the 1996 experiment, and highest in 1997 experiment (almost four times higher). The net result was that highest ration in 1996 was similar to the lowest ration level in 1997 (Table 2a). Therefore, to allow sensible comparisons we identified three ration levels across the two experiments. These ration levels were designated low, intermediate and high (Table 2b), where low and intermediate levels are 45 and 75%, respectively of the highest ration level. We used the average total food intake per individual over the whole experiment, however the experiments ran for different times and the animals differed in age at the termination of the experiments (Table 1). Therefore, to account for these differences, the age of the animals at the end of the experiment was used as a covariate in the analyses. If the age of the individuals was significant the adjusted means of the variable of interest are shown. In the case of *S. elliptica*, two ration levels were used and compared, and all individuals were the same age (Table 2c).

The experiments were terminated either because it was not possible to get sufficient fresh food to support the juveniles, or because the faster growing juveniles were large enough to cause concerns about the rearing container restricting growth. Juveniles were euthanased by chilling to ensure no damage to tissues and that animals were intact for removal of tissues and statoliths. Chilling is the recommended method of euthanasia for tropical cephalopods (Roper and Sweeney, 1983). Only the muscle tissue was analysed.

Table 2
(a) Mean and range of total number of prey items eaten by juvenile *Sepioteuthis lessoniana* in each feeding level at the completion of the two experiments; (b) the categories of feeding levels used in the analysis of the *S. lessoniana* data; (c) the mean and range of the total number of prey items eaten by juvenile *Sepia elliptica* in each feeding level.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Feeding level</th>
<th>Mean total number of prey</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>1</td>
<td>267.50</td>
<td>257–279</td>
</tr>
<tr>
<td>1996</td>
<td>2</td>
<td>126.25</td>
<td>124–128</td>
</tr>
<tr>
<td>1997</td>
<td>1</td>
<td>335.50</td>
<td>247–353</td>
</tr>
<tr>
<td>1997</td>
<td>2</td>
<td>174.33</td>
<td>171–176</td>
</tr>
<tr>
<td>(b)</td>
<td>Feeding level</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>7</td>
<td>348.14</td>
<td>342–353</td>
</tr>
<tr>
<td>Intermediate</td>
<td>7</td>
<td>264.57</td>
<td>247–279</td>
</tr>
<tr>
<td>Low</td>
<td>10</td>
<td>155.10</td>
<td>124–176</td>
</tr>
<tr>
<td>(c)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>12</td>
<td>194.55</td>
<td>185–206</td>
</tr>
<tr>
<td>Low</td>
<td>11</td>
<td>104.33</td>
<td>100–107</td>
</tr>
</tbody>
</table>
given there is no evidence that the digestive gland is an energy storage organ in Sepioteuthis australis (Semmens, 1998).

The percentage water, protein, carbohydrate and lipid were determined using techniques described in Moltschaniwskyj and Martinez (1998). Duplicates were run for all tissue analyses for each individual, and blanks were also run simultaneously. Concentrations of lipid, protein and carbohydrate were expressed as a function of the wet weight of the muscle mass. Mantle muscle tissue was analysed for RNA concentration using a Promega Total RNA isolation system kit (Cat. No. Z5110). RNA content was expressed as a ratio of the protein concentration in the mantle muscle tissue.

2.1. Statistical analyses

A one-way ANCOVA was used to compare the variable of interest among the ration levels using age as a covariate. If there was no effect of the covariate when differences among the feeding levels were significant a Tukey’s honestly significant difference post hoc test was used. Assumptions of ANOVA were checked by visual assessment of the residual and normality plots. Linear relationships between dorsal mantle length and total body weight were compared among the treatments using an ANCOVA.

3. Results

3.1. Sepioteuthis lessoniana

At the end of the experiments there were significant differences in both total body weight \( (F = 130.96, \text{df} \ 2,20, \ P < 0.001) \) and dorsal mantle length \( (F = 76.246, \text{df} \ 2,19, \ P < 0.001) \) of the juveniles among the three feeding levels. Individuals fed at the highest and intermediate rations were very similar in weight and length, but were more than twice the mass and 40% longer than juveniles fed at the lowest ration (Fig. 1). There was no evidence that the length–weight relationships were modified by ration \( (F = 1.35, \text{df} \ 2,17, \ P = 0.285) \), suggesting that the length–weight relationship could not be used as a nutritional condition index for these animals.

Mortality levels were relatively high, with 38% of the juvenile squid dying during the experiment, however, there was no evidence that this mortality was dependent on ration \( (\chi^2 = 2.56, \text{df} \ 2, \ P = 0.278) \).

Small and non-significant differences among the ration levels were found in mantle muscle carbohydrate \( (F = 0.05, \text{df} \ 2,18, \ P = 0.952) \) and lipid content \( (F = 0.14, \text{df} \ 2,18, \ P = 0.873) \). These differences were 7 and 11.6% between the highest and lowest levels of carbohydrate and lipid, respectively. The protein content of the mantle muscle was highly variable among individuals within each treatment. As a result although 45% less protein was detected in the muscle tissue of juveniles fed at the high versus intermediate ration, this was not significant \( (F = 2.93, \text{df} \ 2,18, \ P = 0.079) \). In contrast, the water content was significantly higher in the muscle tissue of individuals reared at the highest ration \( (F = 4.74, \text{df} \ 2,18, \ P = 0.022) \), approximately 9% higher than detected in juveniles at the intermediate ration (Fig. 2).
An examination of the bivariate partial correlations among the variables, controlling for age, found a trend that heavier juveniles (faster growing juveniles) had decreasing concentrations of protein ($r_{adj} = -0.51$, df 15, $P = 0.036$), but increasing concentrations of water ($r_{adj} = 0.72$, df 15, $P = 0.001$).

The RNA:protein ratio was almost two times higher in juveniles fed at the high ration, compared with the intermediate and low food intake juveniles ($F = 4.38$, df 2, 15, $P = 0.032$) (Fig. 2). A positive partial correlation, controlling for the age of the juveniles, was detected between RNA:protein ratio and total body weight ($r_{adj} = 0.60$, df 15, $P = 0.010$). Furthermore, there was a positive correlation between the total number of prey consumed and RNA:protein ratio ($r = 0.54$, $n = 18$, $P = 0.021$).

### 3.2. Sepia elliptica

The difference in ration was sufficient to produce a significant difference in the weight ($F = 5.06$, df 1.20, $P = 0.036$) and dorsal mantle length ($F = 5.64$, df 1.21, $P = 0.023$) between the treatments at the end of the experiment. The average total weight and dorsal mantle length of the high ration juveniles was 22 and 8.7% higher, respectively, than low ration individuals (Fig. 3). However, the length–weight relationships did not differ.
between the two treatments ($F = 1.35, \text{df} = 2,17, P = 0.285$). There was no mortality of juvenile cuttlefish during the experiment.

Negligible differences were found in water ($F = 4.27, \text{df} = 1,21, P = 0.051$) and carbohydrate ($F = 0.0002, \text{df} = 1,21, P = 0.990$) concentrations between the two ration levels. There were also no significant differences in lipid ($F = 3.78, \text{df} = 1,21, P = 0.067$) and protein concentration ($F = 0.21, \text{df} = 1,21, P = 0.649$) between the two ration levels. This was despite concentrations being 20 and 14% lower for lipid and protein, respectively, in juveniles on high rations. However, both variables were highly variable among the juveniles. There was no difference in the RNA:protein ratios between the two ration levels ($F = 0.19, \text{df} = 1,21, P = 0.666$). Furthermore, there was no correlation between specific growth rates and RNA:protein ratios ($r = 0.022, \text{df} = 15, P = 0.934$). In addition, there was no correlation between the RNA:protein ratios and the total number amount of prey eaten ($r = 0.12, \text{df} = 15, P = 0.64$).

4. Discussion

Ration level caused dramatically different growth rates in the juvenile cephalopods, indicating that the experiment did place at least the low ration animals under nutritional stress. However, there was no evidence that the amount of food consumed resulted in
biochemical differences in mantle muscle tissue. We found no evidence that protein, lipid, and carbohydrate content could be used to provide an indicator of feeding history in juvenile Sepioteuthis lessoniana and Sepia elliptica. As a result there is no evidence that these measures of condition at the tissue level can be used to understand the effect of feeding activity on growth rates and survivorship of wild individuals.

Extremely high variability in protein content of field and laboratory reared juveniles has been a feature of previous work on tropical squid and cuttlefish (Moltschaniwskyj and Martinez, 1998; Moltschaniwskyj and Semmens, 2000; Semmens and Moltschaniwskyj, 2000). This experiment explicitly attempted to minimise possible sources of variation among individuals by tracking and recording the growth and nutritional history of each animal. However, high levels of variability in protein concentration were just as evident in this group of experimental animals. Therefore, ration level does not appear to be a major process in determining protein content or variability in these cephalopods.

No difference in lipid, carbohydrate and protein concentrations in the mantle muscle of either species among individuals reared at the different food rations suggests that storage of energy was unlikely to occur in juveniles. Typically, cephalopod muscle tissue contains very low concentrations of glycogen, suggesting this is not a storage product used by cephalopods (Suryanarayanan and Alexander, 1971). During the early stages of the experiments we were confident that juveniles on the highest ration were fed
to satiation. However, towards the end of the experiment all prey items were eaten immediately, suggesting we may have been unsuccessful in providing sufficient food to feed high ration juveniles to satiation. This experiment using *S. elliptica* was unable to produce the difference in carbohydrate concentration seen in a previous experiment (Moltschaniwskyj and Martinez, 1998). In that experiment, juvenile *S. elliptica* fed ad libitum, and presumably to satiation, had higher concentrations of carbohydrate than their lower fed siblings. The absence of mortality of the juvenile cuttlefish in this experiment suggests that we most probably had provided sufficient food for survival, but not enough to see an increase of carbohydrate previously detected. In the case of *S. lessoniana*, specific growth rates over 4% body length per day in this current experiment were comparable with values obtained from laboratory and field populations (Jackson, 1990; Jackson et al., 1993).

A major concern and problem when isolating individuals in separate rearing containers is that growth of the juveniles may become restricted. Analysis of statolith increments from the juvenile *S. lessoniana* used in this experiment revealed a very sharp and dramatic drop in increment width at the point of containment (Jackson and Moltschaniwskyj, in press). This was assumed to be a record of a drop in growth associated with transfer from large tanks to small containers. Although statolith increments never returned to the same width as prior to transfer, a divergence in increment width between the groups of squid was ascribed to a difference in growth due to ration. Therefore, although there is some evidence that the rearing containers may have compromised growth, the difference in growth during the experiment was sufficient to satisfy the aims of the experiment.

Mortality levels near 40% during the experiments using juvenile *S. lessoniana* were higher than desirable. Although there was no evidence that mortality was due to ration level there is insufficient replication required for a rigorous frequency analysis. The increase in feeding levels in the second experiment was explicitly intended to minimise mortalities. The isolation of the animals is an artificial condition, particularly since *S. lessoniana* juveniles display schooling behaviour several weeks after hatching. However, this isolation provided us with the ability to control and record exactly the food intake of each juvenile. We were also able to remove the effects of feeding hierarchies and cannibalism that occurs among individuals when schools of juveniles are maintained in captivity.

RNA:protein ratios in *S. lessoniana* did correlate with growth and the amount of food consumed by the juvenile squid. However, when adjusted for age, the RNA:protein levels explained only 36% of the variation in body size. This provides a weak ecological tool to assess growth or to recognise growth as a function of feeding status in wild individuals. Although age estimates using statolith analysis have been validated and used to generate growth curves for squid (Jackson, 1994), there is no reliable method to estimate growth rates for wild cuttlefish. The use of biochemical techniques as an alternative has been proposed and it was suggested that RNA concentration as a function of fresh body weight should provide an index (Pierce et al., 1999). However, there was no evidence in our work to be able to provide a biochemical measure of growth in cuttlefish *S. elliptica*. The development of similar indices for use with *Sepia officinalis* has been partially successful, in that the correlation of RNA:DNA ratios the growth rate
were evident under one temperature regime, but not another (Clarke et al., 1989). Clearly continued exploration of these indices is needed.

The influence of environmental conditions on growth when developing an assessment tool of condition and instantaneous growth also needs careful consideration. The temperatures used in these experiments were comparable to those in austral spring and autumn in Townsville waters (Kenny, 1974). However growth and condition of an individual will be a function of an interaction between temperature and food in determining growth rates. This was demonstrated when the RNA:protein ratios measured in the cuttlefish feeding experiment of Clarke et al. (1989) were temperature dependent. The usefulness of RNA:protein ratio in assessing instantaneous growth rates or condition appears to be specific to each cephalopod species and the physical environmental conditions (Clarke et al., 1989; Houlihan et al., 1998; Pierce et al., 1999; this study). As such it will be necessary to validate this tool for a range of environmental conditions and life history stages.

In conclusion, despite running experiments with control and knowledge of the food intake of the juveniles there was very little evidence of an effect of feeding history at other than at the whole animal level, i.e. size-at-age of an individual. Unfortunately a number of parameters, biological and physical, have the capability to modify the size-at-age of an individual. Furthermore, size-at-age information provides little information about the growth trajectory taken or the thermal or nutritional history of the individual that results in the observed size-at-age. However, the successful use of ATCase as a biochemical indicator of feeding activity in juvenile cuttlefish (Koueta and Boucaud-Camou, 1999) could provide us with a tool to assess nutritional status in other young planktonic cephalopods.

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References


