

# Cephalopod hatchling growth: the effects of initial size and seasonal temperatures

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**Abstract** Temperature is known to have a strong influence on cephalopod growth during the early exponential growth phase. Most captive growth studies have used constant temperature regimes and assumed that populations are composed of identically sized individuals at hatching, overlooking the effects of seasonal temperature variation and individual hatchling size heterogeneity. This study investigated the relative roles of initial hatchling size and simulated natural seasonal temperature regimes on the growth of 64 captive *Octopus pallidus* over a 4-month period. Initial weights were recorded, and daily food consumption and fortnightly growth monitored. Two temperature treatments were applied replicating local seasonal water temperatures: spring/summer (14–18°C) and summer/autumn (18–14°C). Overall octopuses in the spring/summer treatment grew at a rate of 1.42% bwd<sup>-1</sup> (% body weight per day) compared to 1.72% bwd<sup>-1</sup> in the summer/autumn treatment. Initial size influenced growth rate in the summer/autumn treatment with smaller octopuses (<0.25 g) growing faster at 1.82% bwd<sup>-1</sup> compared to larger octopuses at 1.68% bwd<sup>-1</sup>. This was opposite to individuals in the spring/summer treatment where smaller octopuses grew slower at 1.29% bwd<sup>-1</sup> compared to larger octopuses at

1.60% bwd<sup>-1</sup>. Initial size influenced subsequent growth, however, this was dependent on feeding rate and appears to be secondary to the effects of temperature.

## Introduction

Cephalopod growth is highly variable and influenced by biotic and abiotic factors such as temperature, diet, age, gender and level of maturity (Forsythe 1984, 1993; Forsythe and Van Heukelem 1987; Forsythe and Hanlon 1988). Individual growth variation can influence many facets of a cephalopod population including size and age structure, reproductive dynamics, and survival rate of hatchlings, all of which in turn can affect local abundance levels and therefore fisheries. It is necessary to determine which factors have the greatest impact on growth, in order to understand the complex dynamics of cephalopod populations.

Temperature has a very strong influence on cephalopod growth, as demonstrated in laboratory experiments with controlled temperatures (e.g., Forsythe and Hanlon 1988; Wood and O'Dor 2000; Aguado Gimenez and Garcia Garcia 2002). For example, *Loligo pealeii*, individuals kept at 20°C have mean growth rates 60% higher than those reared at 15°C (Hatfield et al. 2001). Temperature effects have also been observed in wild populations e.g., *Octopus mimus*, where growth is highest in summer for both males and females (Cortez et al. 1999). Captive studies have generally shown a two-phase pattern comprising of a short exponential stage of high growth, followed by a slower, usually power growth stage, where more energy is invested in reproductive development (Mangold 1983).

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Temperature has the greatest potential to influence subsequent growth during the faster exponential stage (Forsythe and Van Heukelem 1987; Hatfield et al. 2001).

Many species spawn during periods of rising temperatures, e.g., spring/summer, where hatchlings encounter dynamic temperatures (Ambrose 1988). Most captive growth studies have used one or several fixed temperature regimes (e.g., DeRusha et al. 1987; Forsythe and Hanlon 1988; Hatfield et al. 2001; Segawa and Nomoto 2002; Iglesias et al. 2004; Miliou et al. 2005), which do not reflect natural temperature undulations. The effects of simulated seasonal temperatures on the rapid juvenile growth phase of cephalopods needs attention and are examined for the first time in this study.

The concept of seasonal temperature change influencing juvenile cephalopod growth was formulated by Forsythe (1993), in what is now referred to as the Forsythe effect: “As hatching occurs over a period of increasing water temperatures, each monthly cohort will encounter warmer temperatures and thus grow significantly faster than cohorts that hatched only weeks previously” (Forsythe 2004). The Forsythe effect has been shown to be an effective explanation for a high proportion of the variability observed in cephalopod growth (Hatfield 2000; Hatfield et al. 2001). However, the Forsythe effect does not explain all the variability, as hatchlings reared under identical conditions can vary in final size by an order of magnitude (e.g., *O. ocellatus* 5.3–16.3 g at 20°C and 7.5–31.5 g at 25°C, Segawa and Nomoto 2002).

Cephalopod growth studies that calculate individual growth as an average over the lifespan, assume that populations are composed of identically sized hatchlings and therefore that growth of all individuals begins from a common starting point (Tracey et al. 2003; Challier et al. 2005). However, species such as *Sepioteuthis australis*, *Sepioteuthis lessonisana*, and *O. digueti* for example can have considerable variation in size at hatching 4.3–7.3 mm (Steer et al. 2003), 4.7–6.2 mm (Ikeda et al. 1999), 4.1–6.0 mm (DeRusha et al. 1987) mantle length (ML), respectively. Pecl et al. (2004) demonstrated theoretically that differences in hatchling size could result in larger hatchlings being double the size of smaller hatchlings after 90 days growing at the same rate, assuming that individuals experiencing similar environmental conditions grow at similar rates, irrespective of initial hatchling size. Pecl et al. (2004) expanded on this, and hypothesised that there may be a definable relationship between hatchling size and growth rate, where for example, smaller hatchlings

grow faster than larger hatchlings (or vice versa). Laboratory experiments monitoring the growth of ‘known sized’ cephalopod hatchlings under identical light and temperature regimes are needed to elucidate the influence of initial size on growth and final size.

The aim of this study was to assess how individual size-at-hatching influences the growth of *O. pallidus* (Hoyle) hatchlings reared under simulated seasonal temperature regimes. This study addresses two questions. (1) Do individuals experiencing similar conditions grow at similar rates irrespective of hatchling size, or is there a definable relationship between growth rate and initial size? (2) Do simulated seasonal temperature regimes have an impact on juvenile growth rate?

A benthic species, *O. pallidus* is of medium size (max 1.2 kg), endemic to southeast Australian temperate waters and found in depths from 7–275 m. Eggs are 11 mm in length and laid in clusters of 150–250 (Stranks 1988).

## Materials and methods

### Specimen collection

Three *O. pallidus* females with egg clutches of approximately 200 eggs each were collected from waters in northwestern Tasmania, Australia on 15 February 2005. The octopuses were caught using a commercial 500 pot bottom set long line 3.7 km in length (40°49.268S; 145°39.774E west and 40°50.240S; 145°42.091E east), at a depth of 45 m, which had been deployed approximately 6 weeks prior. Onboard the octopuses were retained in their pots and provided with a constant flow of water in an 80 l holding tank. After landing they were transferred to a 1,000 l concrete flow-through tank for 48 h and transported in aerated 20 l buckets to the Tasmanian Aquaculture and Fisheries Institute (TAFI) in Hobart. At TAFI the octopuses were individually housed in 250 l cylindrical plastic flow-through tanks supplied with filtered natural seawater. Temperature was maintained at ambient levels (11–22°C) and fluorescent lighting replicated natural daylight hours (0600–1,800 hours light, 1,800–0600 hours dark). The octopuses and their eggs were monitored daily for any signs of stress or hatching.

The first two eggs hatched on 17 May 2005, 91 days after collection from the wild. Hatch rate increased during the following 2 weeks, peaking during 1–5 June 2005. The highest rate of hatches in 1 day was 48 on 5 June 2005. All octopuses used in the experiment hatched during this 5-day period and from a single mother.

**Table 1** Temperature profiles for the spring/summer and summer/autumn temperature treatments for the duration of the experiment

Start	End	Days	Spring/summer (°C)	Summer/autumn (°C)
1/6/05	1/7/05	30	14	18
2/7/05	19/7/05	17	15	17
20/7/05	6/8/05	17	16	16
7/8/05	24/8/05	17	17	15
25/8/05	24/9/05	30	18	14

## Experimental design

The experiment ran from 1 June to 23 September 2005 (114 days). A total of 64 octopuses were used and divided randomly into two treatments of 32 individuals. The octopuses were held individually in 2 l plastic enclosures floating in 250 l cylindrical tanks, with 4–8 enclosures per tank. Each enclosure contained a scallop (*Pecten fumatus*) half shell to act as a den. The tanks were in banks of five, with separate pumps, header tanks and heater/chiller units per bank. The banks formed two temperature-based treatments.

The two treatments replicated the local seasonal water temperatures of northwestern Tasmania. The treatments were spring/summer (14–18°C) and summer/autumn (18–14°C). The octopuses hatched in ambient water (12°C), were transferred to acclimatisation tanks, and then held for 24 h prior to transferral to the treatment tanks. The rate of acclimatisation for the spring/summer treatment was 1°C every 12 h, and 1°C every 4 h for the summer/autumn treatment. No signs of stress (i.e., inking, swimming erratically and rapid colour change) were observed during the acclimatisation period.

Temperatures were controlled by heater/chiller units based at the inflow of each bank of tanks. Temperatures were altered 1°C on five occasions at 30, 17, 17, 17, and 30-day intervals (Table 1). The 30-day periods at the start and the end of the experiment were applied to replicate the stable periods of mid seasons. The temperature change intervals were based on measurements recorded during the spring/summer of 2004/2005 and the summer/autumn of 2005 (see <http://www.marine.csiro.au/remotesensing/oceancurrents>). Temperatures were monitored daily with standard thermometers. Four data loggers, one at each end of each bank monitored continuous temperature records every 15 min.

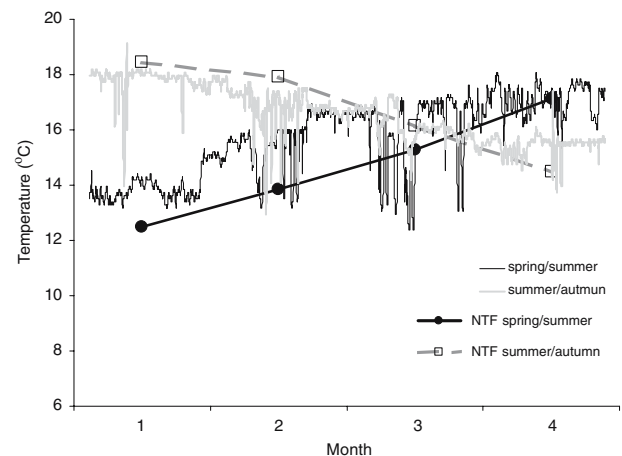
Temperature fluctuated during the experiment, due to faults with the heater/chiller units caused by blockages in water flow. The temperatures attained were slightly lower and varied more than was originally intended. However, the general temperature trend

followed that of increasing and decreasing temperature regimes. Monthly mean surface temperature data from the National tidal facility (NTF) in Burnie in northwestern Tasmania during spring/summer and summer/autumn over the last 10 years displayed similar temperature patterns to the treatments (Fig. 1).

## Feeding

The octopuses were fed every afternoon on wild caught porcelain crabs (*Petrolisthes elongatus*). The crabs were divided into six size classes based on carapace width (Table 2). Crab weight ranges were derived from the live wet weights of 30 individuals from each size class. At completion of the experiment the mean weights for each crab size class were analysed to acquire a general indication of the amount of food consumed at each feeding event.

Each octopus had a constant supply of two crabs. The size of the crabs given to each individual was determined by (i) the size of the octopus, (ii) the sizes of the crabs previously eaten by the octopus and (iii) behavioural observations of the octopus when given a



**Fig. 1** Temperatures recorded every 15 min for the spring/summer (black line) and the summer/autumn (grey line) temperature treatments; mean monthly ocean temperatures recorded at the National tidal facility in northwestern Tasmania spring/summer (black dots, black line) and summer/autumn (white squares, grey dashed line)

**Table 2** Size classes based on carapace width and subsequent mean weight for the crabs (*Petrolisthes elongatus*) used to feed *Octopus pallidus*

Size	Carapace width (mm)	Mean weight (g)	Weight range (g)
S0	<2	0.033	0.011–0.070
S1	2–4	0.079	0.044–0.135
S2	4–6	0.201	0.101–0.366
S3	6–8	0.419	0.225–0.702
S4	8–10	1.040	0.510–1.712
S5	10–12	2.219	1.326–3.810

crab that the researchers believed was in the upper size limits it could prey upon without injury. The number and size of live and/or consumed crabs was recorded each afternoon in order to provide a profile of the octopuses feeding rates. Crab sizes were based on visual estimates using the carapace width scale (Table 2). A *t*-test was performed on the weight of crabs consumed to determine if there was any difference between treatments.

#### Data collection and analysis

The octopuses were weighed individually every 2 weeks to 0.001 g wet weight before feeding, allowing for progressive monitoring of the growth of each individual. A fortnightly timeframe was applied to minimize handling stress and the potential impacts such stresses could have on growth. Using a set routine and a single balance, one researcher performed all the weighing for consistency. Keeping handling to a minimum, each octopus was transported in individual jars and was out of water for a maximum of 10 s.

To calculate growth the following instantaneous growth rate equation was applied:

$$G = \frac{\ln Wt_2 - \ln Wt_1}{\Delta t}$$

where  $Wt_1$  and  $Wt_2$  are individual weights at times  $t_1$  and  $t_2$ , and  $\Delta$  time interval in days between two weighing periods. This equation was applied to enable comparisons with other studies that have taken similar approaches (DeRusha et al. 1987; Forsythe et al. 2001). *t*-Tests were performed to determine if there were any difference between treatments in initial size and final size, all data was transformed (Log<sub>10</sub>) prior to analysis to ensure a normal distribution.

Analyses of co-variance (ANCOVA) were performed to determine if there were any significant differences between the treatments. Using initial size as a covariate, the relationship between treatments for

initial size versus final size, initial size versus instantaneous growth and initial size versus total feed eaten were analysed.

#### Results

Survival rate was 78.12%, with 14 (seven per treatment) octopuses dying during the experiment. The deceased octopuses ages ranged between 26 and 96 days (mean = 58 days,  $7.812 \pm \text{SE}$ , mean weight at hatching was 0.276 g ( $0.013 \pm \text{SE}$ ) and 0.416 g ( $0.033 \pm \text{SE}$ ) at death. Many lost weight prior to death the mean reduction in weight between the last weighing and death was 0.085 g ( $0.036 \pm \text{SE}$ ) a 20% reduction in size.

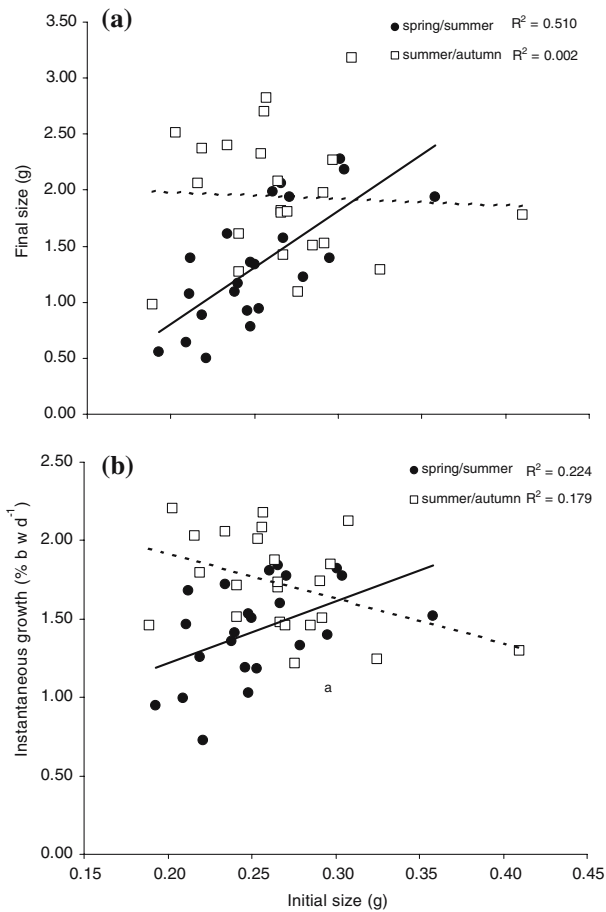
Although randomly allocated, the octopuses in the spring/summer treatment were 6.6% smaller on average than those in the summer/autumn treatment at the beginning of the experiment (Table 3), however, this was not statistically significant ( $t = -1.364$ ,  $df$  25,  $P = 0.185$ ). By the end of the experiment the octopuses in the spring/summer treatment were significantly smaller (31%) on average than those in the summer/autumn treatment (Table 3;  $t = -3.711$ ,  $df$  20,  $P = 0.001$ ).

The treatments showed a significant difference in the relationship between initial size and final size ( $F = 11.878$ ,  $df$  1, 45,  $P = 0.001$ ). The spring/summer treatment displayed a positive relationship ( $r^2 = 0.5104$ ) between initial and final size (Fig. 2a), indicating that initially smaller octopuses (<0.25 g) had a smaller final size range 0.494–1.61 g (mean 1.023 g,  $n = 13$ ) compared to initially larger octopuses (>0.25 g), range 0.94–2.274 (mean 1.75 g,  $n = 10$ ). The summer/autumn treatment, however, displayed no relationship between initial size and final size ( $r^2 = 0.002$ ) (Fig. 2a).

The treatments displayed a significant difference in the relationship between initial size and instantaneous growth (% body weight per day) calculated over the entire experimental period ( $F = 10.599$ ,  $df$  1, 45,

**Table 3** Initial and final size comparisons for *Octopus pallidus* in the spring/summer and summer/autumn temperature treatments

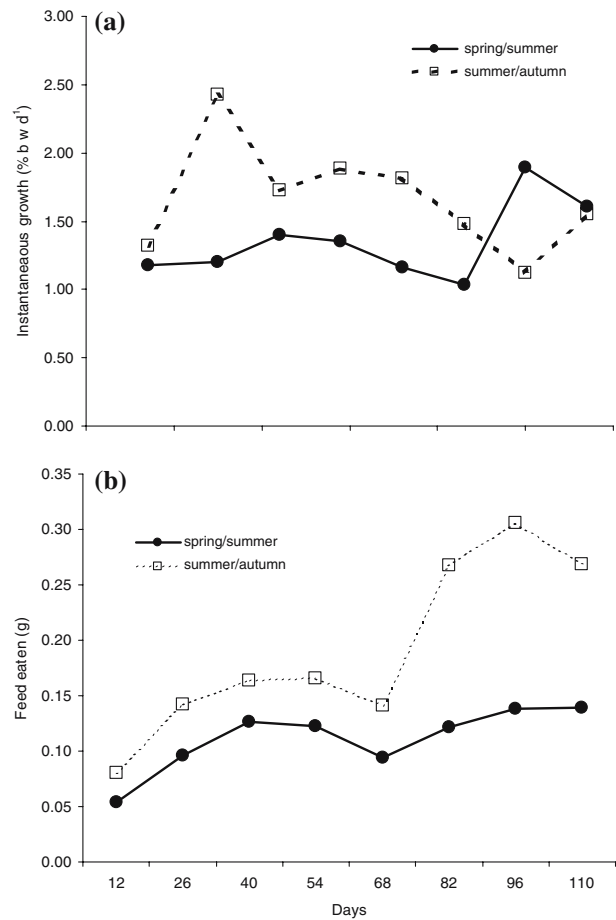
	Spring/summer	Summer/autumn
Initial size		
Range (g)	0.193–0.358	0.189–0.410
Mean (g)	0.256	0.274
SE	0.007	0.01
Final size		
Range (g)	0.494–2.274	0.935–3.177
Mean (g)	1.339	1.938
SE	0.111	0.119



**Fig. 2** **a** Initial size (g) versus final size (g) for *Octopus pallidus* in the spring/summer (black line) and summer/autumn (dashed line) temperature treatments. **b** Initial size (g) versus instantaneous growth rate (% bwd<sup>-1</sup>) for *Octopus pallidus* in the spring/summer (black line) and summer/autumn (dashed line) temperature treatments

$P = 0.002$ ). A positive relationship between growth rate and initial size ( $r^2 = 0.224$ ) was evident in the spring/summer treatment, with initially smaller octopuses (<0.25 g) growing slower at 1.293% bwd<sup>-1</sup> (0.089 ± SE) compared with initially larger octopuses at 1.605% bwd<sup>-1</sup> (0.068 ± SE) (Fig. 2b). This pattern was the opposite for the summer/autumn treatment where a weaker relationship was shown ( $r^2 = 0.1787$ ), with initially smaller octopuses (<0.25 g) growing faster at 1.824% bwd<sup>-1</sup> (0.108 ± SE) compared with initially larger octopuses at 1.684% bwd<sup>-1</sup> (0.079 ± SE) (Fig. 2b).

The spring/summer treatment displayed relatively constant growth in terms of % bwd<sup>-1</sup> until approximately day 100, during the warmest period for that treatment, when a peak occurred followed by a decline at the last weighing. In contrast, the summer/autumn treatment displayed a dramatic peak in mean growth of

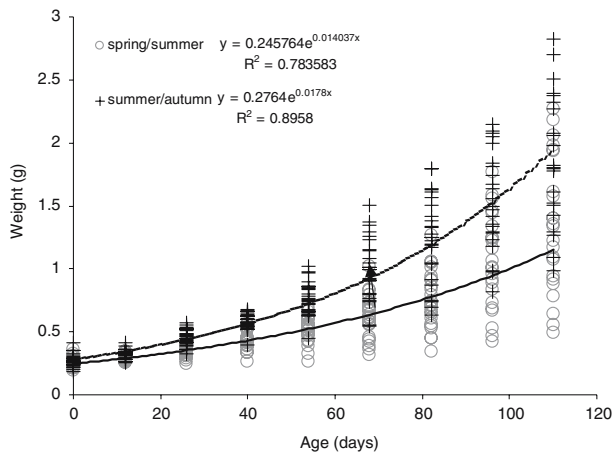


**Fig. 3** **a** Mean instantaneous growth rate (% bwd<sup>-1</sup>) of *Octopus pallidus* at 14-day intervals over 114 days for the spring/summer and summer/autumn temperature treatments. **b** Mean grams eaten over 14-day intervals for *Octopus pallidus* in the spring/summer and summer/autumn temperature treatments

2.428% bwd<sup>-1</sup>, in the first 30 days during the highest temperatures, growth then generally declined until a second peak at the last weighing (Fig. 3a).

Both treatments demonstrated exponential growth, with no evidence of two-phase growth. The mean size difference between treatments increased consistently throughout the experiment. Overall, octopuses in the spring/summer treatment grew at rate of 1.429% bwd<sup>-1</sup> and those in the summer/autumn treatment grew at 1.727% bwd<sup>-1</sup> (Fig. 4). Within treatment growth variation increased with time and was higher in the spring/summer treatment than the summer/autumn treatment for the majority of the experiment.

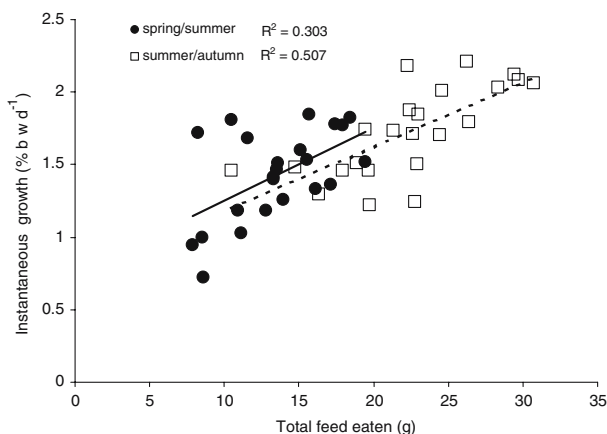
Total feed eaten was significantly different between the treatments ( $t = -7.033$ ,  $df 25$ ,  $P = 0.000$ ). The combined mean weight of crabs eaten per day was 3.58 g (0.143 ± SE), and 5.7 g (0.25 ± SE) for the spring/summer and summer/autumn treatments, respectively. There was little fluctuation in the grams



**Fig. 4** Raw data distribution of weight (g) at 14-day intervals over 114 days for *Octopus pallidus* with fitted exponential growth curves for the for the spring/summer (circle, black line) and summer/autumn (cross, dashed line) temperature treatments

eaten per day by the spring/summer octopuses throughout the experiment, with no evidence of temperature effects. Conversely, the summer/autumn octopuses consistently ate more than the spring/summer octopuses, and a dramatic increase in mean consumption by the summer/autumn octopuses occurred at approximately day 75 and remained for the rest of the experiment, corresponding with the period of lowest temperatures for this treatment (Fig. 3b).

Total feed eaten was positively correlated with instantaneous growth rate calculated over the duration of the experiment for both spring/summer ( $r^2 = 0.3038$ ) and summer/autumn ( $r^2 = 0.5076$ ) octopuses (Fig. 5). However, the relationship between total feed eaten and initial size was significantly different ( $F = 8.510$ ,  $df$  1, 52,  $P = 0.005$ ) between the treatments. In the spring/



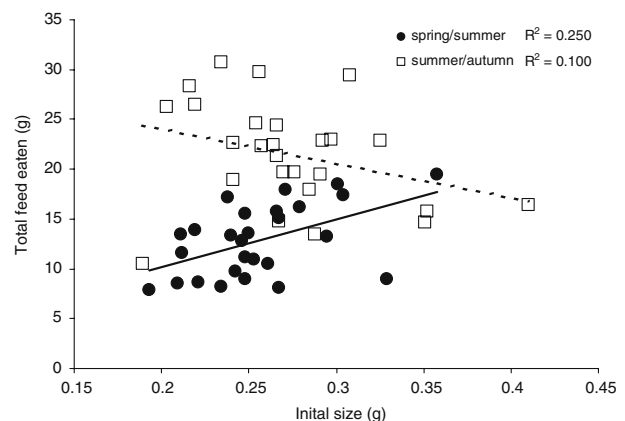
**Fig. 5** Total growth (%  $bwd^{-1}$ ) versus total feed eaten (g) for *Octopus pallidus* in the spring/summer (black line) and summer/autumn (dashed line) temperature treatments

summer treatment there was a positive relationship ( $r^2 = 0.2502$ ) where initially small octopuses ate less food overall than initially larger octopuses. This pattern was reversed in the summer/autumn treatment where a weaker relationship was observed ( $r^2 = 0.1008$ ) with initially smaller octopuses eating more food than their larger counterparts (Fig. 6).

## Discussion

Octopuses in the spring/summer treatment were significantly smaller at the end of the 114-day experiment than those in the summer/autumn treatment, indicating that simulated seasonal temperatures had a strong influence on growth. At the start of the experiment, summer/autumn octopuses had a spike in growth rate, which corresponded with the period of highest temperatures for the treatment. The effects of this initial growth spike separated the two treatments and resonated for the duration of the experiment, even though both treatments had an equal number of degree-days. When temperature was highest for the spring/summer octopuses, a much smaller growth spike occurred, this increase was not sufficient to bridge the size gap between the treatments. These temperature effects on growth support the principals of the Forsythe effect (Forsythe 1993); that cephalopods hatched during periods of higher temperatures will grow faster than those hatched at cooler temperatures. In a seasonal context, this suggests that *O. pallidus* hatched in late summer will grow faster than those hatched in late spring.

Most cephalopod species grow quickly and are short lived (Mangold 1983), at 114 days and an average size



**Fig. 6** Total feed eaten (g) versus initial size (g) for *Octopus pallidus* in the spring/summer (black line) and summer/autumn (dashed line) temperature treatments

of 1.63 g the experimental octopuses would have to grow and develop extremely quickly to approach the maximum size of the species (1.2 kg) and develop approximately 200 eggs each weighing 0.2 g. Two possible explanations for this apparently slow development are that culture conditions stunted growth (Jackson 1994; Pecl and Moltschaniwskyj 1999) or this species lives for a lot longer and has significantly different growth patterns than anticipated.

The largest octopuses were 4.6 and 3.4 times the size of the smallest in the spring/summer and summer/autumn treatments, respectively. Conducted in a controlled environment, all individuals were kept in separate containers, were from the one mother and hatched at the same temperature, the most plausible explanations for within treatment growth variation are the effects of initial size at hatching, feeding (Garcia Garcia and Aguado Gimenez 2002; Segawa and Nomoto 2002), and paternity, or a combination of the three. Genetic differences derived from mixed paternity as observed in *Loligo pealeii* (Buresch et al. 2001) and *Loligo forbesi* (Emery et al. 2001) is unlikely for the 64 octopuses used in the experiment, as they were picked randomly from 150+ individuals from the one mother.

In the spring/summer treatment initially smaller individuals grew 24% slower and remained small, in comparison to initially larger individuals that grew faster and were subsequently larger at the end of the experiment. In the summer/autumn treatment the relationship between growth rate and initial size, showed an opposing trend, where initially small octopuses grew 8% faster than their larger counterparts. The initial growth spike in the summer/autumn treatment, corresponding to the period of high temperatures, lifted the growth rates of the smaller octopuses, and effectively separated the treatments. The different relationships between hatchling size and growth rate, depending on the prevailing temperature regime, indicates that variations in initial size could be responsible for substantial amounts of variation in size-at-age in wild cephalopod populations, as suggested by Pecl et al. (2004).

The sizes of the crabs given to an octopus were proportional to the size of the octopus; therefore larger individuals generally had more available food. The summer/autumn treatment octopuses were larger and consistently ate more food on average than those in the spring/summer treatment. Higher food consumption combined with temperature effects resulted in higher growth in the summer/autumn treatment similar seasonal effects are evident in the on-growing of *O. vulgaris* in floating cages (Rodriguez et al.

2006). In the spring/summer treatment initially smaller octopuses ate less in total for the duration of the experiment than initially larger octopuses. The opposite was observed in the summer/autumn treatment where initially smaller octopuses ate more in total for the duration of the experiment than initially larger octopuses. This feeding pattern mirrors the pattern observed when comparing initial size and instantaneous growth, indicating that temperature, feeding and initial size all influenced the growth of individuals in both treatments.

Two factors not investigated in the present study that potentially influenced growth, were maternal effects and the impact of temperature during embryonic development. Maternal nutrition can influence the condition and size of eggs, if the mother is under nutritional stress smaller and fewer eggs will be laid, and higher mortality rates can occur (Steer et al. 2004). Temperature has an inverse relationship with the duration of embryonic development in many cephalopod species (Ito 1983; DeRusha et al. 1987; Caveriviere et al. 1999) and may influence yolk production. Variation in yolk reserves between different sized hatchlings may have affected the potential for growth during the days prior to and immediately after hatching (Boletzky 1994).

Egg condition and composition may be optimized for growth in relation to surrounding water temperatures and seasonality (Boletzky 1994). If this is a factor then the eggs used may have been 'pre-conditioned' for a particular temperature regime, most likely a regime similar to the low initial temperatures in the spring/summer treatment. The high initial temperatures in the summer/autumn treatment could have displaced the natural growth patterns. The scope of the present study did not allow for investigation into these factors. Additionally, the amount of time the eggs spent in the wild, and temperatures they experienced before removal was unknown. Further research into maternal effects on embryonic development and the subsequent relationship between temperature and hatchling growth is required to fully understand these relationships.

This study has shown that the effects of seasonal temperature change on growth are significant. This emphasises the importance of considering seasonality and initial size heterogeneity when calculating the growth trajectory of individuals within cephalopod populations, particularly in a fishery context. If warm temperatures coincided with the hatching of a cohort in the wild, a 'pulse' of high growth similar to the one observed in the early stages of the summer/autumn treatment could easily occur. The probability of such

an event is high, for many cephalopod species have shortened embryonic phases at higher temperatures (DeRusha et al. 1987).

This study has shown that at lower temperatures octopuses that are small at hatching will end up small and will grow slowly. This pattern is displaced at higher temperatures, where smaller octopuses can grow faster and can have a final size similar to or even larger than octopuses hatched at a larger size. There is obviously a complex but important relationship between hatchling size and subsequent growth rate, however, the impacts of initial hatchling size appear secondary to the effects of temperature.

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