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Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity

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Abstract The relationship between size and age at maturity in cephalopods is unresolved. The most recent interspecific comparison of size and age of cephalopods contradicts two previous studies by concluding that larger species do not live longer. This paper addresses the confounding effects of temperature and phylogeny while answering the question, "Do larger cephalopods live longer?". To test this hypothesis, life-history data from 18 species of cephalopods, from five orders, with sizes at maturity spanning five orders of magnitude, were obtained from the literature. Without temperature consideration and with *Nautilus* spp. included in the sample, regression analysis suggests ($r^2 = 0.376$, $p = 0.007$) that larger cephalopods take longer to reach maturity. Once temperature was controlled by using physiological time (degree-days), the coleoid cephalopods moved closer to the best fit line and the genus *Nautilus* became an outlier. When *Nautilus* was removed and time measured in degree-days, the relationship was very strong ($r^2 = 0.785$, $p < 0.001$). We conclude that coleoid cephalopods achieve larger size by delaying maturity and that temperature, as well as phylogeny, must be considered when making interspecific comparisons.

Introduction

Cephalopods are an ancient molluscan class notable for their active lifestyle and well-developed senses. They range in adult size from *Idiosepius*, an 8 mm long sepiolid genus, to the giant squid, *Architeuthis*, which can grow to over 5 m in length, making it the world's largest invertebrate. Size at maturity is a critical trait, as larger animals can produce more offspring and possibly provide better parental care (Stearns 1992). Cephalopods are found from the poles to the tropics and from the intertidal zone to the abyss. They are also important predators in the world's oceans, with high growth rates and wet weight food conversion efficiencies of 30 to 60% (Clarke 1996; Hanlon and Messenger 1996).

All extant cephalopods (including octopuses, squid, cuttlefish and sepiolids) except *Nautilus* species are classified in the subclass Coleoidea (Sweeney and Roper 1998). Members of the genus *Nautilus*, the only genus in the subclass Nautiloidea, are the only externally shelled cephalopods. They are known to have morphological, behavioral and life-history differences that easily distinguish them from all other cephalopods (Calow 1987; Hanlon and Messenger 1996; Sweeney and Roper 1998).

By comparing different species of cephalopods, several workers have suggested that a positive relationship exists between size and age at maturity. Forsythe (1984) compared six species of octopuses and concluded "that larger octopuses have longer life spans and smaller species such as *Octopus joubini* have shorter life spans." Van Heukelem (1976) examined the life span of cephalopods from four orders and concluded that "in general, the larger species have longer life spans." However, Calow (1987) was the first and only researcher to statistically test this hypothesis. His results differed from the two previous studies. Calow quantified time to maturity and size at maturity for a broader sample of cephalopods from four orders. Unlike the previous two authors, his data set included *Nautilus* spp. and *Bathypolypus arcticus*.

Bathypolypus arcticus is a small octopus that is most common at depths of 200 to 600 m and at low temperatures of 4 ± 2 °C in the Atlantic Ocean (O'Dor and Macalaster 1983). Calow did not find a significant relationship between size at maturity and life span, and therefore concluded that species that are large at maturity achieve their larger size by growing faster. This conflict may have arisen because none of these authors made any attempt to normalize for temperature effects and because the anomalous *Nautilus* genus was not separated from the coleoid cephalopods.

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Temperature is known to have a considerable effect on the metabolism and body size of ectotherms, which make up approximately 99% of the Earth's species (for a recent review of intraspecific effects of temperature see Atkinson and Sibly 1997). Ectotherms require a certain temperature and amount of time for growth to adult size (Begon et al. 1990). For example, *Octopus bimaculoides* kept at 23 °C had their life span shortened by about 20% but were three times larger when 5 months old compared to octopuses raised at 18 °C (Forsythe and Hanlon 1988).

In a changing environment, temperature variation is likely to affect the population biology of short-lived, semelparous cephalopods more than longer-lived, iteroparous fish (Forsythe and Hanlon 1988). Forsythe (1993) developed a model based on laboratory growth rates of *Loligo forbesi* at known temperatures. This model demonstrated that even a 1 °C increase in temperature during the 90-d exponential growth phase causes a doubling of weight. A 2 °C increase in temperature predicted that animals grow five times larger!

The present study investigates the effect temperature has on time to maturation by using physiological time, i.e. degree-days. Degree-days are calculated by multiplying the average daily temperature in degrees Celsius by the time in days (Begon et al. 1990). For example, *Illex illecebrosus* eggs take 16 d to develop at 13 °C (O'Dor and Dawe 1998). This yields 208 degree-days.

A complication, in addition to temperature, is the inclusion of a member of the subclass Nautiloidea, which represents fewer than 1% of all extant species of cephalopods and a group very different from their modern cousins. Calow's (1987) data set included *Nautilus*, the only extant genus of Nautiloidea. Not only do these ectochochleates have an external shell, a primitive eye which is open to the sea and two pairs of gills, their life-history traits also reflect their distant relationship to the other cephalopods. Members of the genus *Nautilus* lay extremely large eggs, have long life spans and are iteroparous polycyclic spawners (Saunders and Landman 1987; Ward 1987). Although there is debate about when Nautiloidea split from the other cephalopods, the scheme presented by Hanlon and Messenger (1996) shows the subclasses Nautiloidea and Coleoidea diverging in the Ordovician period.

Another difficulty with interspecific comparisons of size and age at maturity in cephalopods is the large range of variation within a species. Differences in temperature as well as other abiotic and biotic factors can affect the exponential growth rates of young cephalopods and cause large differences in size and age at maturity (Forsythe and Hanlon 1988; Forsythe 1993). For this reason, we use average sizes at maturity from animals that live at known temperatures. We sought new data to include species that mature over a large range of sizes, which will further decrease the effect of intraspecific differences in size at maturity. Using species from a variety of taxa, as well as habitats, should best represent cephalopods as a group; we have used all available data.

The primary objective of this study was to compare size at maturity and life span of a variety of cephalopods with a modern data set to resolve the question, "Do larger cephalopods live longer?" The secondary objective was to identify confounding factors that can bias this type of interspecific comparison. We analyzed a data set which included temperature as a factor to test the hypothesis that larger cephalopods take longer to reach maturity. Both standard time (days) and physiological time (degree-days) were used in the analysis to examine the importance of controlling for the effect of temperature when studying life-history traits with a time component. As Calow's (1987) data included *Nautilus* spp., our analysis was undertaken both with and without the genus *Nautilus* to determine whether including this ancient group compounded the effect of ignoring the role of temperature in the life-history trends in modern cephalopods.

Materials and methods

Data from the literature

Life-history data were collected from the literature (Table 1) on 18 representative species of cephalopods. The data set included species from five orders: Nautilida (*Nautilus*), Octopodida (octopuses) Sepiida (cuttlefish), Sepiolida (sepiolids) and Teuthida (squid) following Sweeney and Roper (1998). For consistency, most of the species used by Calow (1987) were retained, but in many cases more recent and accurate data were available and used. In some cases, only data from fishery estimates were available, but, whenever possible, data from animals that had been reared through their entire life cycle in the laboratory at constant temperature were used. This insured more uniform adult sizes, as well as increasing the accuracy of the age and temperature data used to calculate degree-days. When several references are summarized in a single value, a simple numerical average was taken across sources (e.g. values of 0.035, 0.04 and 0.045 g reported for hatchling *Octopus* "*joubini*" weights were averaged to 0.04 g). There is some question as to the identity of the octopus that has been referred to as "*Octopus joubini*" in the literature (see Forsythe and Toll 1991).

Although there is considerable within-species variation in cephalopods (Yang et al. 1986), we used average size at maturity at a given temperature, as it best describes a typical member of that species. We avoided using range data, which is much more variable and may not reflect an "average" member of a species. Where published averages of the traits of interest do not exist, the midpoint of range data was used. Bell (1980) used a similar method to compare age at maturity in placental mammals, Squamata (reptiles), amphibians and freshwater fish. As the largest cephalopod in our data set is 100 000 times bigger than the smallest, the methods outlined here should be robust enough to handle some error in size or age at maturity estimates, as errors are small relative to the total range.

Calculations

Life-history traits were quantified, and the following measurements were recorded: size at maturity (weight in grams of a mature female), age at maturity (time in days until first reproduction), physiological age at maturity (time in degree-days until first reproduction), and instantaneous relative growth rate (G) calculated by:

$$G = \frac{\ln W_2 - \ln W_1}{(t_2 - t_1)} \quad ,$$

where W_2 is the weight at maturity, W_1 is the weight at hatching and $t_2 - t_1$ is the time between hatching and maturity (Forsythe and Van

Table 1 Data set of hatchling size, size at maturity, age at maturity, average lifetime temperature, age at maturity, growth rate and physiological growth rate for 18 species of cephalopods. Data from the laboratory (*L*) and from the field (*F*) (*G* growth; *T* temperature)

Taxon	Abbreviation	Data	Hatchling size (g)	Size at maturity (g)	Age at maturity (d)	Average lifetime temperature (°C)	Age at maturity (degree-days)	*G*	*G*/*T*
Subclass Nautiloidea									
Order Nautilida									
Family Nautilidae									
Nautilus belauensis	Nb	L, F	5.9[a]	1157[b]	3978[c]	13[d]	51714	0.13	0.01
Subclass Coleoidea									
Order Octopodida									
Family Octopodidae									
Bathypolypus arcticus	Ba	L, F	0.214[e,f]	70[f]	1400[a]	4.0[f]	5600	0.41	0.103
Octopus bimaculoides	Ob	L	0.07[g]	545[g]	341[g]	23.0[j]	7843	2.63	0.114
Octopus dofleini	Od	F	0.025[h,i]	16300[h,i]	1019[i,j]	10.7[h,i]	10903	1.31	0.123
Octopus sp. "*joubini*"	Oj	L	0.04[k,l,m]	30[k]	182[k]	25[k,l]	4550	3.64	0.145
Octopus maya	Om	L	0.093[n]	3262[n]	257[n]	25[n]	6425	4.07	0.163
Octopus vulgaris	Ov	L, F	0.0014[o]	2417[p]	435[p]	18.3[p]	7960	3.3	0.18
Order Sepiida									
Family Sepiidae									
Sepia officinalis	So	L	0.175[q]	1200[q]	335[q]	22.5[q]	7538	2.64	0.117
Sepia pharaonis	Sp	L	0.1[r]	84.1[r]	110[r]	30[r]	3300	6.12	0.204
Sepiella inermis	Si	L	0.01[r]	36.6[r]	90[r]	30[r]	2700	9.12	0.304
Order Sepiolida									
Family Idiosepiidae									
Idiosepius pygmaeus	Ip	L, F	0.00033[a]	0.175[s]	50[s]	25.2[s]	1260	12.55	0.498
Family Sepiolidae									
Euprymna scolopes	Es	L	0.005[t]	2.67[t]	80[t]	23[t]	1840	7.85	0.341
Order Teuthida									
Family Loliginidae									
Loligo forbesi	Lf	L, F	0.007[u]	910[v]	365[u]	14[a]	5110	3.23	0.23
Loligo opalescens	Lo	L	0.001[w]	21.2[w]	184[w]	16[w]	2944	5.41	0.338
Loligo vulgaris	Lv	F	0.003[x]	447[y]	245[y]	14[a]	3430	4.86	0.347
Sepioteuthis lessoniana	Sl	L	0.044[z]	122.7[r]	90[r]	30[r]	2700	8.81	0.294
Family Ommastrephidae									
Illex illecebrosus	Ii	L, F	0.00015[A]	400[B]	365[C]	12.6[B]	4599	4.05	0.322
Family Thysanoteuthidae									
Thysanoteuthis rhombus	Tr	F	0.002[a]	8966[D]	240[D]	24.5[D]	5880	6.38	0.26

[a] Present paper, [b] Saunders and Spinosa 1978, [c] Landman and Cochran 1987, [d] Saunders and Ward 1987, [e] Wood et al. 1998, [f] O'Dor and Macalaster 1983, [g] Forsythe and Hanlon 1988, [h] Cosgrove 1993, [i] Hartwick 1983, [j] Cosgrove 1976, [k] Hanlon 1983, [l] Forsythe 1984, [m] Forsythe and Hanlon 1981, [n] Van Heukelem 1983, [o] Villanueva 1995, [p] Mangold 1983, [q] Forsythe et al. 1994, [r] Nabhitabhata 1995, [s] Lewis and Choat 1993, [t] Hanlon et al. 1997, [u] Forsythe and Hanlon 1989, [v] Martins 1982, [w] Yang et al. 1986, [x] Packard 1969, [y] Coelho et al. 1994, [z] Hanlon 1990, [A] O'Dor et al. 1986, [B] O'Dor 1983, [C] O'Dor and Dawe 1998, [D] Nigmatullin et al. 1995 (values used in calculations can be obtained upon request from the authors)

Heukelem 1987). Physiological instantaneous relative growth rate (G/T) was defined as simply the above, with time in degree-days.

Estimates

In a few cases, the required data had to be estimated. There are, for example, no published weights of hatchling *Nautilus* spp. The weight of a hatchling *N. belauensis* was estimated using hatchling shell size and a regression analysis of the cubed shell diameter versus the weight of seven young *N. belauensis* that weighed < 50 g (Carlson et al. 1992) in addition to a single hatchling *N. pompilius* that was weighed for the present study on 24 April 1996 at the Waikiki Aquarium. The hatchling *N. pompilius* weighing 4.33 g, with a maximum shell diameter of 26.25 mm, fit a highly significant correlation ($r^2 = 0.990$, $p < 0.001$) between cubed shell diameter and weight, which indicates that a hatchling *N. belauensis* with a 30 mm shell diameter (Carlson et al. 1992) would weigh approximately 5.9 g.

Five preserved hatchling *Idiosepius pygmaeus* were weighed by G. Pecl (James Cook University, Townsville, Australia personal communication), and their average weight of 0.33 ± 0.06 mg used. There are no published hatchling weights for this species.

To estimate hatchling weight for *Thysanoteuthis rhombus*, a value of 80% of egg weight was used. *T. rhombus* egg weight was calculated from the egg diameters reported by Nigmatullin et al. (1995). We assumed these eggs were spherical (volume $= 4/3\pi r^3$) and had a density close to water. *T. rhombus* hatchlings were estimated to weigh 0.002 g. Error in this estimated hatchling weight would affect the comparison of growth and size at maturity (Table 3) but not the size and age at maturity (Figs. 1, 2; Table 2).

Bathypolypus arcticus were included because they were used in Calow's (1987) analysis, and the authors of the present paper have experience with this species. While O'Dor and Macalaster (1983) have published size at maturity of 70 g, size at hatch of 0.15 g, temperature of 4 °C and estimated age at maturity of 2 years, recent rearing studies indicate that age of maturity in their study was significantly underestimated. The hatchlings have very slow growth rates. For example, one juvenile fed crustaceans ad libitum took 583 d to reach 3.8 g at 6 °C (2215 degree-days), which predicts maturation at 1400 d at 4 °C when modeled conservatively. Other individuals grew at similar rates (Wood unpublished data).

Regional temperature for the Azorean *Loligo forbesi* was estimated by averaging temperatures at 200 m depth for 40°N; 28°W and 36°N; 28°W (Fuglister 1960). A depth of 200 m was used as that is where adults are fished and where tagged specimens were

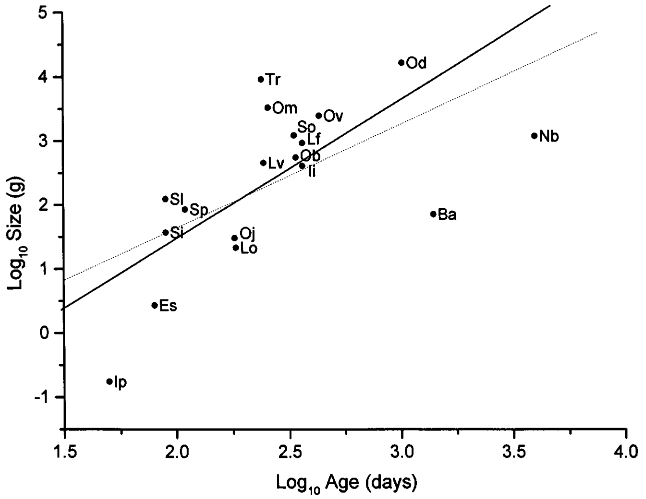

Fig. 1 Log_{10} of weight at maturity versus $\log_{10}$ of age at maturity measured in days for 17 coleoid species and one nautiloid species. With *Nautilus* in the sample ($y = 1.620x - 1.609$, $r^2 = 0.376$), as represented by the *dashed line*. The *solid line* shows the relationship when *Nautilus* is removed from the sample ($y = 2.228x - 2.979$, $r^2 = 0.451$). Abbreviations for names of species, see Table 1

observed (O'Dor et al. 1994). A similar estimate of local temperature was made for the *L. vulgaris* population used.

Statistical analysis

Calow's (1987) hypothesis that larger cephalopods grow faster was investigated by examining the Pearson correlation of growth (G) and growth/temperature (G/T) on size at maturity (Table 3). This was done both with and without *Nautilus* spp. in the sampling data we used for analysis. Life-history data were $\log_{10}$ transformed to prevent heterogeneity of variance.

The hypothesis that larger cephalopods live longer was tested with regression analysis using the Systat 7 statistical package (Table 2). A linear regression analysis was completed using data from Table 1. The analysis was repeated four times thus testing all combinations of time, measured in both days and degree-days, in the presence or absence of *Nautilus* spp. Results of the various analyses were compared.

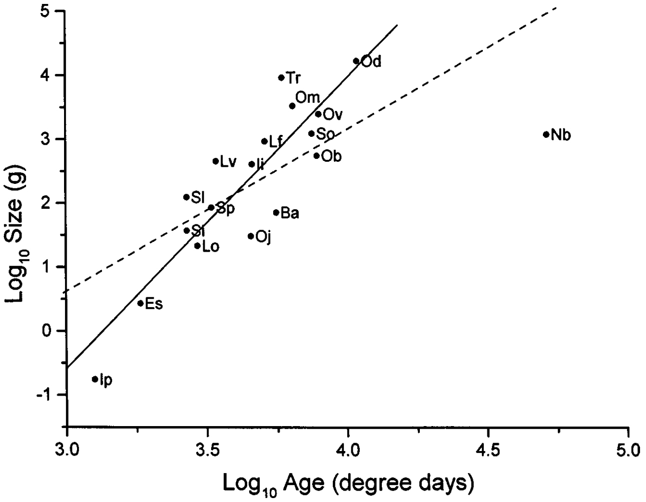

Fig. 2 Log_{10} of weight at maturity versus $\log_{10}$ of age at maturity in degree-days for 17 coleoid species and one nautiloid species. With *Nautilus* in the sample ($y = 2.526x - 7.001$, $r^2 = 0.502$), as represented by the *dashed line*. The *solid line* shows the relationship when *Nautilus* is removed from the sample ($y = 4.546x - 14.238$, $r^2 = 0.758$). Abbreviations for names of species, see Table 1

Table 2 Predicted size at maturity from age in days and age in degree-days for cephalopod groups including and excluding nautiloids (H_0 null hypothesis)

Cephalopod group	R^2	p-value	Conclusion
Age in days			
Coleoid and nautiloid	0.376	$p = 0.007$	Reject H_0
Coleoid only	0.451	$p = 0.003$	Reject H_0
Age in degree-days			
Coleoid and nautiloid	0.502	$p = 0.001$	Reject H_0
Coleoid only	0.785	$p < 0.001$	Reject H_0

An additional regression analysis was done on the life-history traits of coleoid cephalopods at the taxonomic family level. This was done in order to determine if non-independent data from closely related species were responsible for the results. For example, our data set has six species of octopuses all in the same family, and five of these six are in the same genus. It could be argued that these five or six species should be treated as one data point (Harvey et al. 1995). When there was more than one species in a family we used the species that is first alphabetically.

Results

Using our data set, with *Nautilus* in the sample and time in calendar days, we found a significant positive relationship between age and size at maturity in cephalopods ($r^2 = 0.376$, $p = 0.007$, Table 2). While this regression has a significant non-zero slope, Fig. 1 shows a high degree of scatter. Both *N. belauensis* and *Bathypolypus arcticus* take >1000 d to reach maturity although they are not particularly large cephalopods.

When *Nautilus* was removed from the sample, the fit improved ($r^2 = 0.451, p = 0.003$, Fig. 1). *Bathypolypus arcticus* was an outlier in this comparison (studentized residual = −3.7). This may be due to the fact that *B. arcticus* lives at 4 °C, while most of the other species live around 20 °C.

With *Nautilus* back in the sample, measuring time in degree-days improved the relationship ($r^2 = 0.502$, $p = 0.001$, Fig. 2). The use of degree-days brought the coleoid cephalopods including *Bathypolypus arcticus* noticeably closer together, but *N. belauensis* was an outlier in this analysis (studentized residual = −4.5).

Table 3 Correlation between growth rate and size at maturity. Note the negative correlations between growth rate and size at maturity in all cases (G growth; T temperature)

Comparison	Pearson correlation
G vs coleoid and nautiloid size at maturity	−0.663
G vs coleoid size at maturity	−0.662
G/T vs coleoid and nautiloid size at maturity	−0.624
G/T vs coleoid size at maturity	−0.633

For coleoid cephalopods, there was a strong significant relationship between size at maturity and physiological time ($r^2 = 0.785$, $p < 0.001$, Fig. 2). A visual comparison of Fig. 2 with Fig. 1 confirms that there is much less variation in the data around the regression line. The equation of the solid line is $y = 4.546 \pm 0.615(x) - 14.238 \pm 2.240$, with the plus/minus terms indicating the standard errors. Using this equation, five of the six squid are above the line while four of the six octopuses are below. The three cuttlefish are near the line while the two sepiolids are below and near the origin. Of the species for which laboratory data was used exclusively, four were above the line and five below. Where both laboratory and field data were used, the split was even with two above and below the line. However, the three species using exclusively field data (Lv, Tr, Od) were above the line.

This relationship holds when analyzed at the family level ($r^2 = 0.854$, $p = 0.003$) as well. However, the sedentary deep-sea octopus *Bathypolypus arcticus* and the oceanic squid *Thysanoteuthis rhombus* were outliers with studentized residuals of −2.1 and 2.1, respectively (Fig. 3).

We also examined the relationship between growth rate and size at maturity, both with and without *Nautilus* and with temperature in calender days and in degree-days. In all cases, there was a negative correlation between growth rate and size at maturity (Table 3).

Discussion and conclusions

Size and age at maturity

When degree-days are used, results indicate that larger size at maturity in coleoid cephalopods is a consequence of longer life spans rather than faster growth rates. As shown in Table 2, size at maturity is significantly and positively correlated to physiological age. Furthermore, no evidence that supports the hypothesis that larger cephalopods grow faster was found (Table 3). In all cases, the correlation between growth rate and size at maturity was negative in the range of −0.624 to −0.663. If anything, cephalopods that mature at smaller sizes grow faster. We interpret these results as evidence for a life-history tradeoff in coleoid cephalopods between maturing early at a smaller size and maturing later at a larger size. Organisms that mature earlier are more likely to avoid predators and survive to reproduce due to the shorter period between their birth and maturity. Additionally, organisms that mature earlier increase their fitness because the offspring are produced sooner, and these offspring also start reproducing earlier. Delaying maturity leads to higher fecundity, which also increases fitness (Stearns 1992). However, the risk of predation before reproduction is expected to increase as age at maturity increases. For modern cephalopods, our results support Van Heukelem's (1976) and Forsythe's (1984) conclusions that larger cephalopods have longer life spans.

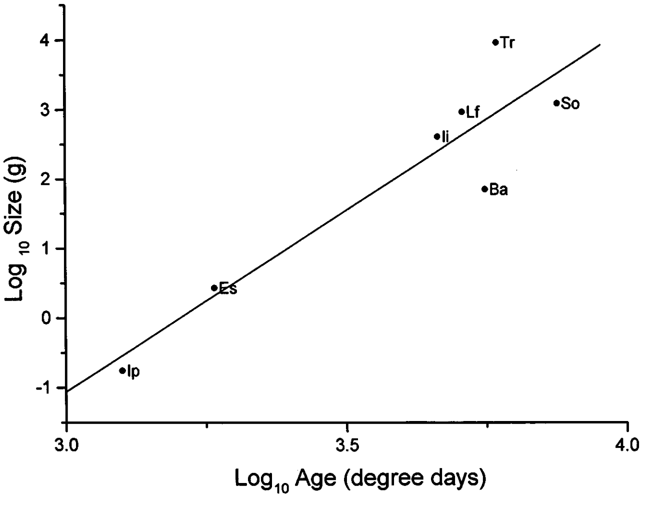

Fig. 3 Log_{10} of weight at maturity versus $\log_{10}$ of age at maturity in degree-days for representatives of seven families of coleoid cephalopods ($y = 5.262x - 16.876$, $r^2 = 0.854$). Abbreviations for names of species, see Table 1

Nautilus as a confounding factor and lineage effects

Members of the genus *Nautilus* represent fewer than 1% of extant cepahlopods. When making the generalization that cephalopods which live longer mature at a larger size, Van Heukelem (1976) likely meant modern cephalopods, as all his examples were coleoids. As shown in Table 2, removing *Nautilus* from the analysis improved the relationship between age at maturity and size at maturity.

The inclusion of Nautiloidea appears to mask the significant correlation in the rest of the group. Fig. 2 graphs size versus age in degree-days. *Nautilus* is an outlier from the trend set by the other cephalopods and is thought to live and reproduce for years after reaching maturity (Saunders and Landman 1987; Hanlon and Messenger 1996). This is unlike coleoid cephalopods which have short life spans and are typically semelparous. Had life span been used instead of age at first maturity, the iteroparous *Nautilus* would have been even more of an outlier. Removing *Nautilus* makes biological as well as statistical sense.

Unlike *Nautilus*, the coleoid cephalopods do not noticeably deviate from our reported trend, nor do all the members of these groups cluster together. Even species in the same genus, such as *Octopus*, are not clustered. However, there may be a small lineage effect in growth rates between Octopodida and Teuthida. Most of the octopuses mature at a lower weight than predicted by the regression line in Fig. 2 and have lower growth rates (Table 1), while five of the six squid have higher growth rates. The cuttlefish appeared between these two. These patterns should be explored as better data become available for a wider variety of species.

Some researchers argue that it is incorrect to apply phylogenetic correction techniques as proposed by

Harvey et al. (1995) in all comparative analyses (Westoby et al. 1995). Although we are arguing for a lineage-specific relationship between size and age in coleoid cephalopods, Harvey et al. (1995) argues that species may not be the appropriate unit for comparison as they are not independent. What if one taxa, say the genus *Octopus* or the family Octopodidae, has a strong relationship between size and age at maturity due to lineage effects while the other groups do not? This would likely be noticed in Fig. 2, but one can alternatively sacrifice sample size to increase the number of independent evolutionary events in the lineage (Stearns 1992).

To eliminate such biases, we used the first species alphabetically for each of the seven coleoid families listed in Table 1 to test the regression of age on size at maturity. As the results ($r^2 = 0.854$, $p = 0.003$) were similar to those found at the species level, the relationship that larger cephalopods live longer holds when the data set is analyzed at the family level.

Importance of temperature

Calow (1987) acknowledged that temperature may affect cephalopod life-history traits. Perhaps because the data were limited, Calow did not control for temperature. In the present study, using degree-days to measure time increased the significant relationship between age and size at maturity. There will be some error in the effect of lifetime temperature estimates in environments where the temperature changes as the cephalopods mature (Forsythe 1993; Rodhouse 1998). This is because seasonal and other changes in temperature will have a greater effect on exponentially growing hatchlings than on older cephalopods. We found that once time was measured in degree-days, 78% of the variability of size at maturity in coleoid cephalopods is predicted by age at maturity. With better data and a more complicated and accurate model that examines age-specific effects of temperature, we expect a further reduction of the unaccounted variability in size at maturity.

Confounding factors can dramatically change results when testing life-history hypotheses or constructing phylogenetic trees based on life-history traits. Temperature affects growth rates in ectothermic animals such as cephalopods. Using physiological time (e.g. degree-days) is one way to test interspecific life-history hypotheses for ectotherms. For example, *Bathypolypus arcticus* is a small octopod that lives at 4 °C. This octopod takes much longer to mature than a similarly sized Florida pygmy octopus (*Octopus "joubini*") which lives at 25 °C. We argue that, while there are significant behavioral, physiological, ecological and life-history differences between these two species, an eightfold difference in life span is not as significant as it first appears. Most, but not all, of the difference in life span is due to the effect of temperature, not any real differences in life-history traits. If temperature is not taken into account and the species examined come from a broad range of environments, an interspecific correlation between size at maturity and life span is primarily a correlation between size at maturity and the temperatures at which the different species live.

Although Forsythe (1984) and Van Heukelem (1976) did not explicitly control for temperature, the effect of temperature on growth rates and life spans of the species that they examined would have been much less. This is because the species that they examined did not live in as wide a range of temperatures as the species examined by Calow (1987) and in the present paper.

Environmental variables

At a given temperature, growth rate and size at maturity increases with resource availability (Atkinson and Sibley 1997). Differences in resource availability are expected to cause some variation in the data. However, cephalopods studied so far seem to be limited by predation, not food. For example, squid may rarely be out of food because, when their preferred foods such as fish and crustaceans are limited, squid will prey on other squid in their school (Dawe and Brodziak 1998). Octopuses spend very little time foraging, which may be optimal behavior if the octopuses are minimizing exposure to predators by limiting their hunting time and not actively defending territories (Mather and O'Dor 1991; Mather 1993). Aronson (1986) showed that the number of octopuses was inversely related to the number of predatory fish present. While food is an important biotic factor, these examples suggest that it is often not limiting the growth of wild cephalopods.

Due to cephalopods' excellent senses, mobility and nocturnal habits, it is especially difficult to make direct observations of cephalopods in the field. Researchers depend largely on laboratory-based culture programs for cephalopod life-history data (Boletzky and Hanlon 1983). Although there are few studies comparing field and laboratory growth rates in cephalopods, much of the available information indicates that the high laboratory growth rates are not abnormal. Animals caught in the wild and transferred to the laboratory often do not feed as readily or grow as fast. "Wild caught cephalopods are particularly prone to mechanical damage," and this is especially true for squid (Boyle 1991). The squid *Loligo opalescens* grows faster in the field than those cultured in the laboratory (Jackson 1994). Pecl and Moltschaniwskyj (1999) found differences in cellular growth mechanisms between the sepiolid *Idiosepius pygmaeus* from the field and those collected and then kept in 30-cm^3 glass aquaria for 7 d. However, many species of coastal cuttlefish and octopus thrive in the laboratory and have been kept for several generations. Van Heukelem (1976) found no difference in growth between branded wild *Octopus cyanea* and well-fed laboratory *O. cyanea*. It is possible that laboratory environments alter growth patterns in pelagic cephalopods like squid, but it is likely that benthic and epibenthic animals like octopuses and cuttlefish are less affected when kept under these conditions.

We found little evidence for differences between the laboratory and field data used in our analysis. Life-history data collected from the laboratory or the laboratory and field accounted for 14 of our 17 species, and both were distributed evenly about the line. There were only three species that used field data exclusively, two squid (Lv, Tr) and an octopus (Od). These appear above the line, although the octopus is almost on the line. Field data frequently underestimate the effect of temperature because of sparse information on what the fast-growing planktonic phase is exposed to and for how long. Temperature data are often based solely on adults, even though influences on the fast-growing young may have a substantial impact on later life. These young may, for example, be found higher in the water column, in warmer waters, than the better sampled adults.

Species are likely to adapt to the temperature and environment at which they live. According to Begon et al. (1990), "the effects of different temperatures on ectotherms follow a typical pattern, though there is variation from species to species." This study, like Calow's (1987), used animals that live at a wide range of average temperatures (4 °C to 30 °C in our case) and a variety of environments. No doubt some of the variation seen in Figs. 1 to 3 is caused by adaptation to environmental conditions. Variation of size at maturity, temperature and phylogenetic differences all can confound the analysis, but once addressed, the "typical pattern" underlying the variation appears.

While the above factors are important, our approach is valid. Our largest cephalopod is 100 000 times heavier at maturity than our smallest. Species from a variety of habitats such as open-ocean, deep-sea and coastal areas from five cephalopod orders were used. This broad sample of species with parameters that vary over six orders of magnitude is robust enough to handle the likely errors in age and size at maturity as well as differences in feeding, local conditions, etc. This process does not ignore adaption; on the contrary, it helps to find it. Species or groups of species can be removed from the analysis if it makes both biological and statistical sense to do so (i.e. *Nautilus*). This method also points to new questions, such as "Why does *Thysanoteuthis rhombus* grow so fast for its size?"

Difficulties

One of the our primary challenges was collecting a data set that could be used for comparison between groups because workers do not measure size in each order in Cephalopoda with units of measurement that are comparable between or even within groups. For example, size in octopuses is usually measured in weight, while size in squid and cuttlefish is measured in mantle length and size in *Nautilus* is measured in shell diameter or shell aperture width. The mantle lengths of one species of squid are usually not comparable to other species of squid due to morphological differences. While there are conversions for many species from mantle length to weight, these conversions are almost always for maturing or mature animals, and we were not willing to extrapolate to hatchlings, as morphology (i.e. the ratio of mantle length to interocular width) often changes with age. Weight is the best measurement for interspecific comparisons of size in cephalopods, as it does not depend on the shape of the animal being measured. Directly measuring weight is the most accurate and sensitive measure of size, as length must be cubed to convert it into weight (Forsythe and Van Heukelem 1987). Locating published cephalopod hatchling weights was the major bottleneck that limited the number of species used in this analysis. In several cases, hatchling weights for well-studied species could not be found although published mantle lengths were abundant.

Another challenge was that ranges, sometimes over an order of magnitude, are often reported for various cephalopod life-history traits. Averages, preferably with standard deviations, are more useful for this type of analysis and were preferentially used. We encourage workers to publish average and standard deviation values accompanied with similar temperature data.

Future directions

There is a need for more basic information for interspecific comparisons. Life-history data from deep-sea and open-ocean species are still rare. Size and age at maturity data are needed for investigating lineage effects between squid, cuttlefish and octopus. Life tables for species are essential so that the effect of age-specific mortality can be investigated. Understanding of basic cephalopod biology becomes more and more critical as cephalopods make up an increasing percentage of the world's fisheries (Pauly et al. 1998).

In focusing on the differences between cephalopods and fish (e.g. O'Dor and Webber 1986), cephalopod biologists may understate the differences among cephalopods themselves. For example, Rodhouse's (1998) comment that cephalopods other than *Nautilus* "are generally short lived (usually 1 year) and have monocyclic reproduction and a semelparous life history" is technically correct, but may mislead non-specialists. Nonetheless, our analysis is consistent with suggestions (Pauly 1998; Rodhouse 1998) that the short, rapid-growth life histories of cephalopods illustrate physiological progenesis. This concept is attractive as it explains the differences between cephalopods and both fish and other molluscs (Bayne et al. 1976; Young and Thompson 1976), but our analyses make it clear that physiological progenesis proceeds on a physiological timescale. Thus, 4 years at 4 °C is still a "short" life span for *Bathypolypus arcticus* in physiological time. The approach described here seems a powerful way of resolving apparent differences among cephalopods from diverse habitats, once we begin to record the right sorts of data.

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