Cephalopod embryonic shells as a tool to reconstruct reproductive strategies in extinct taxa

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ABSTRACT

An exhaustive study of existing data on the relationship between egg size and maximum size of embryonic shells in 42 species of extant cephalopods demonstrated that these values are approximately equal regardless of taxonomy and shell morphology. Egg size is also approximately equal to mantle length of hatchlings in 45 cephalopod species with rudimentary shells. Paired data on the size of the initial chamber versus embryonic shell in 235 species of Ammonoidea, 46 Bactritida, 13 Nautilida, 22 Orthocerida, 8 Tarphycerida, 4 Oncocerida, 1 Belemnoidea, 4 Sepiida and 1 Spirulida demonstrated that, although there is a positive relationship between these parameters in some taxa, initial chamber size cannot be used to predict egg size in extinct cephalopods; the size of the embryonic shell may be more appropriate for this task. The evolution of reproductive strategies in cephalopods in the geological past was marked by an increasing significance of small-egged taxa, as is also seen in simultaneously evolving fish taxa.

Key words: embryonic shell, initial chamber, hatchling, egg size, Cephalopoda, Ammonoidea, reproductive strategy, Nautilida, Coleoidea.

CONTENTS

I. Introduction .............................................................. 270
II. Morphological structure of embryonic shells in extant and extinct cephalopods ........................................... 272
III. Relationship between egg size, embryonic shell size and initial chamber size in extant and extinct cephalopods ........................................................................................................ 274
IV. Evolutionary history of cephalopod reproductive strategies derived from embryonic shell size ........ 278
V. Conclusions .............................................................. 280
VI. Acknowledgements .................................................... 280
VII. References ............................................................ 280

I. INTRODUCTION

Reconstruction of the evolutionary ecology of extinct animals is always a challenging task because it is based on such incomplete evidence. Reproductive biology is a particularly difficult case, as it largely requires preservation of soft parts. However, cephalopod molluscs, as they have a shell, might be a rare exception to this rule, providing an opportunity to track the evolution of reproductive strategies through geological time. Both ectocochleate and endocochleate cephalopods possess a shell – either outer (ammonoids, nautiloids) or inner (squids, belemnites, cuttlefishes) – that records events chronologically in the life of an individual. These records include anything from daily growth bands on squid gladii,
to evidence of change of the entire lifestyle documented in changes of ammonite shell coiling pattern, or signs of the last fatal attack of a predator. One of the most important ecological features of the cephalopod lifestyle is the embryonic shell (ES), which is present in most extinct taxa and extant species, as it reflects the egg size and thus parental investment into individual offspring. Throughout their evolutionary history cephalopods exhibit a variety of body plans and ES morphologies. Generally, in most euctocochleate taxa, the ES consists of an initial chamber (IC) sometimes called the ‘protoconch’ and a few chambers, although in some groups like Ellesmerocerida a distinctive IC is absent (Barskov et al., 2008). In modern coleoids the internal ES represents a structure very similar to that of adults; the sword-like gladius of squid, the broader cuttlebone of Sepiida, the ram’s-horn-shaped spiral structure of Spirula spp., or paired spindle-like stylets in octopods.

Obviously, there is no ES in cephalopod species that have a rudimentary shell or no shell at all, particularly Octopoda and some Sepiolida, but for the rest of the class, the size of the ES might be a suitable tool to reconstruct historical changes in egg and larval sizes, assuming that larger eggs produce hatchlings with a larger ES. Such an assumption is widely used by palaeontologists, e.g. for Palaeozoic nautiloids (Manda & Frýda, 2010), belemnites (Doguzhaeva et al., 2014b), and particularly for ammonites for which the ES ‘ammonitella’ is considered to be a good proxy for egg size (Landman, Tanabe & Shigeta, 1996). Thus, not only is a positive relationship between egg size and hatchling size assumed (which is likely although not yet proven) but also, without any available evidence, this relationship is assumed to be linear.

Not only ES size but also IC diameter is often used to define tentative reproductive strategy as, in contrast to ES size, these data are relatively easy to obtain. Small IC size [ca. 0.5 mm (Nützel, Lehner & Frýda, 2007; Kröger, Servais & Zhang, 2009) although likely up to 1.6 mm as in some ammonites (Laptikhovsky et al., 2013)] is interpreted as evidence for a small amount of yolk in the eggs, and therefore for hatchlings with a planktotrophic strategy, and vice versa [several millimetres (Manda, 2008)]. The fact that any cephalopod hatchling is both lecithotrophic and planktotrophic, and even cephalopods born from the smallest eggs have sufficient yolk reserves to enable them to develop their hunting behaviour (Boletzky, 2003b) is largely ignored in such palaeobiological reconstructions.

These widely held beliefs are not based on any analysis of primary data from recent cephalopods, and are not even accompanied by references to any significant amount of information on the relationship between egg size and hatchling shell size. However, in theory, larger eggs do not necessarily result in larger offspring, as the energy from extra yolk could also be used for organogenesis during the embryonic period – so-called embryogenesis that could be interpreted as delayed hatching with the accomplishment within the egg of developmental processes otherwise occurring after hatching (Crowson, 1981). On the other hand, under some environmental conditions (usually adverse), cephalopod embryos tend to hatch at earlier stages of development, at smaller sizes but with a large outer yolk sac that either might be dropped or consumed, depending on species (Boletzky, 2003b). These processes (embryogenesis and de-embryonisation) might potentially have a strong impact on the evolution of the relationship between egg size and hatching size. Such heterochronies, if they occurred in cephalopods during speciation events, were probably only one of a number of effects, given the likely pleiotropic effects of genes involved in such temporal modifications (Boletzky, 1997).

This review considers all existing data on the relationship between egg size and ES size in recent cephalopods, and aims to verify the assumption that ES size is linearly proportional to egg size. Development of artificial fertilisation and ongoing research in cephalopod culture during recent decades has provided abundant new materials, and to the best of our knowledge this review summarises all existing information on extant cephalopods in which both egg length and ES length at hatching are known. We make similar comparisons between hatching size (mantle length, ML) and egg size in species with a rudimentary shell, to reveal whether the presence/absence of the shell impacts this relationship. During embryonic development, eggs swell and their volume may increase by more than 150% (Boletzky, 1986; Gomi, Masamichi & Tohru, 1986); thus, in our review we use the size of freshly laid eggs, which is nearly the same as that of unfertilised eggs in oviducts.

Secondly, we aim to determine whether hatching size (ML) can be predicted from egg size. In practice it is much easier to catch a mature female and to measure the length of ovulated eggs than to measure hatchlings in planktonic samples. Moreover, as cephalopods grow very rapidly, collected paralarvae could be much bigger than at birth: hatchlings of Stenoteuthis pteropus increase fourfold in ML (and hence, ES) in just two weeks (Laptikhovsky, Arkhipkin & Golub, 1993). For this, we used a separate set of data on egg and hatching size in species that do not possess hard shells, such as octopods and some sepiolids.

The gladius extends exactly from the anterior to the posterior part of the mantle in hatchlings of nearly all Decabrachia, so the ML is effectively the gladius length. There are some rare exceptions that were taken into consideration: in the genus Idasepia a delicate membranous gladius covers only about two-thirds of the ML (Hytleberg & Nateewathana, 1991), in the sepiolids Rossia and Semirosia the gladius extends for some 70–75% of the ML (Bizikov, 2008), and the cuttlefish genus Metasepia have a sepioid of half to two-thirds the ML (Grasse, 2014; B. Grasse, personal communication). However, such exceptions are rare. To estimate relationships between egg size and hatching size we used literature data on embryogenesis of 42 species with an internal shell and 43 species with a rudimentary shell that to the best of our knowledge represents all existing information to date.
Another question we address herein is whether a universal statistically significant relationship exists between IC size and ES size that might allow use of IC, rather than ES, to judge inferred reproductive strategies. For example, although there is abundant information on IC size in the ecologically important Belemnitida, their ES size is poorly known and there is abundant information on IC size in the ecologically judge inferred reproductive strategies. For example, although statistically significant relationship exists between IC size

For this purpose, we used a data set of IC and ES sizes for Ammonoidea and Nautilida from Laptikhovsky et al. (2013), as well as available data for other extinct and extant cephalopod taxa based on an extensive literature search. This resulted in paired data (IC versus ES) in 235 species of Ammonoidea, 46 Bactritida, 13 Nautilida, 22 Orthocerida, 8 Tarphtycerida, 4 Oncocerida, 1 Belemmoidea, 4 Sepiida, and 1 Spirula. To reconstruct the evolution of cephalopod reproductive strategies this data set was supported by non-paired data of either IC or ES in another 324 species of Ammonoidea, 56 Belemmoidea, 9 Coleoidea, 10 Bactritida, 125 Nautilida, 6 Oncocerida, 34 Orthocerida, 9 Pseudorthocerida and 8 Tarphtycerida.

In spite of being heavily biased towards ammonites, as these paired measurements are extremely rare for other groups, the available data set on the relationship between IC and ES size is reasonably complete and sufficient for an initial assessment. For taxonomy we used the reviews of Shevyrev (2006a, b), Allcock, Lindgren & Strugnell (2014) and Hoffmann (2015).

II. MORPHOLOGICAL STRUCTURE OF EMBRYONIC SHELLS IN EXTANT AND EXTINCT CEPHALOPODS

All chambered nautiloids and ammonoids share a shell that is divided into two major parts: (i) the phragmocone which is divided by septa into separate chambers interconnected via the siphuncle; and (ii) the body chamber where the animal lives. In endocochleate cephalopods the shell exhibits various degrees of reduction up to complete absence. Hard ESs of extinct and recent cephalopods differ in structure among taxa (Fig. 1). They generally consist of the IC together with several (0–15) chambers of the phragmocone or proostracum combined with the phragmocone.

The boundary between the ES and post-ES in cephalopods can be clearly seen in some clades (i.e. in ammonites it is marked by a prominent constriction and accompanied by changes in microsculpture), while in others it is poorly known (i.e. belemnoids) or cannot be defined with certainty (some nautiloids s.l.). The following features were used for determination of the ES: (i) nepionic constriction – some bactritoids and Nautilida are characterised by the presence of a wide constriction in the early part of the shell; (ii) septal approximation (decrease in the distance between septa) – this is known in many nautilids and is commonly used for recognition of the ES (Stumbr, 1959; Shimansky, 1975), but as in recent Nautilus the septal approximation lies some one-third of a whorl before the end of the ES (Landman, 1988), such measurements may be slight underestimates; (iii) changes in microsculpture are rarely seen in fossil cephalopods as this relies on excellent preservation, but they were recently reported in taphrocerids by Turek & Manda (2016) who also emphasised very high variability in the ES size of the taxa studied; (iv) shell thickening as a kind of hatching scar and a shift in the shell axis as in some Belemnoidea (Hewitt & Jagt, 1999); (v) the ES of ammonoids, the so-called ammonitella, is finished by a constriction known as the primary constriction, which is accompanied by the nacreous primary varix, indicating appearance of the nacreous layer.

For this study, we tried to use as many features as possible to define ESs, but due to incomplete data about initial shell parts of many taxa, in some cases only a single feature could be used for the determination of ES size.

These ESs can be grouped as follows:

(1) Yanhecerida, Protactinocerida, Iterjocerida (Cambrian – Ordovician) – the earliest cephalopod orders, with few known species. Neither the IC nor the ES is described.
(2) Ellesmerocerida (Cambrian) – the apical initial chamber of the shell is simple, large (~2–3 mm), conical or bluntly rounded, rather rapidly expanding. The larval shell is cylindrical, with several chambers, and no nepionic constriction or hatching scar to define it (Flower, 1964; Dzik, 1984; Barskov et al., 2008).
(3) Endocerida (Ordovician – Early Silurian) – the largest Early Palaeozoic animals, reaching up to 10 m in length (Teichert & Kummel, 1960), an abundant and common taxon. The ES is large, some 5–60 mm in length, inflated, with a chambered apical part and the IC distinctly separated from the post-larval shell (Dzik, 1984; Kröger, 2013).
(4) Oncocerida (Ordovician – Carboniferous) – the IC of the apical end with a slightly larger septal distance than in the following chambers (Kröger, 2007); its maximum diameter is approximately 0.8–1.5 mm. Chambers 2–5 (particularly 3–4) are shorter than the previous and subsequent ones; in our opinion this might be interpreted as marking the end of embryonic development. ES length is 4–7 mm.
(5) Orthocerida (Ordovician – Triassic, ?Cretaceous) – the ES consists of a spherical IC (0.3–1.7 mm) and a single chamber that made it capable of early access to the pelagic zone, before reaching the phragmocone stage (Barskov et al., 2008). ES length is usually 1–5 mm, up to 12 mm in the Triassic Trinocerida.
(6) Pseudorthocerida (Ordovician – Triassic) – in contrast to Orthocerida the IC is conical (Barskov et al., 2008) and 0.5–2 mm, the ES varies between 1 and 14 mm.
Cephalopod reproductive strategies

Fig. 1. Embryonic shells of extant and extinct cephalopods. IC, initial chamber. (A) Ammonoidea; (B) Neocoleoidea: Sepiida (Mississaepia, after Doguzhaeva, Weaver & Ciampaglio, 2014a); (C) Coleoidea: Belemnoidea (Pachybelemnopsis, after Doguzhaeva et al., 2014b); (D) Neocoleoidea: Spirulida (Spirula, after Warnke & Boletzky, 2009); (E) Orthocerida (Archigigasoceras, after Kröger, 2006); (F) Nautilida (Nautilus, after Landman, 1988); (G) Oncocerida (after Kröger, 2007); (H) Pseudorthocerida (Reticycloceras, after Kröger & Mapes, 2004); (I) Neocoleoidea: Oegopsina (Onychoteuthis, after Sweeney et al., 1992); (J) Bactritida (after Mapes, 1979).

(7) Tarphycerida (Ordovician – Devonian) – the IC is large, 1–5 mm, and cup-like on the apical end of the shell; the ES is slightly curved (Turek, 2010), finger-like, and approximately 2.5–16 mm in length.

(8) Lituitida (Ordovician) – the IC is spherical, ~0.7 mm. The ES is not well defined and is ‘a few millimetres’ long (Kröger, 2006).

(9) Actinocerida (Ordovician – Carboniferous) – a large initial part of the shell has a conical IC (Barskov et al., 2008) exceeding 10 mm in diameter (Dzik, 1984).

(10) Ascocerida (Ordovician – Silurian) – the apex of the shell is bullet-shaped without a well-defined ES; the IC is approximately 1–2 mm (Kröger, 2007).

(11) Bactritida (Devonian – Triassic) – the IC is bulbous, from 0.3–0.7 to 1.5 mm, situated at the apical end of the phragmocone. The ES is 1–3 mm in length, includes a few chambers, and is separated by a constriction (Fig. 1) from the juvenile shell (Mapes, 1979).

(12) Discosorida (Ordovician – Devonian) – the IC is 0.8–1.5 mm, the ES is cup-like, separated by a circular or elliptical cicatrix with additional radial depressions (Manda & Turek, 2009). The ES length is 4–7 mm.

(13) Nautilida (Devonian – Present) – the ES consists of a coiled calcified phragmocone and is approximately 4–32 mm in diameter; the proostracum is absent; the IC is cup-like, approximately 1–6 mm long.

(14) Ammonoidea: Anarcestida, Tornocerida, Goniatitida, Clymeniida, Ceratitida, Phyllocerida, Lytocerida, Ammonitida (Devonian – Paleogene (Danian)) – the ES (ammonitella) consists of an IC of 0.2–2 mm that may be spherical, barrel- or spindle-shaped and several chambers covering up to an entire whorl, separated from the adult shell by a primary constriction. Total diameter of the ES (ammonitella) is around 0.5–3 mm.

(15) Coleoidea: Boletzkyyida (Devonian) – the ES consists of a spherical IC of 0.5–0.9 mm and a single septum. The total ES length is ~3–4 mm (Bandel, Reitner & Stürmer, 1983).

(16) Coleoidea: Belemnoidea: Aulacocerida, Phragmoteuthida, Donovanicocida, Belemnitida, Hematicitida (Devonian – Cretaceous) – the ES consists of a globular IC of 0.3–0.7 mm and several chambers. The total length is about 1.5–3 mm (Hewitt & Jagt, 1999; Doguzhaeva et al., 2014b).

(17) Coleoidea: Neocoleoidea: Myopsida, Oegopsida, Bathyteuthida, Sepiolidae, Idiosepiida (Paleogene – Present) and Vampyromorpha (Jurassic – Present) – the ES is the gladius (absent in some Sepiolidae and reduced in Idiosepiida), a pen-like decalcified chitinous proostracum, sometimes bearing remnants of the phragmocone; the IC is absent (Bizikov, 2008; Fuchs & Iba, 2015; Sutton, Perales-Raya & Gilbert, 2016).

(18) Coleoidea: Neocoleoidea: Sepiida (Paleogene – Present) – the ES is the sepion, consisting of a calcified proostracum and a phragmocone with a siphuncular surface of some 4–10 mm at hatching; IC is ovoid or spherical, approximately 0.6–2 mm in length (Bandel & Boletzky, 1979; Doguzhaeva et al., 2014a).

(19) Coleoidea: Neocoleoidea: Spirulida (Jurassic – Present) – the spiralling ram’s-horn-like shell consists of a spherical IC of ~0.7 mm and 2–3 chambers, a cicatrix is absent (Warnke & Keupp, 2005; Lukedener et al., 2008). It is represented by a phragmocone, and lacking a proostracum, with early chambers covered with a thin membrane possibly representing a reduced rostrum (Warnke & Boletzky, 2009; Arkhipkin, Bizikov & Fuchs, 2013).

Some neocoleoid cephalopods, mostly octopods as well as some sepiolids, have a reduced shell. These groups exhibit all possible reproductive strategies from the smallest egg size known for cephalopods (0.6–0.8 mm in Argonauta spp.) to the largest (40 mm in Graneledone boreopacifica).
which is similar to the studied extinct taxa (from 0.5–0.6 mm in some Orthocerida, Ceratitida, Ammonitida and Lytocerida to 50–68 mm in Proterovaginoceras belsenitiforme and Cameroceras turrisoides of Endocerida and in some Nautilida). Unfortunately, they cannot be included this study. However, their exclusion is unlikely to be important as these taxa (judging from the relatively rare occurrence of their very characteristic beaks) were never abundant in seas of the Palaeozoic and Mesozoic, the periods of our primary interest.

III. RELATIONSHIP BETWEEN EGG SIZE, EMBRYONIC SHELL SIZE AND INITIAL CHAMBER SIZE IN EXTANT AND EXTINCT CEPHALOPODS

Analysis of our data on recent cephalopods demonstrated that egg size might be predicted from ES or (in cephalopods with a rudimentary shell) ML size (and vice versa) (Tables 1 and 2, Fig. 2). The mean ± C.I. ratio between egg size and hatchling size was 1.09 ± 0.8 in shell-bearing cephalopods, significantly higher than the mean of 0.85 ± 0.07 in species with a rudimentary shell (Welch two-sample t-test, \( t = 2.4121, \) d.f. = 97.917, \( P = 0.0177 \)). These two relationships thus could be used to estimate the ES or ML of hatchlings from egg size regardless of taxon or reproductive strategy (Fig. 2). For fossil materials, the egg size could be estimated from the ES.

No significant relationship predicting ES size from IC size could be established for all cephalopods (Fig. 3A) although correlations did exist at order and subclass levels in Ammonoidea (Pearson product–moment correlation \( r^2 = 0.948, \) \( P < 0.0001 \)), Bactritida (\( r^2 = 0.662, \) \( P < 0.0001 \)), Tarphycerida (\( r^2 = 0.922, \) \( P = 0.003 \)), and possibly Nautilida (\( r^2 = 0.590, \) \( P = 0.056 \)). The ES to IC ratio is 1.2–2.9 (mean 1.9) in Ammonoidea, 2.7–3.5 (mean 3.1) in Coleoidea (Sepiida, Spirula), 1.9–8.1 (mean 4.2) in Bactritida (Nautilioidea), 2.6–22.3 (mean 9.0) in Nautilida, and 1.8–14.9 (mean 6.3) in Orthocerida. Analysis of covariance (Crawley, 2007) demonstrated that ES size is highly influenced by IC size (\( F = 1191.6, \) \( P < 0.0001 \)), belonging to a particular taxonomic group (\( F = 162.2, \) \( P < 0.0001 \)) and taxa-specific interactions between IC and ES (\( F = 4.9, \) \( P = 0.02 \)) (Fig. 3B).

Among the diversity present in Fig. 3, three evolutionary groups can be identified by principal component analysis (Crawley, 2007). One is represented by the subclass Ammonoidea, another group consists of the order Nautilida (Fig. 4), the third unites the subclass Orthoceratoidea and its descendants – the order Bactritida and the subclass Coleoidea. The evolutionary significance of these three groupings is unclear but possibly is related to shell morphology and hatchling ecology. In Nautilida the shell is external and coiled and the hatchlings demersal. In Ammonoidea the shell is external and the hatchlings pelagic, in the other three taxa the shell may be either external or internal, but is usually straight and streamlined with some very rare exceptions, and hatchlings either pelagic or demersal.

A strict isometric linear relationship between egg size and maximum ES size (length of gladius, maximum distance in Spirula embryonic crescent, or diameter in spheroid nauta) is probably based on some general patterns of shell formation

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Fig. 2. Relationship between egg size and hatchling shell size in cephalopods. Hatchling shell size was measured as embryonic shell (ES) size in shell-bearing cephalopods and mantle length (ML) in those with a rudimentary shell. The southwest Atlantic Benthoctopus eureka was excluded from consideration as an ‘outlier’.

Fig. 3. Relationship between (A) initial chamber (IC) size and embryonic shell (ES) size and (B) changes in ES/IC ratio with initial chamber size in extant and extinct cephalopods.
Table 1. Relationship between egg size and hatchling size (embryonic shell size, ES) in shell-bearing cephalopods. ML, mantle length

| Species                    | Egg size (mm) | Source                                      | Max. shell size (mm) | Source                                      |
|----------------------------|---------------|---------------------------------------------|----------------------|---------------------------------------------|
| **Nautilida**              |               |                                             |                      |                                             |
| *Nautilus belauensis*      | 29            | J. M. Arnold (personal communication in Hanlon & Messenger, 1998) | 28.2–31.8            | Carlson, Awai & Arnold (1992) and Arnold, Landman & Mutvei (2009) |
| *N. macromphalus*          | 26            | Willey (1896)                               | 26.2                 | Arnold *et al.* (2009)                      |
| *N. pompilius*             | 25            | Haven (1977)                                | 23.1–29              | Willey (1902) and Arnold *et al.* (2009)    |
| **Spirulida**              |               |                                             |                      |                                             |
| *Spirula spirula*          | 1.5–1.9       | Sweeney *et al.* (1992) and Warnke & Keupp (2005) | 1.8–2.0              | Sweeney *et al.* (1992) and Lakedener *et al.* (2008) – hatching occurs when shell contains 2–3 chambers; measured in Warnke & Boletzky (2009) |
| **Sepiida**                |               |                                             |                      |                                             |
| *Sepia apama*              | 15            | Cronin (2000)                               | 12.4–13.9            | Cronin (2000) and Payne *et al.* (2013)    |
| *S. elegans*               | 3.7–4.2       | Mangold-Wirz (1963)                         | 3.9                  | Sweeney *et al.* (1992) measured from picture |
| *S. esculenta*             | 5–6           | Siung *et al.* (2010)                       | 5.1–6.4              | Choe (1966)                                 |
| *S. latimanus*             | 11–15         | Okutani (1978)                              | 10–14                | Dan *et al.* (2012)                         |
| *S. lycidas* (=*S. subaculeata*) | 6.0–7.0       | Luo *et al.* (2014)                         | <7                   | Choe (1966)                                 |
| *S. officinalis*           | 6.0–9.0       | Boletzky (1983a)                            | 6.0–8.0              | Vidal *et al.* (2014)                       |
| *S. orbigniana*            | 7.0–9.0       | Naef (1923)                                 | 6                    | Bandel & Boletzky (1979)                    |
| *S. pharaonis*             | 8–15          | Zuev (1971) and Gabr *et al.* (1998)        | 7.7–8.0              | Nabhitabhata & Nilaphat (1999) and Nabhitabhata *et al.* (2005) |
| *Sepiella inermis*         | 3.0–3.5       | Zuev (1971)                                 | 4.3                  | Nabhitabhata *et al.* (2005)               |
| *S. japonica*              | 3.5 (measured on picture) | Gomi *et al.* (1986)                  | 4                    | Zheng *et al.* (2010)                       |
| *S. maindroni*             | 4.0–4.4       | Luo *et al.* (2014)                         | 4.0–5.0              | Choe (1966)                                 |
| **Sepiolida**              |               |                                             |                      |                                             |
| *Rossia macrooma*          | 5.6–9.2       | Laptikhovsky *et al.* (2008)                 | 5                    | Boletzky & Boletzky (1973)                  |
| *R. pacifica*              | 7.9–9.1       | Laptikhovsky *et al.* (2008)                 | 6.0                  | Summers & Colvin (1989)                     |
| **Idiosepiida**            |               |                                             |                      |                                             |
| *Idiosepius* spp.          | 0.9           | Boletzky (2003a)                            | ca. 0.7              | Nabhitabhata & Suwanamala (2008)            |
| **Myopsida**               |               |                                             |                      |                                             |
| *Alloteuthis subulata*     | 1.5–1.9       | Hastie *et al.* (2009)                      | 2.0–3.2              | Hastie *et al.* (2013)                      |
| *Doryteuthis gahi*         | 1.9–3.2       | Guerra *et al.* (2001) and Laptikhovsky & Arkhipkin (2001) | 2.6–3.4              | Arkhipkin, Laptikhovsky & Middleton (2000) and Guerra *et al.* (2001) |
| *D. cf. gahi* (Peru)       | 1.7–2.1       | Cardozo, Baltazar & Bautista (2005)         | 1.9–2.8              | Cardozo *et al.* (2005)                     |
| *D. opalescens*            | 2.0–2.5       | Fields (1965)                               | 2.5–2.7              | McGowan (1954), Sweeney *et al.* (1992) and Vidal *et al.* (2002) |
| *D. pealei*                | 1.6           | Hanlon *et al.* (2013)                      | 1.8                  | Hanlon *et al.* (2013)                      |
| *D. sanpaulensis*          | 1.2–1.3       | Vidal, Marian & Martins (2013)              | 1.4–1.7              | Vidal *et al.* (2013)                       |
| *Heterololigo blekeri*     | 2.6–2.7       | Baeg, Sakurai & Shimazaki (1992)             | 3.0–3.5              | Ikeda *et al.* (2005) and Sweeney *et al.* (1992) |
| *Loligo reynaudi*          | 2             | Sauer *et al.* (2013)                       | 2.3–2.6              | Vidal, Roberts & Martins (2005) and Martins *et al.* (2010) |
| *L. vulgari*               | 1.8–2.7       | Moreno *et al.* (2013) and ICES (2015)      | 2.2–3.3              | Sweeney *et al.* (1992), Sen (2004) and ICES (2015) |
| *L. forbesi*               | 3.06          | Rocha & Guerra (1996)                       | 3.5–4.9              | Sweeney *et al.* (1992) and ICES (2015)     |
| *Uroteuthis duxaucleri*    | 1.3–1.9       | Choi (2008) and Nechta, Anil & Rohini Krishna (2015) | 1.1–1.3              | Nabhitabhata *et al.* (2005) and Choi (2008) |
| *Lolliguncula brevis*      | 1.8           | Hall (1970)                                 | 1.7–2.0              | Perez & Zaleski (2013)                      |
### Table 1. Continued

| Species                     | Egg size (mm) | Source                          | Max. shell size (mm) | Source                          |
|-----------------------------|---------------|---------------------------------|----------------------|---------------------------------|
| *Sepioteuthis australis*    | 5–10          | Pecl (2001)                     | 4.3–7.3              | Steer, Pecl & Moltschanivskyj (2003) |
| *S. lessoniana*             | 3–6           | Zuev (1971), Mhihu, Mgaya & Ngoile (1999) and Deepak & Patterson (2002) | 3.5–7.0              | Choe (1966), Lee et al. (1994), Nabhitabhata et al. (2005) and Vidal et al. (2014) |
| *S. sepioidea*              | 5–6           | Zuev (1971)                     | 5                    | Sweeney et al. (1992)           |
| *Dosidicus gigas*           | 1.1           | Rosa et al. (2013)              | 0.9–1.3              | Sakurai et al. (2013)           |
| *Ommastrephes bartrami*     | 1.1           | Sakurai et al. (1995)           | 1.0–1.5              | Sakurai et al. (1995) (measured from picture) and Yatsu & Mori (2000) |
| *Sthenoteuthis oualaniensis*| 0.84          | Sakurai et al. (1995)           | 1.4                  | Sakurai et al. (1995) (measured from picture) |
| *Illex argentinus*          | 1             | Rodhouse et al. (2013)          | 1.6                  | Rodhouse et al. (2013)          |
| *I. coindeti*               | 0.8–1.3       | Gonzalez & Guerra (2013)        | 1.4                  | Gonzalez & Guerra (2013)        |
| *I. illecebrosus*           | 0.9–1.1       | O’Dor & Dawe (2013)             | 1.1–1.25             | O’Dor & Dawe (2013)             |
| *Todarodes pacificus*       | 0.8           | Watanabe et al. (1996)          | 0.95–1.1             | Bower & Sakurai (1996), Watanabe et al. (1996) and Sakurai et al. (2013) |
| *Abralia trygonura*         | 0.9           | Young & Mangold (1994)          | 1.2                  | Bigelow (1992)                  |
| *Thysanoteuthis rhombus*    | 1.0–1.2       | Sabirov et al. (1987)           | 0.9–1.3              | Sabirov et al. (1987)           |

![Fig. 4](image)

**Fig. 4.** Principal component analysis of the ratio between embryonic shell size and initial chamber size (ES/IC). Numbers define observed ES/IC ratio calculated to the nearest number below (e.g. 1 corresponds to the range from 1.0 to 1.9999). AMM, Ammonoidea; BAC, Bactritida; COL, Coleoidea; ORT, Orthoceriida; NAU, Nautiloidea.

During embryogenesis that are shared by all cephalopods. One possible explanation is the expression of the *engrailed* gene universal in all molluscs for delimiting the boundaries of shell-forming fields during embryogenesis, although in cephalopods also involved in the production of evolutionary novelties such as the tentacles, eyes and funnel (Baratte, Andouche & Bonnaud, 2007). The presence of a shell possibly affected the ratio between egg size and hatching size, which is higher in shelled species as detailed above.

A strong correlation between ES (= hatching) size and egg length in cephalopods (Fig. 2) is consistent with observations from gastropods that lack adelphophagy (intra-capsular cannibalism), in which the shell length of hatchlings is correlated with egg length (Ito, 1997; Collin, 2003). This might be caused by scaling of the ectoderm invagination in proportion to yolk volume at shell formation. Unfortunately, there is no information available to support this suggestion. Despite the conservation of the early shell-forming developmental program across molluscan classes, little is known about the underlying fine-scale cellular or molecular processes (Hohagen & Jackson, 2013). The initial contact between endoderm and dorsal ectoderm that precedes shell gland invagination has been observed in representatives of Gastropoda, Bivalvia, Scaphopoda and Cephalopoda. In species with a rudimentary shell, shell gland development ceases during dorsal ectoderm invagination, and the shell field never forms. In cephalopods with an internal shell, the shell gland is also internalised forming a ‘shell sac’, whereas *Nautilus* retains an external shell throughout embryogenesis (Kniprath, 1981; Tanabe & Uchiyama, 1997; Hohagen & Jackson, 2013). However, cephalopod eggs differ from those of other molluscs in the presence of large yolk stocks, strongly impacting embryonic development, therefore there might be underlying cephalopod-specific developmental patterns.

Hatchlings of the deep-sea Southwest Atlantic *Benthoctopus eureka* have very small ML of 3 mm but hatch from eggs of a final size of 23–25 mm (Laptikhovsky, 2001). Initial
Table 2. Relation between egg size and hatchling size (mantle length, ML) in cephalopods with a rudimentary cartilaginous shell

| Species | Egg size (mm) | Source | Hatchling ML (mm) | Source |
|---------|---------------|--------|-------------------|--------|
| **Octopoda** | | | | |
| Argonauta argo | 0.6–0.8 | Sweeney et al. (1992) | 0.75–0.9 | Sweeney et al. (1992) |
| A. hians (= A. boettgeri) | 0.7–1 | Sweeney et al. (1992) | <1–1.25 | Sweeney et al. (1992) |
| Amphioctopus aeguina | 3.0–3.3 | Igua et al. & Srinivasan (2006) | 3.1 | Igua et al. & Srinivasan (2006) |
| A. burryi | 2.2–2.5 | Sweeney et al. (1992) | 1.5 | Sweeney et al. (1992) |
| Bathypolipus baideri | 11 | Wood, Kenchington & O’Dor (1998) | 7.7 | Wood et al. (1998) |
| Benthoctopus eureka | 20–30 | Ignatius & Srinivasan (2006) | 3.1 | Ignatius & Srinivasan (2006) |
| Callistoctopus macropus | 3.0–3.3 | Ignatius & Srinivasan (2006) | 3.1 | Ignatius & Srinivasan (2006) |
| Eledone cirrhosa | 6.0–9.0 | Sweeney et al. (1992) | 3.7–4.5 | Mangold, Boletzky & Frösch (1971) and Sweeney et al. (1992) |
| Enteroctopus dofleini | 6.0–8.0 | Sweeney et al. (1992) | 3.0–5.5 | Villanueva & Norma (2008) |
| E. megalocyathus | 8.35 | Uriarte et al. (2014) | 8.38 | Ortiz, R & M (2006) |
| Granulectone bainatla | 15–32 | Robison, Seibel & Drazen (2014) | 23–30 | Voigt & Drazen (2004) |
| Macroctopus maorum | 5.0–8.0 | Sweeney et al. (1992) | 2.3 | Sweeney et al. (1992) |
| Macrotritopus burryi | 1.5–2.1 | Sweeney et al. (1992) | 1.3–1.5 | Sweeney et al. (1992) |
| Octopus bimaculatus | 2.5–4.0 | Sweeney et al. (1992) | 2.6 | Sweeney et al. (1992) |
| O. briareus | 10.0–14.0 | Jereb et al. (2014) | 5.5–7.5 | Mangold et al. (1971) and Jereb et al. (2014) |
| O. chierchiae | 3.8 | Rodaniche (1984) | 3.5 | Rodaniche (1984) |
| O. cyanea | 2.0–3.0 | Sweeney et al. (1992) | 1.2–2.0 | Sweeney et al. (1992) |
| O. fitchi | 4.0–6.0 | Sweeney et al. (1992) | 2 | Sweeney et al. (1992) |
| O. insularis | 1.66 | Alejo-Plata & Alejo (2014) | 1.22 | Alejo-Plata & Alejo (2014) |
| O. laqueus | 2.6 | Mangold et al. (1971) | 1.7 | Mangold et al. (1971) |
| O. latacius | 2.0–3.0 | Sweeney et al. (1992) | 2.3 | Sweeney et al. (1992) |
| O. rubescens | 3.0–4.0 | Sweeney et al. (1992) | 1.7–2.0 | Sweeney et al. (1992) |
| O. salutii | 5.2–6.0 | Sweeney et al. (1992) | 3.5–4 | Sweeney et al. (1992) |
| O. tetricus | 2.4 | Sweeney et al. (1992) | 1.3–1.6 | Sweeney et al. (1992) |
| O. vulgaris | 1.5–2.7 | Sweeney et al. (1992) | 1.5–2.0 | Sweeney et al. (1992) |
| O. maya | 6–17 | Van Heukelem (1983) | 7 | Van Heukelem (1983) and Sweeney et al. (1992) |
| O. mimicus | 2.03 | Warnke (1999) | 2.0–2.4 | Warnke (1999) |
| Paroctopus aeguina | 6.0–10.0 | Sweeney et al. (1992) | 4.5–6.5 | Jereb et al. (2014) |
| Robsonella australis | 2.0–2.8 | Sweeney et al. (1992) | 2.2–2.3 | Sweeney et al. (1992) |
| R. fontaniana | 3.1–3.8 | Uriarte et al. (2009) | 2.2 | Sweeney et al. (1992) |
| Scaeurhus patagiatus | 2.0–2.5 | Sweeney et al. (1992) | 21.5 | Sweeney et al. (1992) |
| Scaeurhus unicirrhus | 2.0–2.5 | Sweeney et al. (1992) | 2 | Sweeney et al. (1992) |
| Tremoctopus violaceus | 1.5–2.0 | Laptikhovsky & Salman (2003) | 1.5 | Sweeney et al. (1992) |
| **Sepiolida** | | | | |
| Sepiola atlantica | 2.5–3.0 | Yau & Boyle (1996) and Jones & Richardson (2010) | 1.1–1.9 | Jones & Richardson (2010) and Rodrigues, Guerra & Troncoso (2011) |
| Euprymna berriyi | >2 | Choe (1966) | 2.4–2.8 | Choe (1966) |
| Euprymna scolopes | 2 | Arnold, Singley & Williams-Arnold (1972) | 1.6–1.9 | Hanlon et al. (1997) |
| Sepiella obscura | 2.1–2.5 | Deicke (2009) | 2.0–3.0 | Deicke (2009) |
| Sepiella neglecta | 1.4–2.8 | Lefkaditou & Kaspis (1998) | 2.0–2.7 | Boletzky et al. (1971, figure 1) |
| Sepiola rondeletii | 2.5–3 | Mangold-Wirz (1963) | 3.5–4.5 | Boletzky et al. (1971, figure 1) |
| Sepiola ligulata | 2.6 | Naef (1928) | 1.9–2.7 | Boletzky et al. (1971, figure 1) |
| Sepiola robusta | 2.2–2.4 | Boletzky (1938) | 2.0–2.6 | Boletzky et al. (1971, figure 1) |
Egg size in this species is 17–19 mm (Gleadall et al., 2010). This species has unusually long arms of about 2.5 times the mantle length; in other octopods arm length is about the same as mantle length or less, with marked similarity in body proportions between hatchlings of pelagic and merobenthic octopods (Boletzky, 1997). The very small mantle length relative to body size in B. eureka might be a heterochrony that resulted in accelerated phenotypic expression of adult features (see Boletzky, 1997). Appearance of this heterochrony could result from inactivity of engrailed with respect to the determination of ML from shell size, as the shell is reduced in octopods. It is difficult to judge whether such heterochronies might be possible in other cephalopods. There are examples of the opposite process: partial reduction of the shell not affecting the final hatching size, with the mantle extending well beyond the skeletal elements (in Metasepia, Idiosepius, Rossia, Semirossia). This evolutionary direction could presumably lead to the eventual disappearance of the internal shell. In such ‘half-shelled’ cephalopods the soft-body size, rather than shell size, might be predicted more accurately from the egg size, with the use of ES measurements to predict egg size leading to slight underestimates.

The size of the IC cannot be used to predict ES size (Fig. 3), although significant correlations were observed within some orders and subclasses, as well as in some gastropods (in which the ES is termed the protoconch II) (Nützel et al., 2007). The relationship between IC size and ES size (and hence egg size) differed among different cephalopod taxa (see above). Further measurements of these variables in a wider range of species will hopefully allow the establishment of a statistical correlation between IC and ES with appropriate uncertainty estimates (confidence intervals or credible intervals) to allow the estimation of egg size in extinct cephalopod taxa.

IV. EVOLUTIONARY HISTORY OF CEPHALOPOD REPRODUCTIVE STRATEGIES DERIVED FROM EMBRYONIC SHELL SIZE

The evolutionary history of Palaeozoic and Mesozoic cephalopod life forms and lifestyles has been reviewed in detail elsewhere (e.g. Barskov et al., 2008; Kröger et al., 2009; Wani, 2011; Ritterbush et al., 2014; Servais et al., 2016). However, these reviews considered only the evolution of adult life forms. The life forms of cephalopod hatchlings and early juveniles can be very different from those of adults (Nesis & Nigmatullin, 2003) and their evolution could involve entirely different processes. For example, octopods of the family Octopodidae, with nearly identical adult lifestyles, can produce either small eggs with paralarval hatchlings that spend up to four months in the pelagic layers (e.g. Enteroctopus dofleini), or large eggs with ‘crawl-away’ demersal young (Sweeney et al., 1992; Villanueva & Norman, 2008).

Egg size reflects numerous adaptations. It is usually inversely related to fecundity (see Vance, 1973a,b) as well as to offspring survival and hence population dynamics. Cephalopods with smaller hatchlings (and thus smaller eggs) have broader latitudinal distribution ranges (Villanueva et al., 2016). The reproductive strategies of most marine invertebrate taxa cover an adaptive range from relatively highly fecund species with small eggs to relatively low-fecundity species with large eggs. Within this range, two more or less separate categories of small- and large-egged species exist. The mathematical model of Vance (1973a,b) predicted only the extremes of the range of egg size and method of nutrition (i.e. planktotrophy, lecithotrophy) to be evolutionarily stable. This model was developed further (Christiansen & Fenichel, 1979; Roughgarden, 1989), confirming that intermediate egg sizes are at a disadvantage.

A recent review by Villanueva et al. (2016) found the mean ± S.D. ML of planktonic hatchings to be 2.5 ± 1.5 mm (range 0.6–8.4 mm), and that of benthic hatchlings to be 6.5 ± 4.6 mm (range 1.5–28 mm). Eggs of intermediate size are relatively rare among cephalopods and generally are produced by either small-sized species with large eggs (e.g. Octopus microturgus) or large species with relatively small eggs (e.g. Euteropopus magnificus, E. dofleini) (Sweeney et al., 1992; Boletzky, 2003a). Given that hatching size is roughly equivalent to egg size, to a first approximation we can assume that taxa with eggs of <4–5 mm are characterised by planktonic early stages, whereas cephalopods with larger eggs produce benthic offspring.

Analysis of egg sizes across a wide range of cephalopod taxa potentially allows exploration of the evolution of reproductive strategies of this class in relation to abiotic and abiotic events such as glaciations, global warming events, continental sea expansions and retreats, and appearances and extinctions of competitors and predators. Because of uncertainties in measurement of ES size in Cambrian cephalopods we begin from Ordovician cephalopods following the taxonomy of Sepkoski (2002) as given in the online genus database (http://strata.geology.wisc.edu/jack/).

During the Ordovician planktonic revolution when the proportion of planktonic organisms increased, particularly in the Early to Middle Ordovician (Servais et al., 2016), the adult stages of many cephalopods evolved to live in the pelagic layers (Kröger et al., 2009). The entire life cycles of many such cephalopods became pelagic. Orthocerida were the first to evolve a small spherical chamber (the IC), which might represent a crucial element of assuming a pelagic lifestyle in hatchlings. The IC allowed them to develop a functional hydrostatic apparatus before reaching the phragmocone stage, and thus to inhabit open waters earlier (Barskov et al., 2008), presumably immediately after hatching. This reproductive pathway was followed later by Ammonoidea, Bactritida, Belemnoidea and some other groups.

Early Ordovician cephalopods were represented mostly by large-egged species (K strategists): Ellesmerocerida, Endocerida, and Actinocerida, likely with demersal hatchlings as large pelagic eggs would be easily predated. Small-egged r-strategist Orthocerida and Pseudorthocerida represented 5–15% of genus diversity in the early Ordovician, increasing to 30–40% in the second half of the period (Fig. 5).
The occurrence of large eggs both in number of genera and in percentage occurrence of $K$ strategists decreased steadily from the early Ordovician through the Silurian and Devonian, mostly due to the demise of archaic large-egged taxa such as Actinocerida and Oncocerida and the simultaneous emergence of pelagic hatchlings. The $r$ strategy of pelagic spawning of small eggs peaked in terms of percentage occurrence in the late Devonian with the first appearance of Ammonoidea, and large-egged taxa reduced to just four genera. During the Devonian, evolutionary trends toward tighter coiling and some reduction of ES size occurred in several lineages of ammonoids (Bogoslovsky, 1969; De Baets et al., 2012; see also fig. 1 in Laptikhovsky et al., 2013).

A gradual decline in prevalence of the small-egged $r$ strategy during the early Palaeozoic was coincident with the evolution of armoured predators: the Placodermi, joined in the Devonian by cartilaginous and bony fishes (Friedman & Sallan, 2012). Agile sharks and bony fishes could forage in both pelagic and benthic environments, whereas heavy and slow-moving armoured fishes were restricted to a benthic lifestyle. Therefore, immobile food sources like carrion and benthos (including benthic eggs) would represent important food sources. Placodermi were declining in the Late Devonian, and eventually became extinct at the onset of the Carboniferous (Friedman & Sallan, 2012).

In the late Palaeozoic (Carboniferous – Permian) large-egged cephalopods became increasingly common due to the evolution of the new large-egged taxon Nautilida, as well as an increase in egg size in Orthocerida, of which some by the end-Cretaceous extinction, the number of large-egged genera varied between 90 and 120 from the Triassic to the Cretaceous, declining to 50–64 genera in the late Triassic – early Jurassic. This decline (mirrored in general cephalopod biodiversity) coincided with an explosion of diversification of teleost fish from the middle Triassic onwards (Romano et al., 2016). Intensive competition with teleosts, particularly Holostei and ‘Subholostei’ that became predominant in marine habitats from the mid-Triassic (Romano et al., 2016) might underlie this decline.

Both fishes sensu lato and cephalopods diversified from the late Cambrian onwards, their ecology and biodiversity reacting to similar environmental and biotic factors. A general trend in both taxa is a gradual shift from the production of large eggs to the production of smaller eggs. Small-egged species predominated among cephalopods from the Devonian, and by the Triassic, the number of large-egged species represented only 3–9% of genus richness (Fig. 5). By contrast, early fishes such as Agnatha, Placodermi, Chondrichthytes and archaic Osteichthyes that produced huge eggs (Smith, 1986; Johanson & Trinajstic, 2014), predominated until the end of Permian. The Acanthodii (about which we have no information on reproduction) were not sufficiently diverse to impact this pattern. A small-egged $r$ strategy became increasingly important from the mid-Triassic, but until the end-Cretaceous extinction, teleost and elasmobranch fishes had similar genus richness (Friedman & Sallan, 2012). However, a large-egged $K$ strategy may have shown greater resilience to catastrophic environmental change within cephalopods (Laptikhovsky et al., 2013).
The evolution of reproductive strategies in both cephalopods and fishes can be shown to have similar general patterns, with a gradual increase in occurrence of small-egg r strategies in both taxa. Both small- and large-egg strategies are common among cephalopods with some predominance in diversity of taxa producing small eggs and offspring.

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