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Intra- and interspecific variability in offspring size in nautilids

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LETHAIA

Hatching size has been considered of great importance in the evolution of externally shelled cephalopods. However, our knowledge of how hatching size varies in response to biotic and abiotic factors is largely lacking. We present a comprehensive overview of hatching size in all known species of modern nautilids (225 specimens, representing eight species). Hatching size ranges from 22 to 33 mm, with the smallest hatchlings in *Nautilus pompilius suluensis* and the largest hatchlings in *Nautilus belauensis*. There is no significant difference in hatching size between males and females in the same species. In addition, hatching size does not affect the morphology of the embryonic shell; smaller hatchlings are identical in morphology to larger hatchlings in the same species. Although information pertaining to temperature and duration of embryonic development are limited, we conclude that there is no clear correlation between hatching size and the temperature at which embryonic development takes place. In contrast, there is a weak correlation between hatching size and the duration of embryonic development. In the Late Cretaceous nautilid *Eutrephoceras* for which data on hatching size are available, species in colder climates exhibit a larger hatching size than those in more temperate climates. A comparison of hatching size and adult size among modern nautilid species reveals a positive correlation, largely driven by *N. pompilius suluensis*, at one end of the spectrum, and *N. belauensis*, at the other. This relationship may be rooted in parental care strategy and/or predation pressure. ☐ *Cephalopods, nautiloids, evolution, development, ecology, body size*

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The size of an organism is a subject of much attention because it reflects different aspects of ecology, physiology, and evolution. Previous studies have documented a link between change in size and ecological factors such as predation pressure (Abrams & Rowe 1996), temperature (Gardner *et al.* 2011; Klug *et al.* 2015), intraspecific competition (Allen *et al.* 2008), oviposition, and parasitoidism/parasitism (Church *et al.* 2019). Relationships between size and developmental factors (e.g. duration of embryonic development) have also been reported (Steele & Steele 1975; Sargent *et al.* 1987). The size of offspring (i.e. eggs, hatchlings) is of particular interest to many biologists. The size represents the maximization of reproductive potential operating under physical and biological constraints and, therefore, the size of offspring provides insights into different reproductive and life history strategies (Neuheimer *et al.* 2015). Offspring size is also often discussed in the context of evolution and macroecology (De Baets *et al.* 2012, 2015; Tajika *et al.* 2018; Fuchs *et al.* 2020; Tajika *et al.* 2020a).

Cephalopod molluscs have a long geological record, originating in the Cambrian (Kröger *et al.* 2011). To learn about reproductive strategy and ecology, the eggs of cephalopods have often been studied. For instance, egg size has been examined in modern cephalopods (octopuses and squids) in relation to environmental factors (Arnold *et al.* 1987; Villanueva 1992; Laptikhovsky & Nigmatullin 1993; Sakai *et al.* 1998; Boletzky *et al.* 2006; Collins & Rodhouse 2006; Ortiz *et al.* 2006; Ibáñez *et al.* 2018). Egg size is also important to many paleontologists to gain insights into the reproductive strategies of fossil cephalopods. Although the eggs of fossil cephalopods (e.g. ammonoids) are occasionally preserved (Tanabe *et al.* 1993; Etches *et al.* 2009; Mironenko and Rogov 2016), such fossils are rare. Alternatively, the embryonic shell is usually used as a proxy for the size of eggs. The embryonic shell is generally preserved at the apex of the shell owing to accretionary growth. The point of hatching is recorded by morphological changes that include the formation of a constriction (called ‘primary constriction’ in ammonoids and ‘nepionic constriction’ in nautilids;

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Fig. 1). A large number of studies have reported the size of embryonic shells in ectocochleate cephalopods and have discussed its ecological, biological, and evolutionary meaning (Landman 1982; Landman *et al.* 1983; Tanabe *et al.* 1994; De Baets *et al.* 2012, 2015; Fuchs *et al.* 2020). These studies have demonstrated wide variation in the shape and size of embryonic shells. On the basis of these findings, some studies have suggested that egg size is one of the most important factors in ammonoid extinction and nautiloid survival at the K/Pg extinction event (Laptikhovski *et al.* 2013; Tajika *et al.* 2018, 2020a). The two distinct reproductive strategies—small but a large number of eggs in ammonoids as opposed to large but a small number of eggs in nautilids— are known as r- and K-selections (Pianka 1970), which correspond to two different types of survivorship curves.

Nautilids are the only extant ectocochleate cephalopods with a phragmocone. Nautilids differ from other extant cephalopods in many aspects such as external morphology, low metabolism, long gestation, and long life span (~20 years; Saunders 1984; Boutilier *et al.* 1996). In contrast to modern coleoids, however, the size of eggs, embryonic shells, and hatchlings of modern nautilids has received little attention (Arnold *et al.* 1987). In particular, little is known about the intra- and interspecific variability in hatching size and the link with development, ecology, and phylogeny. Improving our knowledge of these aspects contributes to a better understanding of the evolution of this group. Such knowledge may be of relevance to support conservation efforts given that modern nautilids are protected by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Modern nautilid eggs have not been discovered in nature. Some questions regarding egg size/hatchling size can be answered by utilizing shells in museum collections worldwide. In this study, we examine hatching size in all known species of modern nautilids by applying computed tomography. We aim to answer the following questions: 1, what is the variation in hatching size within and between species; 2, can hatchlings of nautilid species be morphologically distinguished; 3, does the pattern of hatching size among nautilid species correspond to phylogeny; 4, is there a link between ecological factors and hatching size; and, 5, are hatching size and adult size correlated within and between species and is the same pattern visible in fossil cephalopods?

Methods

We examined a total of 225 conchs of modern nautilid specimens including the following species: *Allonautilus perforatus* (Conrad, 1847), *Allonautilus scrobiculatus* (Sowerby, 1849), *Nautilus macromphalus* Sowerby, 1849, *N. stenomphalus* Sowerby, 1849, *N. pompilius* Linnaeus, 1758, *N. pompilius suluensis* Habe & Okutani, 1988, *N. belauensis* Saunders, 1981, and *N. repertus* Iredale, 1944. Details of the studied material are summarized in Table 1. All specimens were CT-scanned at different research institutions, which yielded image stacks. We obtained the median section of each specimen from the image stacks and the median section was used to measure the hatching size.

In modern nautilids, hatching is marked by some morphological changes including the formation of a constriction (dubbed 'nepionic constriction'; Fig. 1A–G). However, the nepionic constriction is not

Table 1. Studied material. AMNH = American Museum of Natural History. MCM = Mikasa City Museum. YNU = Yokohama National University. PIM = Paleontological Institute and Museum, University of Zurich. NMNS = National Museum of Nature and Science (Japan). UMUT = University Museum, University of Tokyo.

Species	**Geographical region**	**Age**	**Sample size**		**Sex**			**Repository**
			all	adult	female	male	unknown	
Allonautilus perforatus	Indonesia	modern	4	2	0	0	4	AMNH
Allonautilus scrobiculatus	Papua New Guinea		13	12	0	1	12	AMNH
	Solomon Islands		3	3	0	0	4	AMNH
	Unknown		3	1	0	0	1	MCM
Nautilus macromphalus	New Caledonia		21	17	1	9	11	AMNH
Nautilus stenomphalus	Lizard Island, Australia		5	5	2	3	0	AMNH
Nautilus pompilius	Papua New Guinea		14	14	0	11	3	AMNH
Nautilus pompilius	Fiji		4	4	1	3	0	AMNH
Nautilus pompilius	Vanuatu		21	21	0	0	21	AMNH
Nautilus pompilius	Indonesia		23	23	0	0	23	YNU
Nautilus pompilius	Malaysia		33	33	0	0	33	YNU
Nautilus pompilius	Philippines		34	6	0	0	34	AMNH, MCM
Nautilus pompilius	Unknown		1	1	0	0	1	PIM
Nautilus pompilius suluensis	Philippines		6	4	0	0	6	AMNH, MCM, NMNS
Nautilus belauensis	Palau		20	20	8	12	0	MCM, UMUT
Nautilus repertus	Western Australia		20	20	9	11	0	AMNH

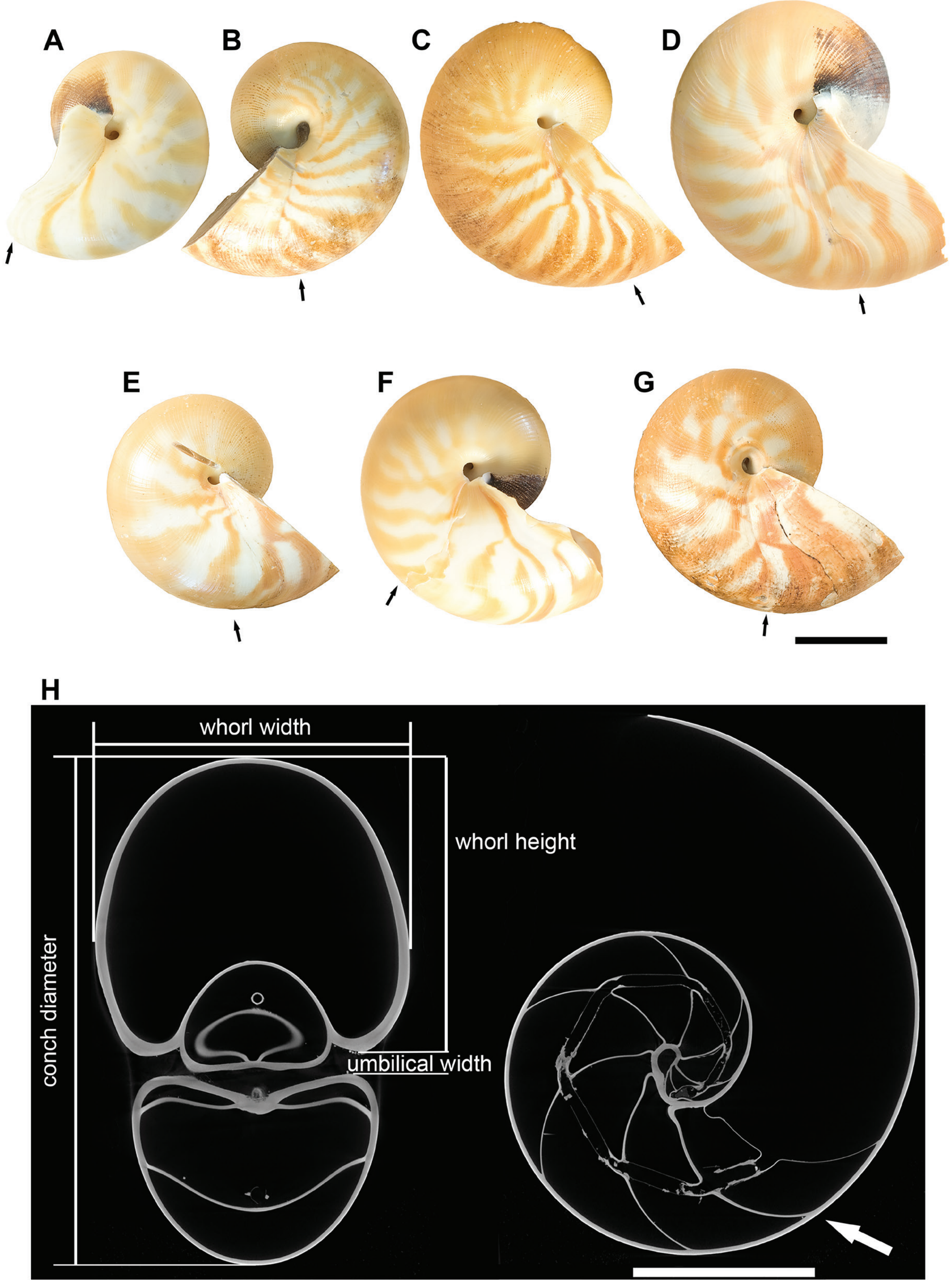


Fig. 1. Embryonic shells of modern nautilids. A, *Nautilus macromphalus* (Delaware Natural History Museum 19937). B, *Allonautilus scrobiculatus* (AMNH 94912), aperture filed down. C, *N. repertus* (AMNH 82718), aperture filed down. D, *N. belauensis* (AMNH 43031). E, *N. pompilius* from Papua New Guinea (AMNH 81960), aperture filed down. F, *N. pompilius* from the Philippines (SUI 40059). G, *N. pompilius* from Vanuatu (AMNH 131865), aperture filed down. H, CT-scan of *N. pompilius* from the Philippines (SUI 42473). AMNH = American Museum of Natural History. SUI = State University of Iowa. Scale bars are 10 mm. Arrows indicate the point of hatching in A–G and the septal approximation in H.

detectable in CT-scans of large specimens (with more than ~2.5 whorls) because the succeeding whorls cover the constriction. Therefore, we applied an alternative methodology to estimate the conch diameter. We measured hatching size based on septal approximation because it is well documented that septal crowding marks the point of hatching in modern nautilids (Fig. 1H; Davis & Mohorter 1973; Landman *et al.* 1983). Measuring the exact body chamber length at the point of hatching is difficult using CT-scans of large specimens. We discovered that: 1, the body chamber length in juvenile and mature specimens is not representative of the body chamber length at hatching; and that, 2, the body chamber length at hatching in specimens exhibiting the nepionic constriction averages 116° with no clear species-specific pattern (Fig. 2). Accordingly, we used 116° as the body chamber length in our calculations. Note that we define the body chamber length as a rotational angle between the aperture and the ventral point at

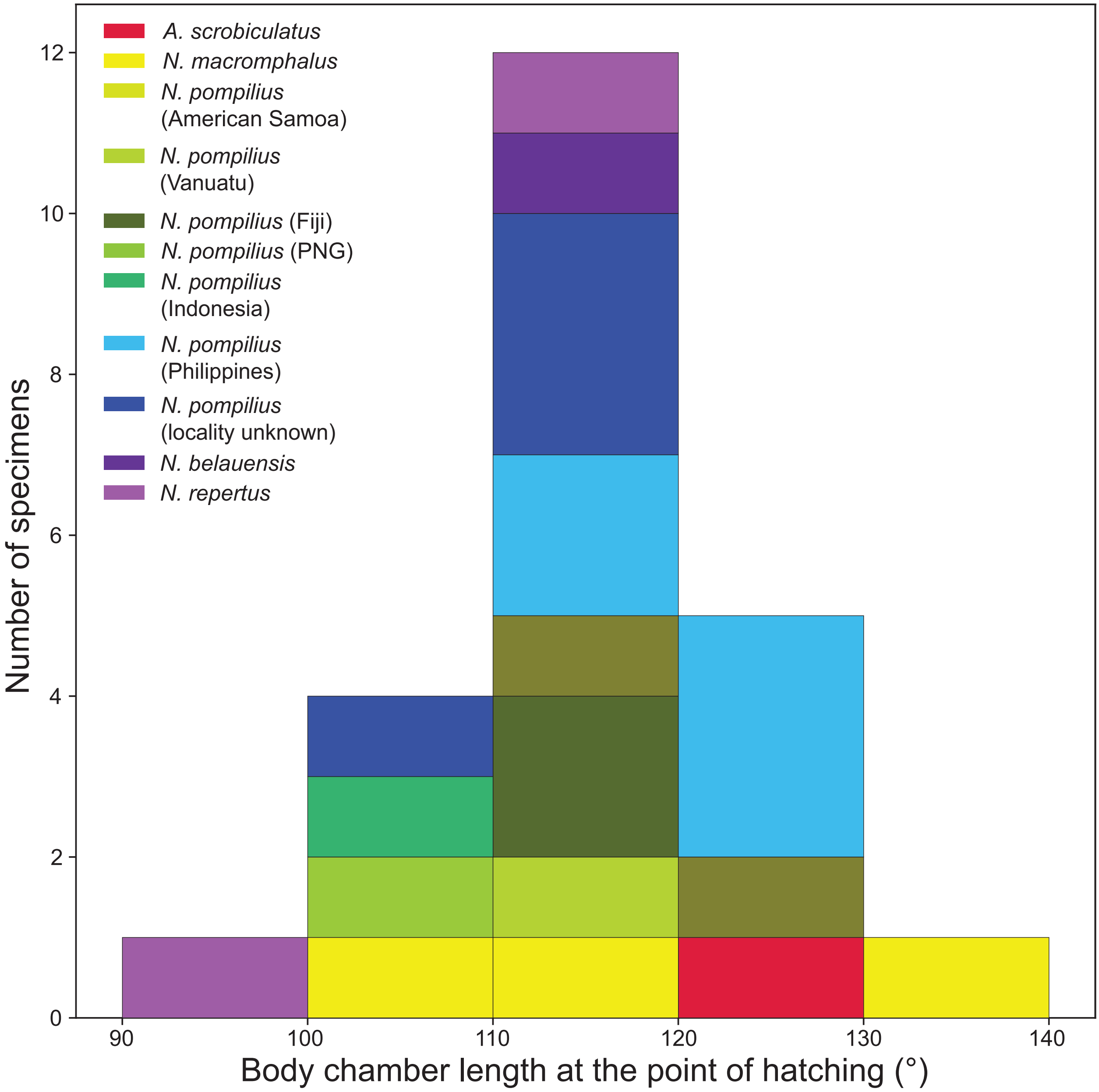


Fig. 2. Histogram of body chamber length at the point of hatching in modern nautilids. Data include *Allonautilus scrobiculatus* (n = 1), *Nautilus macromphalus* (n = 3), *N. pompilius* from American Samoa (n = 1), *N. pompilius* from Vanuatu (n = 1), *N. pompilius* from Fiji (n = 2), *N. pompilius* from Papua New Guinea (n = 2), *N. pompilius* from Indonesia (n = 1), *N. pompilius* from the Philippines (n = 5), *N. pompilius* from unknown locality (n = 4), *N. belauensis* (n = 1), and *N. repertus* (n = 2).

which the last septum and outer shell intersect in median section (see for example, Tajika & Klug 2020). In addition to hatching size, we measured the whorl width (ww), whorl height (wh), and umbilical width (uw) at the point of hatching. Then, we calculated the following ratios: whorl width index (WWI: ww/wh), conch shape (CS: ww/dm), and umbilical width index (UWI: uw/wh). Conch diameter and whorl width at maturity were also measured to determine if there is a correlation between hatching size and adult size. We regarded specimens with a black band at the aperture as adult (Collins & Ward 1987; Klug 2004). The resulting hatching sizes provided with CT-scans were compared to those obtained by direct measurement of specimens used in Figure 1.

We plotted conch diameter at hatching versus conch diameter at maturity and whorl width at hatching versus whorl width at maturity. To test if adult size and hatching size are correlated, we calculated the Pearson's correlation coefficient. This was examined in all species/geographic populations with a sample size > 10. These tests were performed with the Statistics and Machine Learning Toolbox of Matlab 2020b (MathWorks). For groups in which the correlations were significant, an allometric equation was calculated using the reduced major axis in PAST 4.0 (Hammer *et al.* 2001).

Although some studies have examined phylogenetic signals of egg size in cephalopods (Ibáñez *et al.* 2021), we decided not to do such an analysis. This is because the phylogenetic tree of modern nautilids is complex (i.e., some species do not clearly separate out into separate branches; e.g. Combosch *et al.* 2017). Alternatively, we used the three genetically and geographically separated clades in nautilids: Coral Sea (Australia, Papua New Guinea), Indo-Pacific (Indonesia, Malaysia, Philippines, and Western Australia), and South Pacific (Fiji, New Caledonia, Vanuatu; *sensu* Combosch *et al.* 2017) to test if there is a significant difference between them. To this end, we carried out an analysis of variance (ANOVA) and multiple comparison tests to detect which pairs of clades show a significant difference.

Results

Size

The distributions with kernel density estimation of conch diameter and whorl width both at the point of hatching and maturity are shown in Figure 3 and the Supplementary Table. These results are nearly congruent to the hatching sizes that we directly measured (Supplementary Table). The conch diameter at the point of hatching tends to be highly variable and the ranges commonly overlap between species, although there appears to be a species-specific pattern (Fig. 3A). The results of ANOVA reveal a significant difference among species ($p < 0.05$; Supplementary Table). *Nautilus belauensis* possesses the largest hatchlings (Supplementary Table). By contrast, *N. pompilius suluensis* has the smallest hatchlings, although the sample size of this species is small (n = 6). The range of hatching size between female and male does not differ in any species for which the sex is recorded (Fig. 3A). The differences among species are more conspicuous with respect to conch diameter at maturity (Fig. 3B). *Nautilus repertus* is the largest species with respect to adult size, while *N. pompilius suluensis* is the smallest, which is consistent with the report by Saunders (1987). *Nautilus pompilius* shows the highest variation in adult conch diameter and the adult diameter tends to overlap between different geographic populations. Differences in adult size between female and male are apparent within a species (*N. macromphalus*, *N. pompilius*, *N. stenomphalus*, *N. belauensis*, and *N. repertus*). The whorl width at hatching and maturity has a pattern similar to that of conch diameter at hatching and maturity (Fig. 3C, D).

The conch diameter at the point of hatching is plotted against the conch diameter at maturity in Fig. 4A. The conch diameter at the point of hatching increases with increasing adult conch diameter in a comparison of all species ($p < 0.001$; Table 2). We also compared hatching size and adult size within species/geographic populations with sample sizes > 10. Results reveal two different patterns. *Allonautilus scrobiculatus* from Papua New Guinea and *Nautilus macromphalus* each show a positive correlation. However, the hatching size (dm) is independent of adult size (dm) in other groups (Table 2). For the two species with a positive correlation (*A. scrobiculatus* and *N. macromphalus*), we analysed linear dependencies of log-transformed hatching size and adult size (Table 2). Both species show a slope of slightly less than 1.0. The whorl width at the point of hatching is plotted against the whorl width at maturity in Figure 4B. There is no correlation within a species/geographic population except for *A. scrobiculatus* and *N. macromphalus* (Table 3). In comparing all species/geographical populations, the whorl width at the point of hatching and maturity is correlated (Table 3). ANOVA reveals that the three geographically (i.e. genetically) isolated groups—Coral Sea, Indo-Pacific, and South Pacific (sensu Combosch *et al.* 2017)—show a significant difference (Fig. 4A, B; Supplementary Table). Multiple comparison tests show that the Coral Sea group has a significantly smaller hatching size than the Indo Pacific and South Pacific groups. The range of hatching size

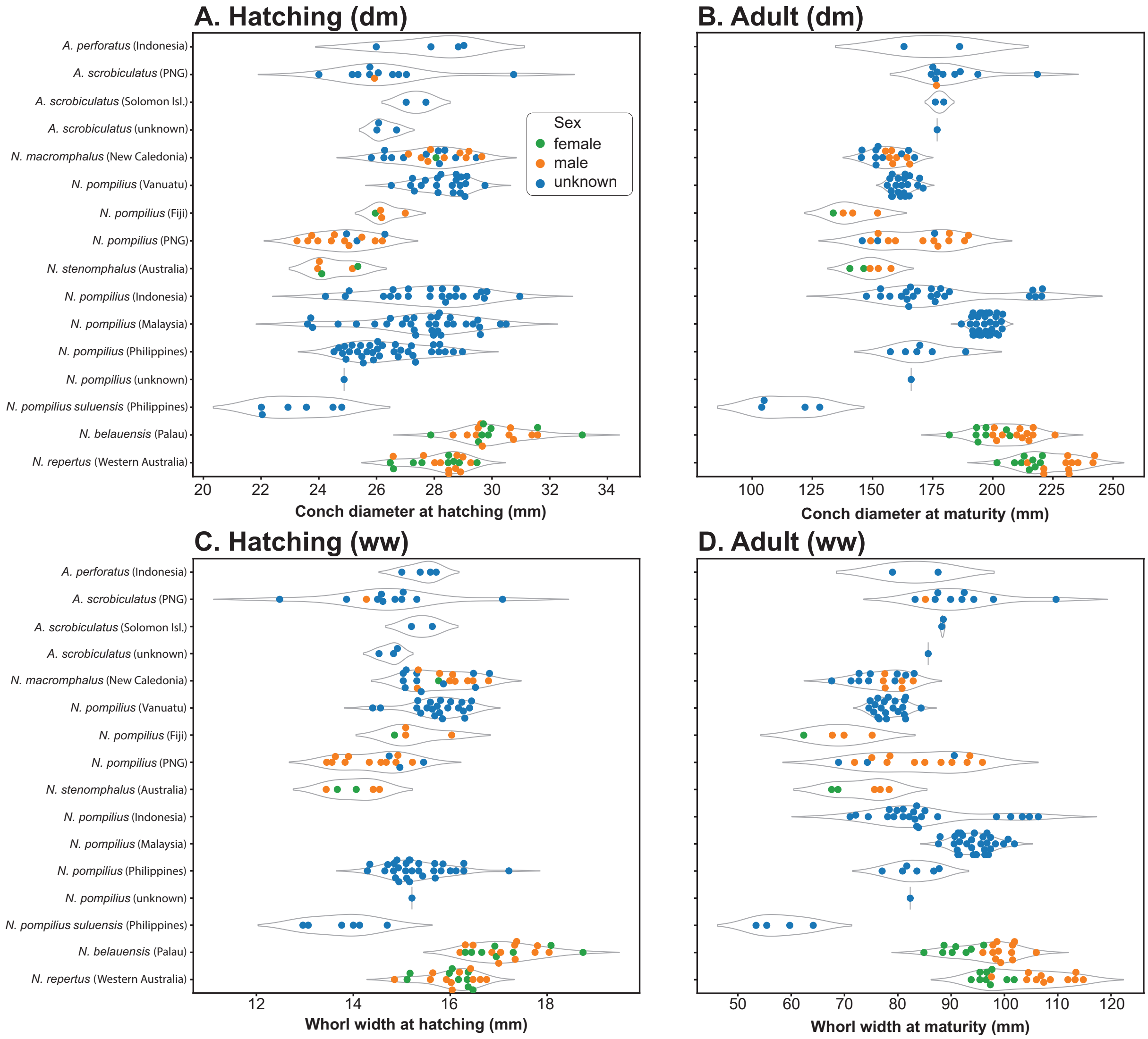


Fig. 3. Hatching and adult size in modern nautilids. A, conch diameter (dm) at hatching. B, conch diameter (dm) at maturity. C, whorl width (ww) at hatching. D, whorl width (ww) at maturity.

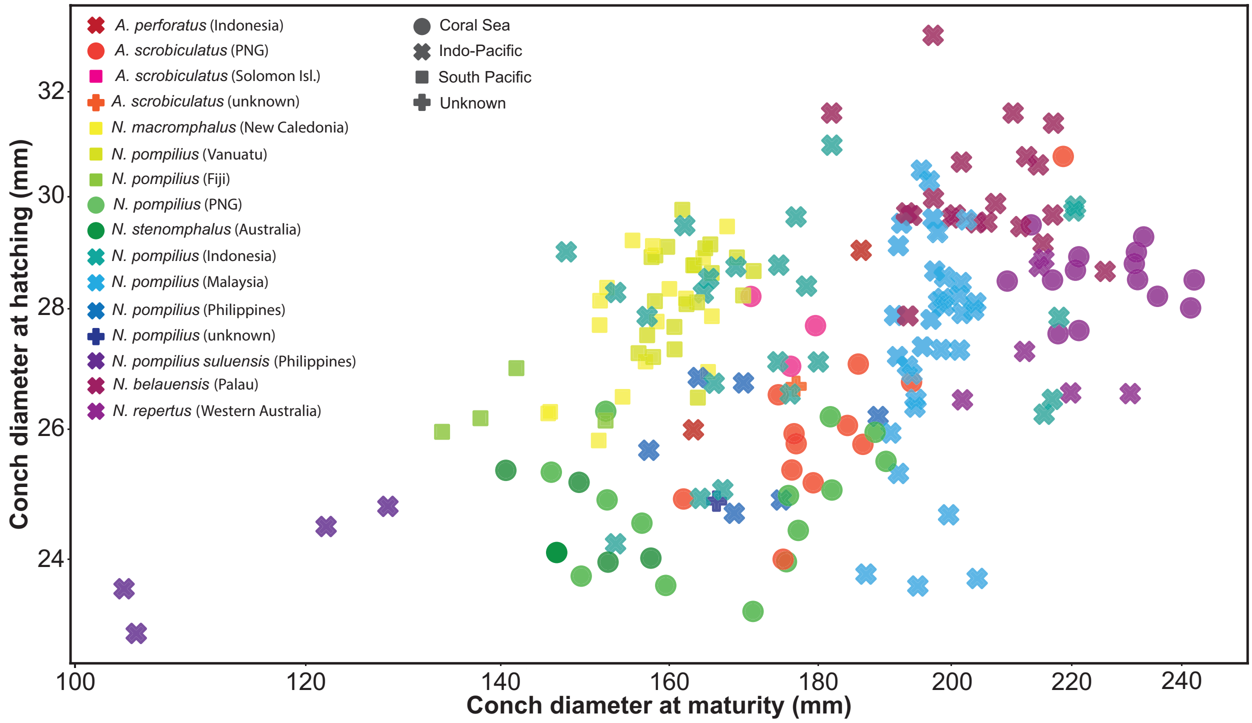
in the Indo Pacific is the highest. This is because this group includes *N. belauensis* and *N. pompilius suluensis*, which have the largest and smallest hatching sizes, respectively.

The link between hatching size and latitude in different geographic populations is somewhat unclear because the exact coordinates of the locations at which the specimens were collected are lacking and some of the populations (e.g. Indonesia, Malaysia, and Papua New Guinea) are located at a similar latitude. Yet, the hatching size between some latitudinally distant geographic populations (e.g. from the Philippines and Australia) exhibit a similar hatching size. Additionally, the hatching size between the latitudinally proximate geographical populations (e.g. from the Philippines and Palau) is significantly different. These results suggest that there is no clear correlation between hatching size and latitude of geographical populations.

Morphology at hatching

The conch shape, whorl width, and umbilical width index at the point of hatching are shown in Figure 5 (A, B and C, respectively). Overall, each conch parameter is highly variable within a species/population and the range tends to overlap among species. Indeed, the results of ANOVA and multiple comparison tests reveal that significant differences only occur among a few groups (Supplementary Table). For example, the value of conch shape is higher in *Nautilus pompilius suluensis* than in *Allonautilus scrobiculatus* and *N.*

A. Conch diameter



B. Whorl width

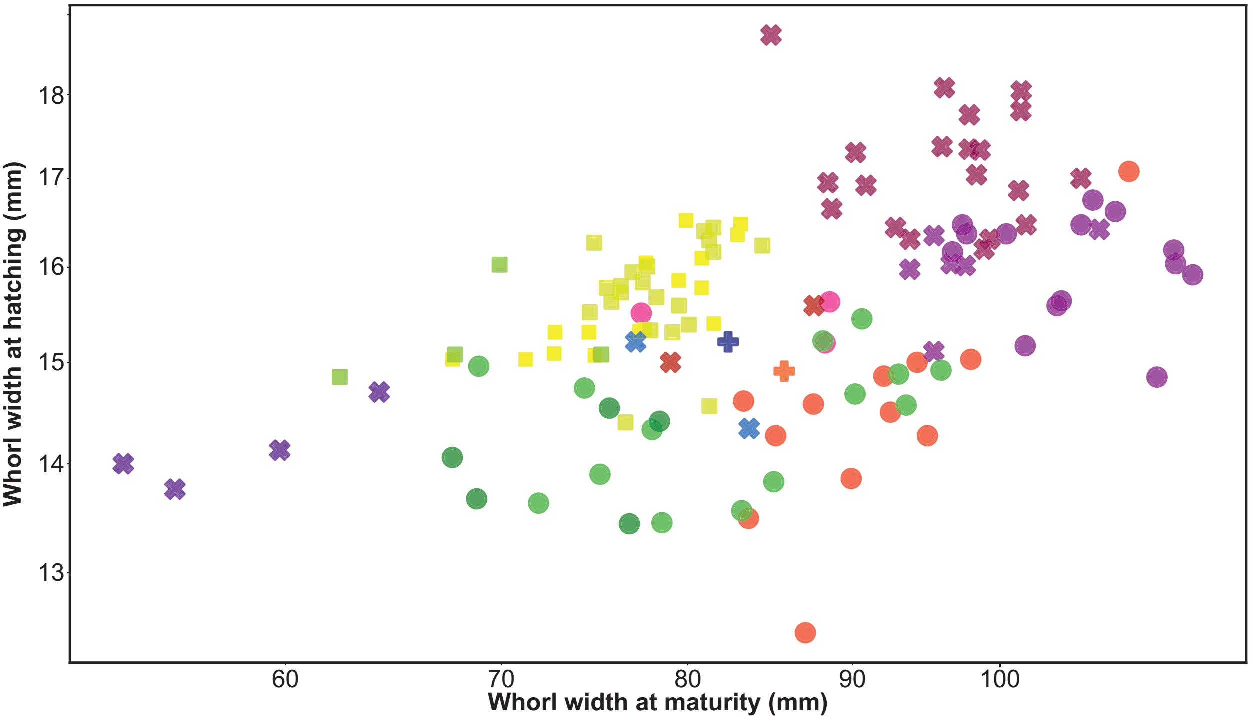


Fig. 4. Hatching size plotted against adult size in modern nautilids on logarithmic axes. A, conch diameter. B, whorl width.

pompilius. The value of the whorl width index is lower in *N. macromphalus* than in other species (Fig. 5B). Among conch parameters, the umbilical width index appears to be the best way to distinguish species. The value in *Allonautilus* is significantly higher than other groups, while the value in *N. macromphalus* is significantly lower than in other groups (Fig. 5C and Supplementary Table).

Table 2. Results of statistical tests of hatching size vs. adult size (conch diameter; mm) in modern nautilids.

Species	**Geographical region**	**Pearson's correlation coefficient**		**Reduced major axis regression**	
		p	**value**	**slope**	**intercept**
A. perforatus	Indonesia	—	—	—	—
A. scrobiculatus	Papua New Guinea	1.70E-04	0.8784	0.83516	-0.47037
	Solomon Islands	—	—	—	—
	Unknown	—	—	—	—
N. macromphalus	New Caledonia	0.0194	0.5598	0.93639	-0.61209
N. stenomphalus	Lizard Island, Australia	—	—	—	—
N. pompilius	Papua New Guinea	0.4316	0.2287	—	—
N. pompilius	Fiji	—	—	—	—
N. pompilius	Vanuatu	0.1972	0.2931	—	—
N. pompilius	Indonesia	0.4579	0.1628	—	—
N. pompilius	Malaysia	0.0548	0.3375	—	—
N. pompilius	Philippines	—	—	—	—
N. pompilius	Unknown	—	—	—	—
N. pompilius suluensis	Philippines	—	—	—	—
N. belauensis	Palau	0.5208	-0.1526	—	—
N. repertus	Western Australia	0.3616	0.2155	—	—
all modern species	all regions above	3.37E-10	0.4398	0.48079	0.35396

Table 3. Results of statistical test of hatching size vs. adult size (whorl width; mm) in modern nautilids.

Species	**Geographical region**	**Pearson's correlation coefficient**		**Reduced major axis regression**	
		P	**value**	**slope**	**intercept**
A. perforatus	Indonesia	—	—	—	—
A. scrobiculatus	Papua New Guinea	0.0071	0.7857	0.97375	-0.74666
	Solomon Islands	—	—	—	—
	Unknown	—	—	—	—
N. macromphalus	New Caledonia	2.28E-04	0.7956	0.5714	0.11563
N. stenomphalus	Lizard Island, Australia	—	—	—	—
N. pompilius	Papua New Guinea	0.1273	0.4276	—	—
N. pompilius	Fiji	—	—	—	—
N. pompilius	Vanuatu	0.3247	0.2259	—	—
N. pompilius	Indonesia	—	—	—	—
N. pompilius	Malaysia	—	—	—	—
N. pompilius	Philippines	—	—	—	—
N. pompilius	Unknown	—	—	—	—
N. pompilius suluensis	Philippines	—	—	—	—
N. belauensis	Palau	0.5427	-0.1447	—	—
N. repertus	Western Australia	0.8997	-0.301	—	—
all modern species	all regions above	1.49E-08	0.4799	0.47875	0.26674

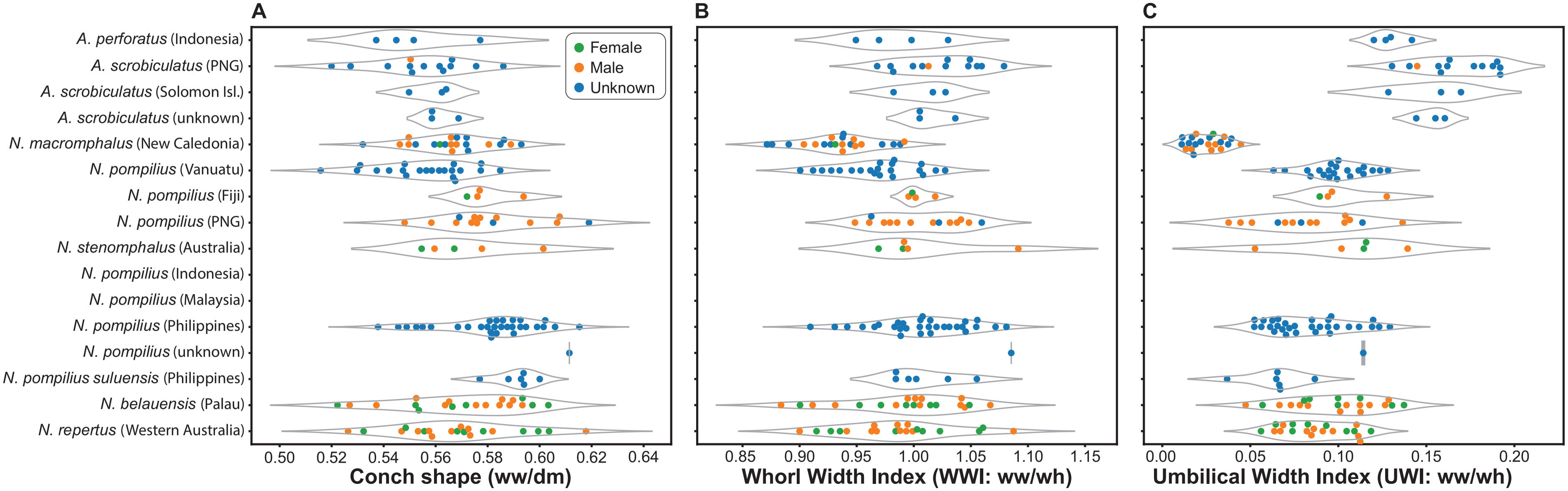


Fig. 5. Morphological parameters of modern nautilids at the point of hatching. A, conch shape (CS; whorl width / conch diameter). B, whorl width index (WWI; whorl width / whorl height). C, umbilical width index (UWI; umbilical width / whorl height).

Discussion

Potential biases and errors

Some potential biases and errors may have occurred during data acquisition and need to be taken into consideration when discussing the results. First, a certain degree of error occurs when estimating the body chamber length to detect the point of hatching. As mentioned in the methods section, we used 116° for body chamber length of all individuals, although the body chamber length varies to some extent (Fig. 2). This introduces some errors in the estimate of hatching size. As shown in Figure 2 and the Supplementary Table, the body chamber length ranges from 94° to 134°, resulting in a maximum possible error of approximately ±1 mm. Nevertheless, the histogram of body chamber length follows a normal distribution ($p < 0.01$), and therefore the maximum error does not occur frequently. Also, our data are nearly congruent with those reported by Arnold *et al.* (1987) and our results based on direct measurement, suggesting that the error is minimal.

Second, we included CT-scans with a relatively low resolution and contrast in our analysis, which also introduces some error. Specifically, the voxel size for the majority of CT-scans is < 100 μm, whereas it is approximately 300–500 μm for CT-scans for *Nautilus pompilius* from Indonesia and Malaysia, and some specimens from the Philippines (for details of these specimens, see Tajika *et al.* 2015; Tajika *et al.* 2018). Thus, we tested if the difference in scanning resolution results in significant errors using the CT-scans of the same specimen with a high and low resolution. Results reveal that the maximum error is ~1% (approximately < 0.3 mm). Therefore, we assume that the error does not significantly affect our interspecific comparison. We excluded CT-scans with low resolution from the analysis for whorl width and umbilical width due to low contrast. However, an error may occur even in highly resolved CT-scans when the contrast between the whorl at the point of hatching and the succeeding whorl is not sufficient. Nevertheless, we suppose that this error also is up to ~0.1 mm.

Morphology

Previous studies documented geometric constraints on the shape of the eggs in various organisms including both vertebrates and invertebrates. During evolution, eggs become wider with increasing size in some groups, while eggs become longer with increasing size in other groups (Kratochvíl & Frynta 2006; Bilder & Haigo 2012; Stoddard *et al.* 2017; Church *et al.* 2019). No data are available to directly compare eggs and hatchlings in nautilids. Nevertheless, discussing the shape of the embryonic shell/hatchling is meaningful as the hatching size is often used for estimating overall egg size (De Baets *et al.* 2012; Tajika *et al.* 2018). In addition, the morphology of the egg may be partially reflected in the overall shape of the embryonic shell. Therefore, we discuss whether the hatching size has an influence on shell morphology in modern nautilids. Additionally, we discuss whether the various species of nautilids can be distinguished.

As shown in the results section, the hatching size (conch diameter, whorl width index) overlaps among species (Fig. 3A, C). *Nautilus belauensis* is the only taxon that possesses a slightly larger hatching size than that of other species. The morphology of the hatchling in *N. belauensis* is highly variable, and the morphological parameters overlap those of other groups (CS, WWI; Fig. 5A, C). *N. pompilius suluensis* possesses a smaller hatching size than that of all other species. However, the morphology (CS, WWI) does not differ from that of other groups. The variation of morphological parameters in *N. pompilius suluensis* is also most likely underestimated due to the small sample size (n = 6). These results suggest that there is no clear relationship between hatching size and morphology (CS, WWI). The umbilical width index (UWI) is the only parameter that illustrates a more conspicuous pattern—*N. macromphalus* and the two species of *Allonautilus* (*A. perforatus* and *A. scrobiculatus*) separate out from the other groups. Considering that *N. macromphalus* and both species of *Allonautilus* are not distinguishable from other species in hatching size, this morphological difference cannot be explained by size. The difference in UWI more likely reflects the phylogenetic relationships among modern nautilid species (Vandepas *et al.* 2016; Combosch *et al.* 2017; Tajika *et al.* 2021a). The hatchlings of other nautilid species (*N. pompilius* from different geographic regions, *N. pompilius suluensis*, *N. belauensis*, *N. repertus*) cannot be easily separated based on the conch parameters CS, WWI, and UWI. This also holds true for the species of *Allonautilus* (*A. scrobiculatus* and *A. perforatus*). These results indicate that there are no morphological constraints on shell shape (conch shape, whorl width index, and umbilical width index) with respect to hatching size.

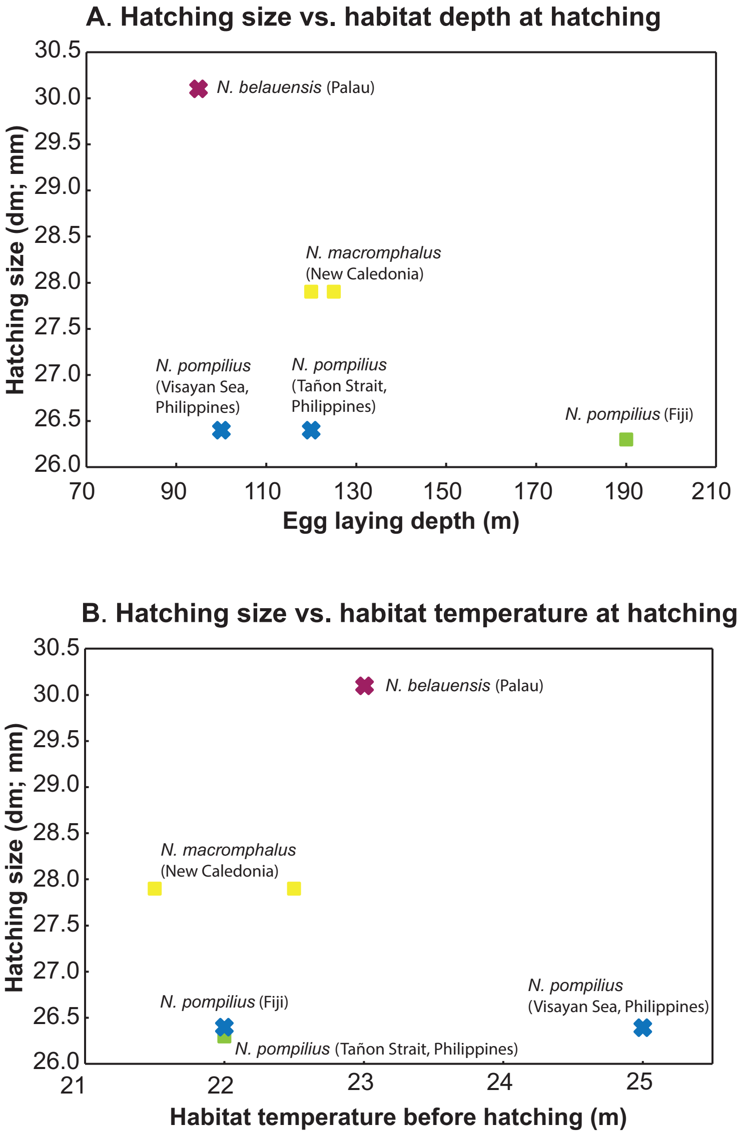
Phylogeny

Ibáñez *et al.* (2021) have examined egg length, body length, and fecundity in 90 modern cephalopod species that include two nautilid species (*N. pompilius* and *N. macromphalus*). They found that the egg length shows a highly significant phylogenetic signal. Our results show that hatching size in nautilids has a more complex pattern. When comparing the three allopatric clades (Coral Sea, Indo Pacific, and South Pacific), there is a statistical difference in hatching size between the Coral Sea clade and the other two clades. However, the Indo Pacific clade shows high variation that brackets the range of the Coral Sea and South Pacific clades. This suggests that the distribution of hatching size in nautilids may not have a clear phylogenetic signal unlike the pattern in coleoid cephalopods, as shown by Ibáñez *et al.* (2021). One reason may be rooted in the fact that the Indo Pacific clade has multiple species with a variety of hatching sizes including the two species with the largest and smallest hatching size (*Nautilus belauensis* and *N. pompilius suluensis*). This may support the hypothesis of an ongoing episode of diversification and speciation in *Nautilus* (Wray *et al.* 1995; Bonacum *et al.* 2011; Combosch *et al.* 2017). Further examination of egg size in combination with a molecular analysis of the same individuals may shed new light on the relationship between hatching size and phylogeny.

In fossil nautilids, different taxa in different times are known to exhibit different hatching sizes (e.g. Wani *et al.* 2011). However, such data are still limited and, thus, do not allow us to examine the phylogenetic influence on the hatching size. Furthermore, some species within a single genus are also known to exhibit different hatching sizes (e.g. *Eutrephoceras* from the Cretaceous Cichowolski *et al.* 2005; Wani *et al.* 2011; Landman *et al.* 2018). Nevertheless, only few data are available regarding the hatching size of contemporaneous nautilid species. At this point, we cannot conclude whether or not species in fossil nautilids possessed a species-specific pattern.

Temperature

In many modern coleoids, higher temperature at the time of embryonic development causes reduced hatching size (Gowland *et al.* 2002; Ibáñez *et al.* 2018). In addition, eggs laid in winter are significantly larger than those laid in summer (Arkhipkin *et al.* 2000). Regarding modern nautilids, details about the effects of temperature and water chemistry on egg size are still not clear. One approach to investigate the habitat and life history of nautilids is the analysis of stable carbon and oxygen isotopes ($\delta^{13}C$, $\delta^{18}O$) preserved in the shell. The value of $\delta^{18}O$ provides information on the temperature of the water in which the shell was formed, and thus is a useful tool to reconstruct the habitat of nautilids. Precise reconstruction of the habitat requires knowledge of the chemistry and temperature of the water column, which is often difficult to obtain. Only a few studies reconstructed the temperature of the habitat in nautilids using such information. Oba *et al.* (1992) examined *Nautilus pompilius* from Fiji and the Philippines together with data on the temperature and chemistry of the water column. They discovered a distinct difference in the temperature/habitat depth between the two geographic populations of *N. pompilius*. The depth at which *N. pompilius* from the Tañon Strait, Philippines, hatched was reconstructed as ~ 75 m (26 °C). The depth at which *N. pompilius* from Fiji hatched was reconstructed as ~350 m (15 °C), which seems unusually deep. Landman *et al.* (1994) stated that the values calculated by Oba *et al.* (1992) were based on ad hoc relationships to calculate temperature, which corresponded to neither aragonite nor calcite water equations. Accordingly, the temperature/habitat depth was recalculated by Landman *et al.* (1994) as ~120 m (22 °C) for *N. pompilius* from the Philippines and as ~190 m (22 °C) for *N. pompilius* from Fiji. Similarly, Tajika *et al.* (2021b) reconstructed the depth at which *N. macromphalus* from New Caledonia hatched using information on the temperature and chemistry of the water column. They concluded that *N. macromphalus* hatched at a depth of ~125 m (~21.5 °C). Although information on the temperature and chemistry of the water column is lacking (i.e., the value of $\delta^{18}O$ of seawater was only estimated), Landman *et al.* (1994) calculated the hatching depth/temperature in some other species: for *N. pompilius* from the Visayan Sea, Philippines, < 100 m (25 °C), for *N. belauensis* from Palau, 80–110 m (23 °C), and for *N. macromphalus*, 110–130 m (22–23 °C). We plotted hatching size against the mean values of habitat depth and temperature during embryonic development using these published data in Fig. 6. Results show that hatching size and habitat depth and temperature during embryonic development are not correlated ($p > 0.05$; Supplementary Table). These results suggest that the water temperature and depth at which individuals hatch are unrelated to hatching size. As mentioned, coleoids seem more sensitive to temperature during embryonic development (Arkhipkin *et al.* 2000; Ibáñez *et al.* 2018). This difference between nautilids and coleoids may be rooted in the difference in physiology, growth, and lifestyle such as habitat depth (Tajika *et al.* 2020a). Nevertheless, at this point little is known regarding other factors such as food availability and water chemistry that may affect the size of organisms. Also, available data for temperature (including the seasonal variation and change due to migration) are very scarce at present, and therefore it is difficult to draw conclusions.


A. Hatching size vs. habitat depth at hatching

B. Hatching size vs. habitat temperature at hatching

Fig. 6. Relationships between hatching size and habitat depth/temperature during embryonic development. A, hatching size vs. depth. B, hatching size vs temperature.

Temperature is also known to affect the period of embryonic development in modern coleoids (Pecl *et al.* 2004; Uriarte *et al.* 2012). Few data are available with regard to the duration of embryonic development versus temperature in nautilids. Okubo *et al.* (1995) published data on the temperature and duration of embryonic development in *Nautilus belauensis* from Palau that were reared in Shima Marineland. Two individuals hatched after 449 days and another individual hatched after 457 days at ~24.4 °C, although the temperature was kept at ~18.3 °C for the first few days/weeks. Uchiyama & Tanabe (1999) reported a range in the duration of embryonic development with different incubating temperatures for *N. macromphalus* from New Caledonia in the Toba Aquarium. One specimen hatched after 362 days at ~24 °C, whereas other specimens hatched between 265 and 316 days at a temperature of ~25 °C for the first 100 days and then at a gradually lowered temperature (21–24 °C). Landman *et al.* (1994) studied two specimens of *N. belauensis* in the Waikiki Aquarium and showed that the specimens hatched after 380 and 420 days, respectively at 22.2 °C. Contrary to coleoids, the relationship between temperature and duration of embryonic development in nautilids seems unclear with our current knowledge. Based on the above studies, however, it is possible that there is a difference in the duration of embryonic development between

N. macromphalus and *N. belauensis* (i.e., 265–362 days in *N. macromphalus* and 380–449 days in *N. belauensis*), although there is high intraspecific variation (up to 97 days). We assume that this difference in the duration of embryonic development is linked to their difference in hatching size. Namely, *N. belauensis* with a longer duration of embryonic development produced larger eggs. If this is the case, the relatively wide range of hatching size among modern nautilid species may reflect, at least partially, variation in the duration of embryonic development. Nevertheless, all the previously published data on the duration of embryonic development were produced using aquarium-reared individuals. It is likely that such individuals may not exhibit the same pattern as those in the wild. Further investigation is needed to better understand the relationship between the duration of embryonic development and hatching size.

The hatching size in fossil nautilids has sometimes been reported (e.g. Cichowolski 2003; Cichowolski *et al.* 2005; Wani *et al.* 2011; Landman *et al.* 2018; Tajika *et al.* 2020b). Because fossil nautilids had a worldwide distribution in the geological past (e.g. in the Cretaceous: Landman *et al.* 2014), it allows us to compare the hatching size from different climatic conditions. The hatching size (conch diameter) of late Campanian *Eutrephoceras nebrascensis* from the Western Interior Seaway (South Dakota, USA) is 10.1 mm (Landman *et al.* 2018). Stable oxygen isotopes ($\delta^{18}O$) of ammonite shells from the same strata indicate that the temperature in this area at this time was 19–26 °C (Landman *et al.* 2018), which indicates a temperate climate. Cichowolski *et al.* (2005) reported that the hatching sizes of Campanian *E. subplicatum* (later synonymized into *E. dorbignyanum* by Nielsen & Salazar 2011) and *E.* sp. from the James Ross Basin, Antarctica, are 20 mm and 32 mm, respectively. Stable oxygen isotopes ($\delta^{18}O$) of benthic foraminera and (nekto-) benthic molluscs indicate that the temperature in this region at the time was 4–8.5 °C and 13.6 °C according to Barrera *et al.* (1987) and Pirrie & Marshall (1990), respectively. These results suggest that species of *Eutrephoceras* may have larger hatching size in colder regions during the Campanian, although the assignment of *Eutrephoceras* for the species from Antarctica may be debated. Laptikhovski *et al.* (2013) compiled published data on nautiloids from the Paleozoic to Mesozoic and found a similar pattern: hatching size is larger in colder water. In contrast, Wani and Ayyasami (2009) reported a relatively large hatching size in *E. clementianum* (20 mm) from the Turonian of India. The exact temperature of this area during the Turonian is unclear, but it likely represents a temperate climate considering the paleolatitude. Thus, further study is needed to elucidate the pattern of hatching size in nautilids with regard to temperature.

Adult vs hatching size

The relationship between adult size and offspring size, and the ecological implication in various organisms are of great interest (Moles *et al.* 2005; Falster *et al.* 2008; Neuheimer *et al.* 2015). This topic has often been discussed in the context of trade-offs between the number of offspring (fecundity, reproductive rate) and probability of survival (Smith & Fretwell 1974). Ectocochleate cephalopods exhibit two distinctively different reproductive strategies. The extinct ammonoids are characterized by small eggs (approximately 0.5–3.0 mm), high fecundity, and, in many instances, very large adult body size (up to ~2 m; De Baets *et al.* 2012; Tajika *et al.* 2018). In contrast, modern nautilids are characterized by much larger eggs, lower fecundity, and moderate adult body size (up to 25 cm; Ward 1987; Arnold *et al.* 1989) and this strategy was already present in the Mesozoic nautilids (Wani 2011). Yet, little is known about the factors that control variation within a taxon. Our results reveal that: 1, modern nautilids show a pattern in which hatching size increases as adult size increases among species; and, 2, this pattern is not visible within a species (intraspecific variation) except in a few cases (*Nautilus macromphalus* and *Allonautilus scrobiculatus*). Assuming that hatching size reflects egg size, at least partially, the former pattern may be related to parental care strategies (Neuheimer *et al.* 2015). Larger adults can invest a higher amount of energy and resources in the production of eggs, which may result in larger offspring. Larger eggs with more yolk may help the embryos survive for a longer embryonic period on the substrate. Increased size of eggs may also increase the survivorship after hatching under food-impoverished conditions as in crustaceans (Gliwicz & Guisande 1992).

Predatory pressure may be another explanation for different adult and hatching sizes of modern nautilids, as documented in other organisms (Blumenshine *et al.* 2000; Palkovacs 2003; Saunders *et al.* 2010). Larger body size of hatchlings may have helped mitigate the risk of attacks from predators. Although frequent attacks on nautilids were reported in multiple geographic regions (Tanabe *et al.* 1988; Yomogida & Wani 2013), the data are insufficient to discuss the potential influence of predation on adult and hatchling size. As mentioned, the proportional relationship between hatching size and adult size is not apparent in most species of modern nautilids (Tables 2, 3). *Allonautilus scrobiculatus* and *Nautilus macromphalus* are the only taxa that show this relationship. As these two species are known to differ both morphologically and genetically from other *Nautilus* species (Vandepas *et al.* 2016; Combosch *et al.* 2017; Tajika *et al.* 2021a), the difference in hatching size-adult size strategy may be linked with phylogeny. The invariant relationship between hatching size and adult size may have only developed in *N. pompilius* and species closely related to it.

In the fossil record, only a few studies have investigated adult size and hatching size in nautilids (Matsumoto *et al.* 1984; Chirat & Rioult 1998; Cichowolski 2003; Wani & Ayyasami 2009; Tajika *et al.* 2020b). We plotted hatching size against adult size using published data (Fig. 7). We find that fossil nautilids show a proportional relationship between adult size and hatching size as in modern nautilids ($p < 0.01$; Supplementary Table). Landman (1987) found a similar pattern in the Late Cretaceous heteromorph ammonoid *Scaphites*. In his study, each of the two species *S. whitfieldi* and *S. larvaeformis* seems to show an invariant relationship between ammonitella diameter (hatching size) and adult phragmocone diameter. By contrast, ammonitella size and adult phragmocone size are positively correlated when comparing six species (*S. carlilensis*, *S. larvaeformis*, *S. preventricosus*, *S. warreni*, *S. whitfieldi*, and *Clioscaphites vermiformis*). Contrary to these results for ectocochleate cephalopods, Neuheimer *et al.* (2015) discovered no correlation between egg size and adult size (mass) in teuthid cephalopods. Furthermore, Ibáñez *et al.* (2021) examined 90 species (7 orders, 31 families) of cephalopods including data on two modern nautilid species and found no relationship between body length and egg length. We assume that the data on modern nautilids in the latter study are insufficient and thus, a nautilid-specific pattern was likely masked by the dominant pattern produced by coleoids. Identifying the reason for the different life history strategies between ectocochleate and coleoid cephalopods needs further investigation. Perhaps, it may be rooted in some constraints caused by the possession of a rather inflexible external conch. Identifying the exact constraints that determine the range of hatching size requires adequate information on ecology. Discovering nautilid eggs in the wild is key to improving our understanding of the reproductive strategy in modern nautilids. In turn, detailed knowledge of the life history of modern nautilids can help us better support the conservation efforts of this group (Broard 2015).

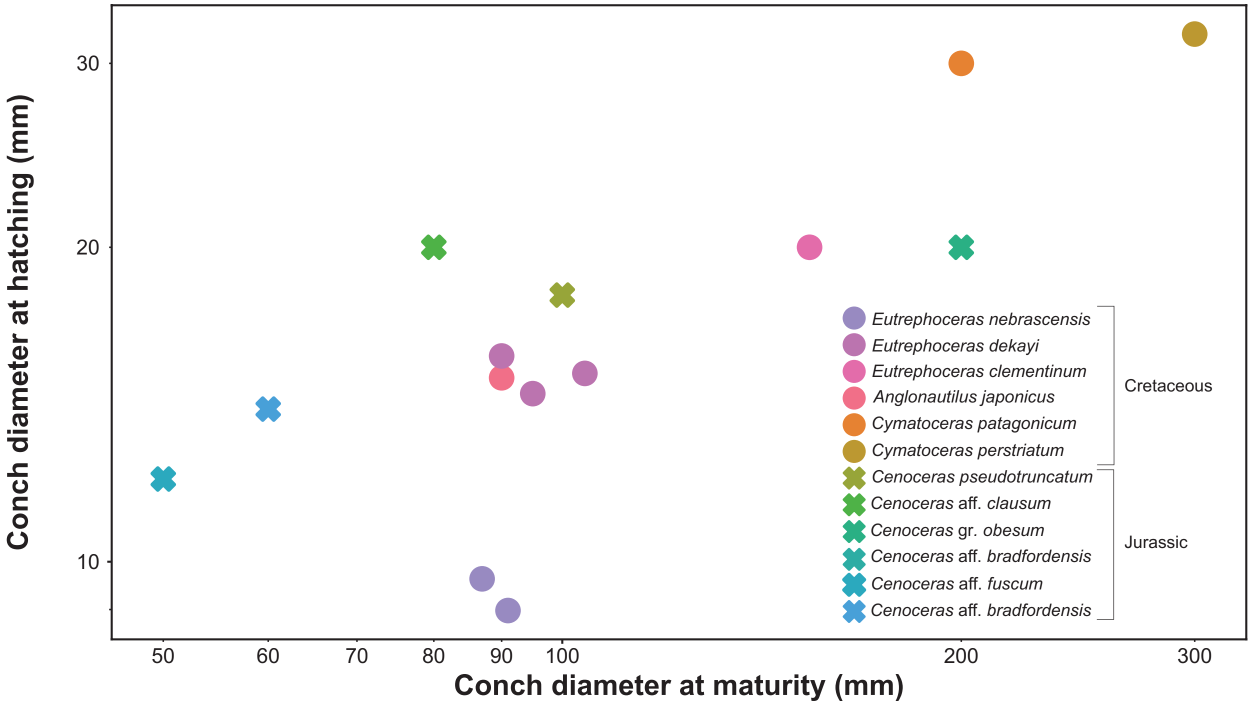


Fig. 7. Hatching size plotted against adult size (conch diameter) on logarithmic axes in fossil nautilids. Data are retrieved from Cichowolski (2003), Chirat & Rioult (1998), Matsumoto *et al.* (1984), and Wani & Ayyasami (2009).

Conclusions

We examined hatching size and its intra- and interspecific variation in all known species of modern nautilids. Summarizeing our discoveries:

1. The hatching size in modern nautilids ranges from 22 to 33 mm, which is consistent with previously published data. Intraspecific variation is reasonably high and the ranges often overlap among species. Hatching size is statistically larger in *Nautilus belauensis* than in other species, whereas hatching size is statistically smaller in *N. pompilius suluensis* than in other species. There is no clear difference in hatching size between males and females in the same species.
2. Hatching size and the morphological parameters conch shape (CS), whorl width index (WWI), and umbilical width index (UWI) at the time of hatching are not correlated. The species of *Allonautilus* (*A. scrobiculatus* and *A. perforatus*) and *N. macromphalus* can be distinguished from other nautilid species based on UWI. The species are nearly indistinguishable using CS and WWI.
3. When comparing hatching size and phylogeny, the distribution of hatching size does not seem to show a clear phylogenetic pattern. This may partially result from the larger Indo Pacific clade that includes species with a wider range of hatching size.
4. When comparing our results and previously published data on aquarium-reared specimens and stable oxygen isotopes, it seems that the hatching size in modern nautilids is not influenced by temperature. Variation in hatching size may be better explained by variation in the duration of embryonic development. The fossil record shows that more or less contemporaneous species of *Eutrephoceras* from temperate and cold climates have distinctively different hatching sizes.
5. Overall, hatching size increases as adult size increases in modern nautilids. This relationship also exists in fossil nautilids and, at least, in some ammonoids. However, this pattern is not common in modern nautilid species. A proportional relationship between hatching size and adult size is visible only in *N. macromphalus* and *A. scrobiculatus*, whereas other species show an invariant relationship. Although the exact reason is unclear, it may be rooted in parental caring strategies and/or predatory pressure. In some coleoids (e.g. teuthids), the relationship between egg size and adult size is invariant, suggesting that ectocochleate cephalopods may have a life history strategy different from coleoids.

Modern nautilids are considered as being endangered. Enhancing our knowledge on the various ecological aspects of nautilids is a key to supporting future conservation efforts. Further study is urgently needed.

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Supporting Information

Additional supporting information is available online in the Supporting Information section at the end of the article.

Supplementary Table. Raw data and results of statistical test.

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