

Research



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# Ecological pressures and the contrasting scaling of metabolism and body shape in coexisting taxa: cephalopods versus teleost fish

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Metabolic rates are fundamental to many biological processes, and commonly scale with body size with an exponent ( $b_R$ ) between 2/3 and 1 for reasons still debated. According to the 'metabolic-level boundaries hypothesis',  $b_R$  depends on the metabolic level ( $L_R$ ). We test this prediction and show that across cephalopod species intraspecific  $b_R$  correlates positively with not only  $L_R$  but also the scaling of body surface area with body mass. Cephalopod species with high  $L_R$  maintain near constant mass-specific metabolic rates, growth and probably inner-mantle surface area for exchange of respiratory gases or wastes throughout their lives. By contrast, teleost fish show a negative correlation between  $b_R$  and  $L_R$ . We hypothesize that this striking taxonomic difference arises because both resource supply and demand scale differently in fish and cephalopods, as a result of contrasting mortality and energetic pressures, likely related to different locomotion costs and predation pressure. Cephalopods with high  $L_R$  exhibit relatively steep scaling of growth, locomotion, and resource-exchange surface area, made possible by body-shape shifting. We suggest that differences in lifestyle, growth and body shape with changing water depth may be useful for predicting contrasting metabolic scaling for coexisting animals of similar sizes.

This article is part of the theme issue 'Physiological diversity, biodiversity patterns and global climate change: testing key hypotheses involving temperature and oxygen'.

## 1. Introduction

Metabolism is the biochemical transformation of material and energy from the environment into biological structure and functions and is therefore important for understanding ecological and physiological processes [1]. As aerobic respiration is the main contributor to metabolic energy production in heterotrophic organisms and is strongly related to body size [2,3], emphasis continues to be placed on quantifying and explaining the relationship between body mass ( $M$ ) and aerobic respiration rate ( $R$ ) [4,5]. This relationship is most commonly described as a power function,  $R = aM^{b_R}$  [5,6], where  $a$  is the scaling coefficient, and  $b_R$  is the scaling exponent that describes how respiration rate changes with body mass. The assertion of a universal value of  $b_R$ , and hence a scaling 'law' [7], has come under serious scrutiny owing to the growing evidence that  $b_R$  varies extensively both between and within species in relation to taxonomic affiliation, lifestyle, developmental stage, physiological state and ecological factors [8–12].

To help explain variation in metabolic scaling, the 'metabolic-level boundaries hypothesis' (MLBH) [3,12,13] proposes that  $b_R$  is affected by the relative

influence of surface area-related and volume-related metabolic processes. The relative influence of either of these processes is mediated by metabolic level ( $L_R$ ), as represented by the elevation of a metabolism–mass relationship [3,12], which can be estimated as the mass-specific metabolic rate at the geometric midpoint of a metabolic rate–body mass scaling relationship [12,14,15]. Specifically,  $b_R$  is predicted to vary inversely with  $L_R$  at resting or low routine levels [3,12,13]. According to the MLBH, the metabolic scaling of organisms with relatively high maintenance and routine activity costs is limited primarily by surface area-related fluxes of resources and wastes or by internal transport of resources to metabolizing cells. In such organisms, if size increases isomorphically (without changing shape), surface-dependent processes (e.g. material and heat exchange) cause  $b_R$  to approach 2/3 [16], or 3/4 when limitations of internal resource-distribution networks predominate [2,7]. By contrast, organisms with low maintenance costs meet metabolic demands amply by surface-related processes, and the influence of volume-related processes should increase, resulting in  $b_R$  approaching 1.

The MLBH is supported by observations across species of teleost fishes whose ontogenetic  $b_R$  values during rest or minimal routine activity are inversely related to  $L_R$ , which is in turn correlated with lifestyle and ambient temperature [15]. Fish species living at increasing oceanic depths, including pelagic, benthopelagic, benthic and bathypelagic lifestyles, exhibit decreasing  $L_R$  and increasing  $b_R$  [15]. Hence, the MLBH mechanistically links ecology with metabolic rates and metabolic scaling [3,11–13], as ecological and environmental factors that influence  $L_R$  can also help to explain variation in  $b_R$ .

However, besides surface area limitations proposed by the MLBH, whole-body metabolic demands at routine levels may also result in  $b_R$  values that approach 2/3 or 3/4. For instance, relatively low  $b_R$  values may occur when the body-size scaling of energy-expensive growth is non-isometric [6,17], thus suggesting that a decrease in mass-specific metabolic demand with size may also contribute to lower  $b_R$ . We will later discuss how specific metabolic demands (e.g. from growth) may help explain our observations of cephalopod metabolic scaling.

In pelagic invertebrates, metabolic rates typically decline with increasing water depth [18–20]. However, within a phylum (e.g. cnidarians, molluscs, arthropods and chordates), and in contrast to teleost fish, pelagic species often have higher intraspecific  $b_R$  values than those of related benthic counterparts [8,21]. Among cephalopods, epipelagic families tend to have higher inter- and intraspecific  $b_R$  values than deep-living families [8], which contrasts with the pattern observed in teleost fish. This difference in how ecological lifestyle influences  $b_R$  suggests that metabolic scaling might not vary in similar ways when comparing coexisting taxa in similar marine environments. However, to our knowledge, no published study has quantitatively investigated the effect of  $L_R$  on  $b_R$  among closely related marine invertebrate species within a taxonomic clade.

Variation in  $b_R$  among diverse pelagic invertebrates has been shown to correlate closely with body-shape change and surface area enlargement during growth [10,22]. In organisms that exchange materials across the external body surface (e.g. skin or cuticle—which can include partially internalized gills and inner-mantle surfaces), the correlation arises because body-shape change during ontogeny affects

the relative surface area. Changes in surface area, expressed as the scaling exponent of surface area in relation to body mass ( $b_A$ ), could influence body surface-related material exchange capacity required for metabolism.

As  $b_A$  is rarely quantified within species, body mass–length scaling exponents ( $b_L$ ) have been used to formulate Euclidean predictions of  $b_A$ , assuming constant mass–density [10,22–24]. The mass to length relationship is commonly described by  $M = xL^{b_L}$  where  $M$  is body mass,  $L$  is the length, often measured as the longest linear dimension of the body, and  $x$  and  $b_L$  are empirically determined constants. When shape remains constant during growth, then  $b_L = 3$  and the surface area should scale as  $M^{2/3}$  (and  $b_A = 2/3$ ), resulting in a predicted  $b_R$  of 2/3. However, relative elongation or flattening of the body shape during growth results in  $b_L$  values less than 3. At the extremes, pure elongation or pure flattening in body shape during growth results in  $b_L$  values of 1 or 2, respectively. In both cases, the surface area will scale as  $M^1$  [10]. As a result, body-shape changes during growth that result in  $b_L < 3$  will cause  $b_A$  to shift from 2/3 towards 1 [10]. If surface area affects metabolic supply capacity,  $b_R$  may predictably increase in the same way.

Many cephalopods have  $b_L$  values centred around 2.5 [23], implying non-isomorphic growth ( $b_A > 2/3$ ). Although cephalopods also use gills for exchange of respiratory  $O_2$  supply [25,26], more than 50% of  $O_2$  uptake in cephalopods may be cutaneous [26]. Hence, shape shifting potentially increases the scaling slope for resource supply capacity across the body surface above 2/3, which is likely the case in epipelagic squids [8,25]. A next step is therefore to test whether  $b_L$  and  $b_R$  covary among cephalopod species with different body plans and lifestyles. However, recent experimental work on physically constrained adult squid has questioned the importance of the outer mantle surface for respiration [27]. Later, we discuss the implications of those findings for interpreting our own results (see §4a).

Cephalopod species co-occur with fish from polar to tropical environments, at various depths including surface waters, bathypelagic and benthic habitats. However, despite their coexistence in similar habitats, cephalopods and fishes exhibit very different life histories. Many of the most active pelagic cephalopod species are semelparous, exhibit exponential mass increase over much of their short lifespans [28,29] and lack a distinct asymptotic growth phase [30,31]. By contrast, fishes are typically iteroparous, show an asymptotic von Bertalanffy growth trajectory [32] and generally live longer lives [33]. These and other biological differences between these taxa prompted us to compare their ontogenetic metabolic scaling relationships, particularly any differences in responses to metabolic level, activity demands, water temperature and depth, relevant life-history traits and ontogenetic changes in body shape.

Specifically, we collated literature data on cephalopods to test the MLBH and a growth-scaling prediction that the metabolic scaling exponent ( $b_R$ ) should correlate negatively with metabolic level ( $L_R$ ). Alternatively,  $b_R$  may positively covary with  $L_R$  if shape shifting (measured as reduced  $b_L$ ) correlates with increasing  $b_R$ . We further investigated whether  $L_R$ ,  $b_R$  and  $b_L$  show systematic differences among ecological lifestyles. Our study reveals a correlation between  $L_R$  and  $b_R$  that is associated with shape shifting and further compares and contrasts these results with those obtained previously for teleost fish [15].

## 2. Material and methods

### (a) Data collection

Cephalopod respiration–mass scaling exponents ( $b_R$  values) were obtained by searching the literature for ordinary least-squares (OLS) regressions of log-respiration rates versus log-body mass. Literature searches were carried out with Web of Science and Google Scholar using a range of search terms such as cephalopod + oxygen + consumption, cephalopod + respiration and [*<species or taxon name>*] + respiration. We also identified related studies from reference lists in relevant papers. All regressions were based on wet body mass, with the exception of one study where dry mass was used [34]. In this case, the dry mass was converted to wet mass (WM) using conversions described in the original study. Any  $b_R$  values in which the reported correlation coefficients ( $r$ ) were less than 0.8 were subsequently excluded from our analyses (electronic supplementary material, table S3), given the greater variability associated with lower correlation coefficients [10]. Additional screening criteria and the experimental conditions in each study included here are detailed in the electronic supplementary material, table S1.

The distinction between standard metabolic rates ( $R_{\text{standard}}$ ) and routine metabolic rates ( $R_{\text{routine}}$ ) arises because  $R_{\text{routine}}$  includes spontaneous movement in experimental chambers [15]. After temperature correction to 15°C using residuals from the Arrhenius plot (see §2b), we found no statistical difference between  $R_{\text{standard}}$  and  $R_{\text{routine}}$  values in either  $b_R$  or metabolic levels ( $L_R$ , unpaired  $t$ -tests,  $t = 0.833$ , d.f. = 9.031,  $p = 0.427$  for  $b_R$ ;  $t = 0.748$ , d.f. = 10.784,  $p = 0.471$  for  $L_R$ ) across all species and within or across lifestyles. Hence, we included both measurement types and conservatively refer to the respiration rates reported as  $R_{\text{routine}}$ , as spontaneous activity during the experiments was possible [8]. Variation in spontaneous activity levels during measurement may therefore contribute to differences in  $L_R$ .

Mass–length exponents ( $b_L$  values) were obtained from published OLS regressions between the WM and dorsal mantle length of cephalopods. WM was chosen for determining  $b_L$  for two reasons: (i)  $b_L$  values from WM come closer to representing volume–length relationships than other mass units, and will therefore better capture body-shape changes; and (ii) WM matches the units used to determine respiration rate to mass relationships, which improves comparability. Some of the values were previously compiled in the dataset of Hirst *et al.* [10]. Additional values were obtained from the literature using Web of Science and Google Scholar, adopting search terms including cephalopod + length + weight, [*<species or taxon name>*] + length + mass, squid + length + mass, and from personal communications with authors. Following the screening criterion for  $b_R$  values, we excluded regressions between mass and length with reported correlation coefficients less than 0.8 (electronic supplementary material, table S4). When multiple  $b_R$  and  $b_L$  values were available for a single species, we determined arithmetic means of each of these values to avoid over-representation of more commonly measured species and to improve the accuracy of the parameter assessment. For lifestyle comparisons, we categorized cephalopods into a pelagic, benthopelagic, benthic or bathypelagic lifestyle (see electronic supplementary material for categorization details). As species may undergo ontogenetic depth migrations or exhibit lifestyle transitions between life stages, our lifestyle classification, based on readily available data and descriptions, is simplistic. Although ontogenetic variation may obscure some lifestyle differences, our classification is still useful for identifying broad patterns and making comparisons with fish [15].

### (b) Data analysis

All respiration rates ( $R$ ) were converted to  $\mu\text{l O}_2 \text{ind}^{-1} \text{h}^{-1}$  for comparability. Metabolic level ( $L_R$ ,  $\mu\text{l O}_2 \text{gWM}^{-1} \text{h}^{-1}$ ) was defined as the mass-specific respiration rate at the geometric

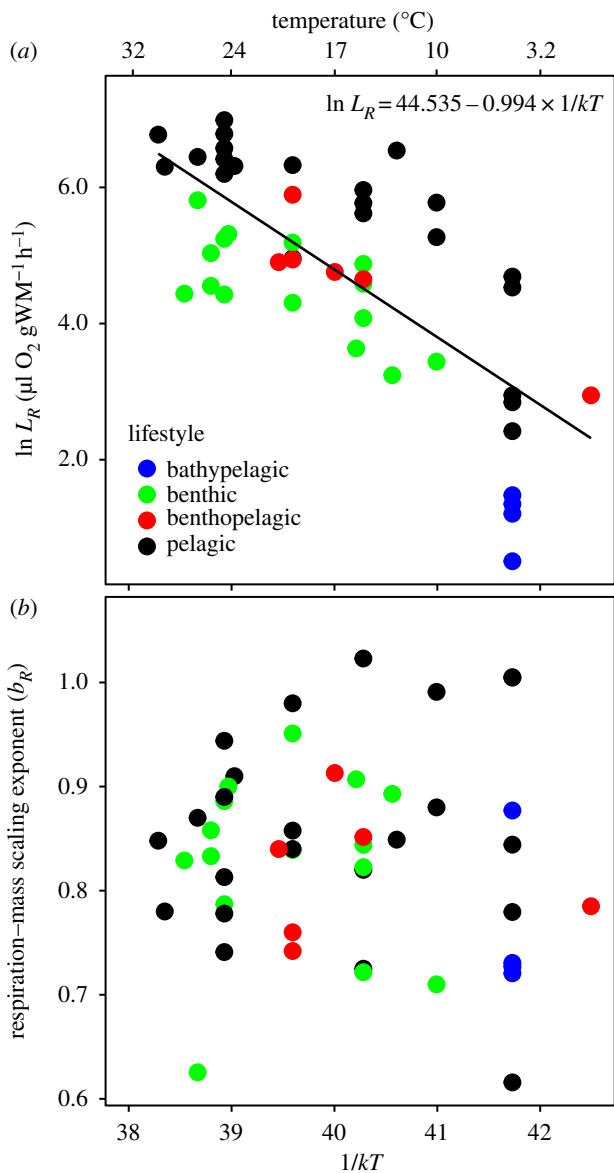
midpoint of the body mass range of the respiration–mass relationship [12,15]. As the scaling coefficient  $a$  and the scaling exponent ( $b_R$ ) are not independent of each other, the use of  $L_R$  to represent metabolic level avoids this problem and is more appropriate [12,14,35].

Statistical analyses were performed using the statistical software package R. The level of significance was set at  $p \leq 0.05$  for all tests. OLS regression was performed to investigate the relationships between  $\ln L_R$  and  $1/kT$ , and between  $b_R$  and  $1/kT$ , where  $T$  is the temperature in Kelvin and  $k$  is the Boltzmann constant ( $8.62 \times 10^{-5} \text{ eV K}^{-1}$ ). Reduced major axis (RMA) regressions were performed with the RMA software version 1.21 [36] to investigate the relationships between  $b_R$  and  $\ln L_R$ , and between  $b_R$  and  $1/b_L$  in the non-benthic cephalopods. Benthic octopuses were excluded because these typically have less permeable body surfaces and are more reliant upon gills for respiratory gas exchange, as compared to pelagic cephalopods [37,38]. RMA regressions were used, as these do not rely on definite dependent and independent variables, and  $\ln L_R$ ,  $b_R$  and  $b_L$  are likely measured with a similar error. The analysis was repeated with phylogenetic generalized least-squares (PGLS) to control for phylogenetic non-independence. We compiled a tree based on published phylogenies (see electronic supplementary material, S1 and figure S1). In both PGLS regressions,  $\lambda$  was not significantly different from 0 ( $p = 1$  and  $p = 0.629$ ), but significantly different from 1 ( $p < 0.0001$  and  $p = 0.003$ ), indicating that the residuals of the model had a weak phylogenetic signal. With the additional phylogenetic correction, the relationship between  $b_R$  and  $1/b_L$  is marginally insignificant ( $p = 0.054$ ), but the result of the relationship between  $b_R$  and  $\ln L_R$  is not altered. As the PGLS regressions produced very similar conclusions, we report only the results of the RMA regressions.

Linear mixed effects models (LME) using the package ‘lme4’ were constructed to investigate the effect of lifestyle on  $\ln L_R$  and  $b_R$ , with these as dependent variables, and lifestyle, temperature and the interaction between lifestyle and temperature as fixed variables. Taxonomy (order, family and species) was included as a nested (hierarchical) random effect, as species share evolutionary histories and are not completely statistically independent. This phylogenetically informed method was used instead of phylogenetic contrasts [39] because the phylogenetic relationships among higher cephalopod taxa are still unresolved [40]. For additional comparisons of lifestyle effects on  $\ln L_R$  without the influence of measurement temperature, the residuals of the Arrhenius plots for  $L_R$  were expressed relative to the fitted equation value at 15°C to standardize  $L_R$  to 15°C (following [15]). To investigate the effect of lifestyle on  $b_L$ , we used  $b_L$  as a dependent variable, lifestyle as a fixed variable and taxonomy as a nested random effect in an LME model. We compared LME models with linear models without taxonomy as a random effect to determine the importance of taxonomic differences. We used the AICc function in the ‘MuMIn’ package for model comparisons, and we regarded the best model as the one with the lowest AIC (AICc) score, corrected for small samples. We estimated  $p$ -values of LME models using the Satterthwaite approximation in the ‘lmerTest’ package. We also carried out multiple pairwise comparisons between lifestyles using the ‘multcomp’ package, with Bonferroni adjustments to  $p$ -values. PGLS was carried out with the ‘caper’ package.

## 3. Results

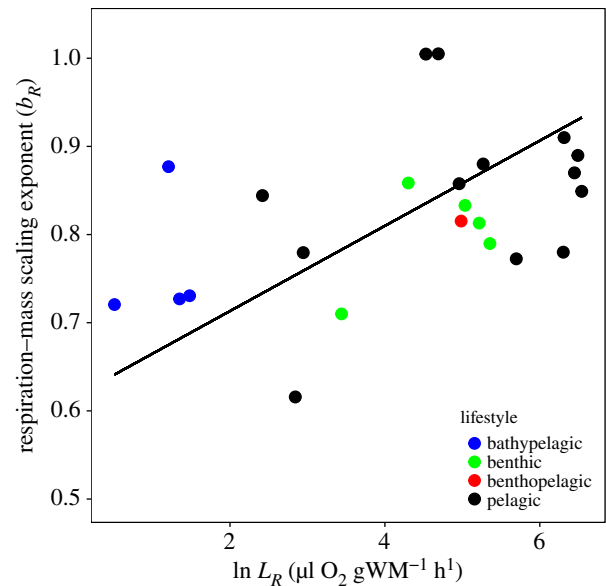
Metabolic exponents,  $b_R$ , ranged from 0.616 to 1.005 (mean =  $0.824 \pm 0.019$  s.e.) among all 24 sampled cephalopod species. Cephalopod body mass ranged over six orders of magnitude, from 0.01 gWM to 12 200 gWM, which was also the mass range for the largest species, *Dosidicus gigas*. Measurement temperature affected metabolic level (as  $\ln L_R$ , figure 1a) with an



**Figure 1.** Arrhenius plots between (a) metabolic level as  $\ln L_R$  and  $1/kT$  ( $r^2 = 0.528$ ,  $p < 0.0001$ ,  $n = 47$ ), and (b) metabolic scaling exponent  $b_R$  and  $1/kT$  ( $r^2 = 0.003$ ,  $p = 0.716$ ,  $n = 48$ ), where  $T$  is the measurement temperature in Kelvin and  $k$  is the Boltzmann constant ( $8.62 \times 10^{-5}$  eV  $K^{-1}$ ). Four ecological lifestyles are colour-coded.

Arrhenius activation energy of  $0.994$  eV ( $\pm 0.14$  s.e.). However, there was no significant relationship between measurement temperature and  $b_R$  (figure 1b). Without temperature correction,  $L_R$  across 23 species varied 417-fold, from  $1.66$  to  $693.07$   $\mu\text{l O}_2 \text{ gWM}^{-1} \text{ h}^{-1}$ . For one species,  $L_R$  could not be calculated, as the mass range for the scaling relationship was not reported.

We found a significant positive relationship between  $b_R$  and  $\ln L_R$  among all sampled species (figure 2,  $r^2 = 0.194$ ,  $p = 0.035$ ). As  $L_R$  values increased 417-fold,  $b_R$  increased approximately 1.5 times, from  $0.64$  to  $0.93$ . We also found a significant positive relationship between  $b_R$  and  $1/b_L$  (figure 3a,  $r^2 = 0.392$ ,  $p = 0.030$ ), and therefore a positive body mass scaling relationship between metabolic rate and body shape, across the 12 non-benthic cephalopod species for which we had both  $b_L$  and  $b_R$  values. The 95% confidence interval of this RMA regression slope (slope =  $1.437$ , 95% CI:  $0.647, 2.227$ ) was significantly different from the lower boundary slope (slope =  $0.5$ ) that predicted metabolic scaling based on different degrees of body elongation. However, it was not



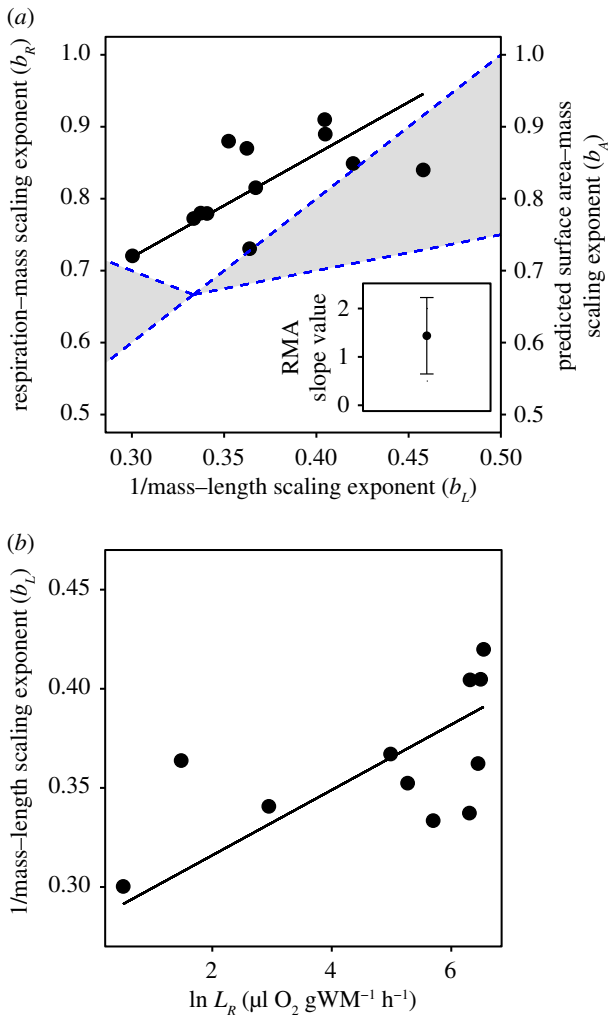
**Figure 2.** Reduced major axis (RMA) regression comparing metabolic scaling exponent  $b_R$  and metabolic level as  $\ln L_R$  for 23 cephalopod species in this study. All  $L_R$  values are without temperature corrections. [RMA regression,  $r^2 = 0.194$ ,  $p = 0.035$ ,  $b_R = 0.617$  (95% CI:  $0.525, 0.708$ ) +  $0.048$  (95% CI:  $0.029, 0.068$ )  $\times \ln L_R$ ]. Four ecological lifestyles are colour-coded.

significantly different from the upper boundary slope (slope =  $2$ ) that predicted metabolic scaling from body-shape flattening only. In non-benthic cephalopods, the relationship between  $\ln L_R$  and  $b_L$  was also significant (figure 3b,  $r^2 = 0.367$ ,  $p = 0.048$ ). An additional screening step that excluded  $b_R$  values for regressions when the mass range covered less than one order of magnitude, or was not reported, excluded two species and one family, and did not significantly alter the results (electronic supplementary material).

Metabolic level (as  $\ln L_R$ ) differed between lifestyles (figure 4a). The best model describing variation in  $\ln L_R$ , which had the lowest AICc score, incorporated lifestyle as a factor and temperature as a covariate, but not the interaction term between lifestyle and temperature. This indicates that the positive effect of temperature on  $L_R$  is similar across lifestyles. Both lifestyle ( $p = 0.001$ ) and temperature ( $p < 0.0001$ ) had significant effects on  $\ln L_R$ , even when taxonomy was included as a random effect. In general,  $\ln L_R$  decreased across pelagic, benthopelagic, benthic and bathypelagic lifestyles. Mean  $L_R$  was lowest in bathypelagic species ( $3.31 \pm 0.59$   $\mu\text{l O}_2 \text{ gWM}^{-1} \text{ h}^{-1}$ , s.e.), which was significantly lower than that for the other three lifestyles (figure 4a, versus benthic:  $p = 0.006$ ; versus benthopelagic  $p = 0.006$ ; versus pelagic:  $p < 0.0001$ ). At the extreme, mean  $L_R$  observed in bathypelagic species was less than 1/100th of the mean value for pelagic species ( $433.59 \pm 64.76$   $\mu\text{l O}_2 \text{ gWM}^{-1} \text{ h}^{-1}$ , s.e.). However, mean  $\ln L_R$  did not differ significantly between pelagic and benthopelagic species ( $p > 0.9$ ), nor between pelagic and benthic species ( $p > 0.9$ ). Pelagic species had a significantly higher mean  $\ln L_R$  ( $266.63 \pm 45.43$   $\mu\text{l O}_2 \text{ gWM}^{-1} \text{ h}^{-1}$ , s.e.) than that of benthic species ( $54.31 \pm 8.31$   $\mu\text{l O}_2 \text{ gWM}^{-1} \text{ h}^{-1}$ , s.e.) when  $\ln L_R$  was corrected to a common temperature of  $15^\circ\text{C}$  ( $p = 0.005$ ).

We found no significant lifestyle ( $p = 0.19$ ) or temperature ( $p = 0.74$ ) effect on  $b_R$ . However, mean  $b_R$  values decreased across pelagic (mean  $b_R = 0.860 \pm 0.021$ , s.e.), benthic ( $0.827 \pm 0.022$ , s.e.), benthopelagic ( $0.815 \pm 0.026$ , s.e.) and bathypelagic ( $0.764 \pm 0.038$ , s.e.) species (figure 4b).





**Figure 3.** Relationships between metabolic scaling exponent ( $b_R$ ) and the inverse of the mass-length scaling exponent ( $1/b_L$ ), and between  $1/b_L$  and metabolic level as  $\ln L_R$ . (a) RMA regression comparing  $b_R$  and  $1/b_L$  for non-benthic cephalopod species [RMA regression,  $r^2 = 0.392$ ,  $p = 0.030$ ,  $b_R = 0.287$  (95% CIs:  $-0.007$ ,  $0.582$ ) +  $1.437$  (95% CIs:  $0.647$ ,  $2.227$ )  $\times 1/b_L$ ]. The blue dashed lines enclose the prediction envelope for the surface area to mass scaling powers ( $b_A$ ) based on  $b_L$  values from the Euclidean model from [10]. The inset shows the slope ( $\pm 95\%$  CI) of the RMA regression between  $b_R$  and  $1/b_L$ , and the slopes for the lower [ $b_A = 0.5 + 0.5(1/b_L)$ ] and upper [ $b_A = 2 \times (1/b_L)$ ] boundaries of the prediction envelope. (b) RMA regression comparing  $1/b_L$  and  $\ln L_R$  for non-benthic cephalopod species [ $r^2 = 0.367$ ,  $p = 0.048$ ,  $1/b_L = 0.283$  (95% CIs:  $0.231$ ,  $0.335$ ) +  $0.016$  (95% CIs:  $0.007$ ,  $0.026$ )  $\times \ln L_R$ ].

Across 60 species, lifestyle appeared to have an effect on the scaling of body shape, measured as  $b_L$ , although this was not statistically significant (figure 4c,  $p = 0.078$ ). We found no significant pairwise differences between  $b_L$  values among lifestyles following a Bonferroni correction for multiple comparisons.

## 4. Discussion

Across a diverse range of cephalopod species with differing lifestyles, the ontogenetic body mass scaling exponent for respiration ( $b_R$ ) correlates positively with metabolic level ( $L_R$ , figure 2). This positive relationship contrasts with the negative relationship observed among teleost fish (figure 5; [15]), despite both taxa having broadly overlapping body-size

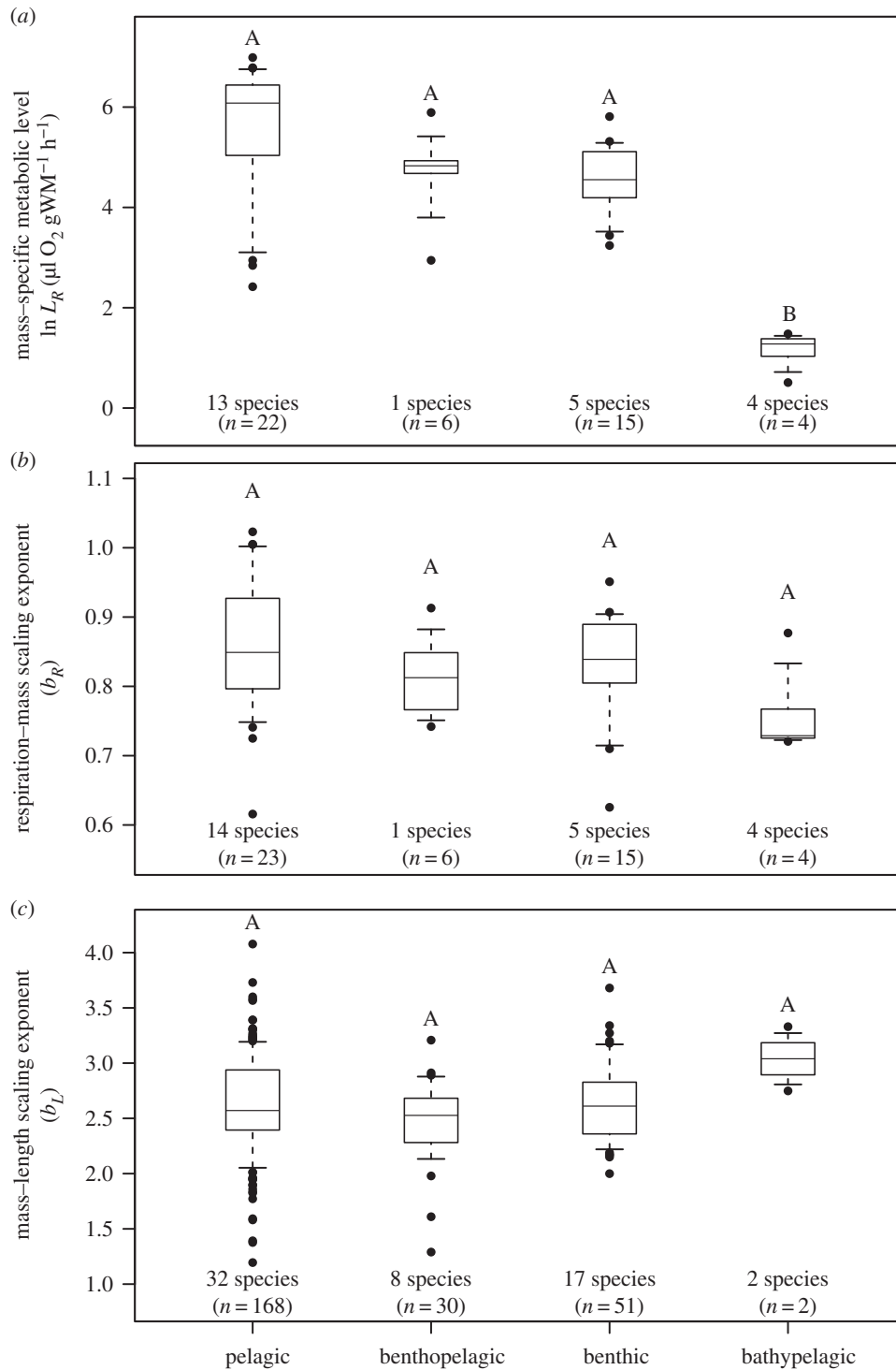
ranges and co-occurring in the same habitats. Moreover, across the non-benthic cephalopods,  $b_R$  correlates positively with increasing body-shape elongation or flattening, and hence increased relative surface area (as quantified by  $1/b_L$ , figure 3). Indeed, the RMA slope relating  $b_R$  with  $1/b_L$  is statistically indistinguishable from predictions of a Euclidean body surface area model based on body-shape flattening. This relationship with body shape reinforces existing evidence that across a diverse taxonomic range of open water invertebrates that use cutaneous exchange of respiratory gases, nutrients and (or) metabolic wastes, the body mass scaling exponents for rates of metabolism (including both respiration and soluble nitrogen excretion) are correlated with shape change and associated surface area enlargement [10,22,41].

We present two explanations for the contrasting relationships between  $b_R$  and  $L_R$  observed among fish and cephalopods. First, the MLBH predicts that at rest or during routine activity, as metabolic level increases across species,  $b_R$  should become increasingly influenced by surface- rather than volume-dependent processes. Increased influence of surface-dependent process would lead to a negative correlation between  $b_R$  and  $L_R$  among species in which surface area for resource or waste exchange (e.g. gills) typically scales hypoallometrically with body mass, as is observed in teleost fish [15]. However, if the scaling of surface area for exchange of resources or wastes is not isomorphic, and high-energy species display steeper scaling of this surface area, a positive correlation between  $b_R$  and  $L_R$  may arise, as is observed in cephalopods. Body-shape shifting in cephalopods may allow  $b_A$  to increase in high  $L_R$  species, thus permitting the steeper scaling of whole-body metabolic demand resulting from ecologically favoured, elevated levels of sustained activity or growth, or both, to exert a greater influence on  $b_R$ , as predicted by the MLBH.

Second, an alternative or complementary explanation for the contrasting metabolic scaling relationships between teleosts and cephalopods emerges from focusing only on the scaling of whole-body metabolic demands, specifically growth demands with body mass at routine levels. As overhead costs of growth contribute strongly to metabolic rate, even at resting levels [42,43], a decrease in mass-specific growth demand with size may also contribute to lower  $b_R$  (the ‘growth-scaling’ hypothesis). In species such as teleost fish whose specific growth rate declines during ontogeny, fast-growing species will have a high proportion of metabolism determined by growth costs, and hence be predicted to have a low resting or routine metabolic scaling exponent, compared with animals with slower growth throughout ontogeny. However, if growth is rapid and sustained throughout ontogeny, as is observed in epipelagic cephalopod species [30,31],  $b_R$  should also be high, as we have observed. Many studies of diverse animals have also shown similar effects of exponential growth on  $b_R$ , as reviewed in [3,11]. We next discuss how life-history differences between cephalopods and teleosts at different habitat depths may, at least in part, explain the contrasting  $b_R$  and  $L_R$  correlations found (figure 6).

### (a) Life history and energetic contrasts within well-lit waters

Metabolic level ( $L_R$ ) is significantly affected by temperature and lifestyle (figures 1a and 4a) and generally declines with increasing depth in many taxa (cephalopods [19], crustaceans

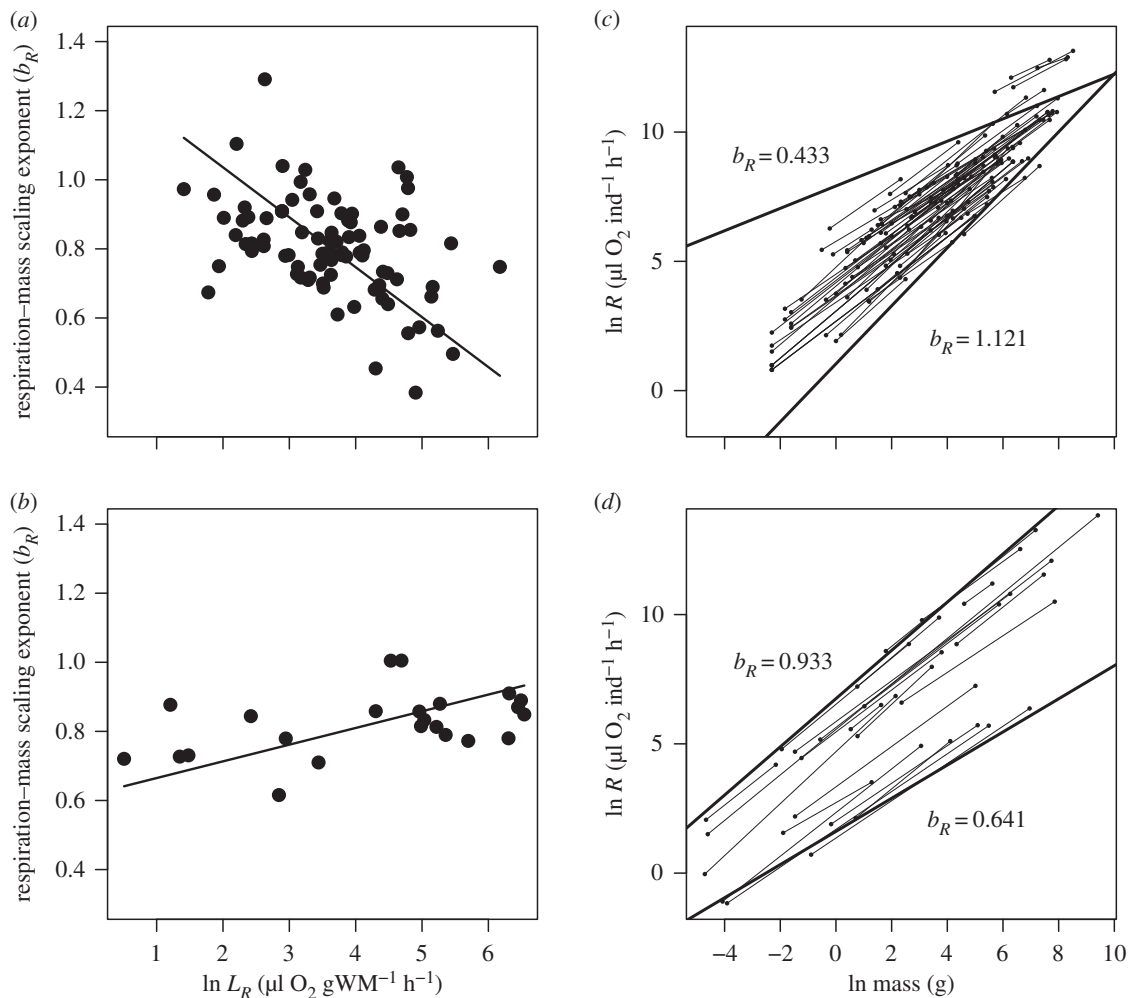


**Figure 4.** The effect of lifestyle on the metabolic level as (a)  $\ln L_R$  (23 species,  $n = 47$ ), (b) metabolic scaling exponent  $b_R$  (24 species,  $n = 48$ ) and (c) mass-length scaling exponent  $b_L$  (59 species,  $n = 251$ ). The lower and upper edges of the boxes represent the 25th and 75th percentiles, respectively, and the black lines within the boxes represent the median. The error bars extend to the 10th and 90th percentiles. Values beyond the 10th and 90th percentiles are indicated as individual points. Different letters indicate significant differences between the lifestyles ( $p \leq 0.05$  after Bonferroni adjustment for multiple comparisons).

[18] and teleost fish [15]). Pelagic, benthopelagic and benthic cephalopods have significantly higher metabolic levels ( $\ln L_R$ ) than bathypelagic cephalopods. The similar metabolic levels ( $\ln L_R$ ) of pelagic and benthopelagic cephalopods may relate to the well-lit pelagic and neritic (near shore) environments that they inhabit.

For both cephalopods and teleosts in well-lit waters, visual predation and feeding interactions are likely important and are associated with rapid locomotion [19,44], rates of growth and metabolism (or metabolic level). The relatively steep metabolic scaling observed in many of the most active pelagic

cephalopod species is likely associated with exponential mass increases throughout ontogeny, including during adulthood [28,30,45]. Although a general growth model for cephalopods remains elusive [31], many shallow water species commonly achieve exponential growth [30,31], which contrasts starkly with the systematic decline in mass-specific growth rate over ontogeny as seen in the von Bertalanffy growth trajectories of most fish species [32]. Hence, the growth-scaling hypothesis predicts that growth demands will affect metabolic scaling in cephalopods and teleost fish differently because of their different growth patterns (figure 6).

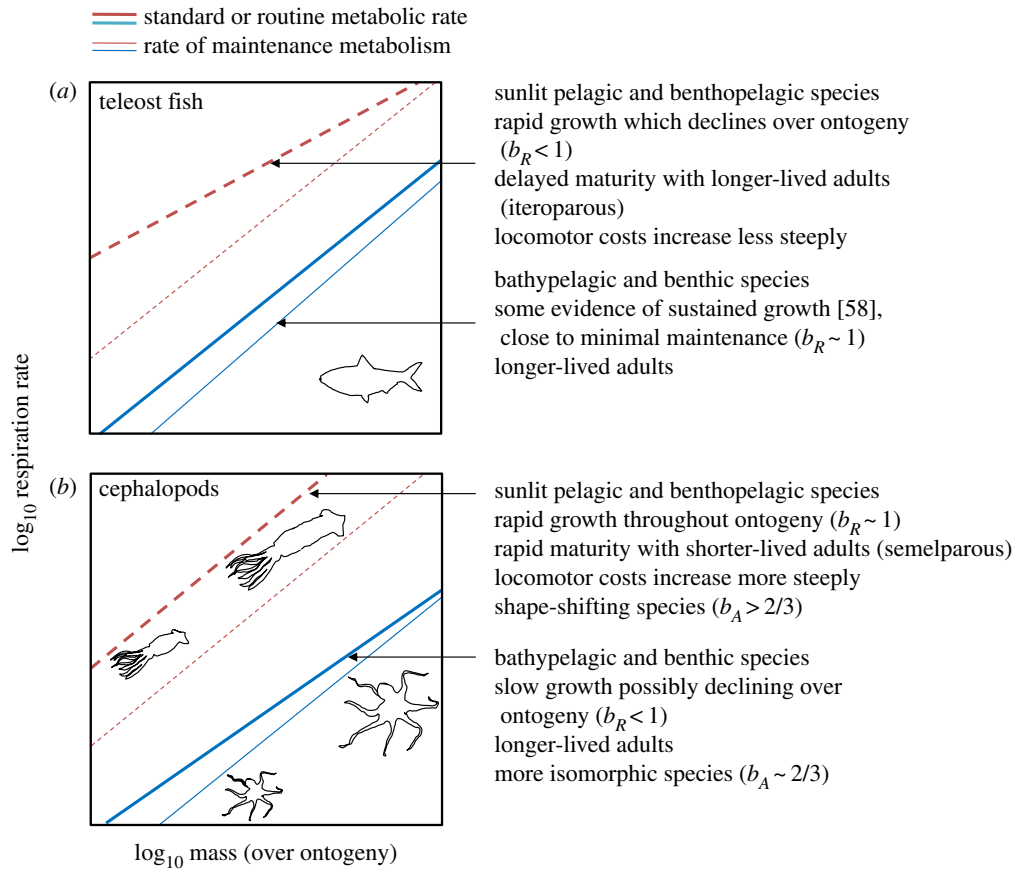


**Figure 5.** Comparisons of intraspecific body mass scaling of respiration (metabolic rates) ( $R$ ) among teleost fish and cephalopod species. (a) RMA regression between metabolic scaling exponent  $b_R$  and metabolic level as  $\ln L_R$  for 89 fish species (without temperature correction) obtained from [15], [ $r^2 = 0.18$ ,  $p < 0.0001$ ,  $b_R = 1.325$  (95% CIs: 1.221, 1.429)  $-0.145$  (95% CIs:  $-0.173$ ,  $-0.117$ )  $\times \ln L_R$ ]. (b) RMA regression between  $b_R$  and  $\ln L_R$  values for 23 cephalopod species (without temperature correction) obtained from our study [RMA regression,  $r^2 = 0.194$ ,  $p = 0.035$ ,  $b_R = 0.617$  (95% CI: 0.525, 0.708)  $+ 0.048$  (95% CI: 0.029, 0.068)]. (c) Intraspecific relationships between  $\ln R$  and WM ( $\ln WM$ ) for fish species, as previously compiled [15]. (d) Intraspecific relationships between  $\ln R$  and  $\ln WM$  for cephalopod species, as compiled in our study. For species with multiple  $b_R$  values based on multiple mass ranges, we took the average minimum and maximum masses as the mass range shown here (refer to electronic supplementary material). The thick black lines in (c,d) illustrate the approximate upper and lower boundaries for the scaling relationships between respiration rate and body mass of fish and cephalopods, respectively. We predicted these boundaries by applying values obtained from the minimum and maximum  $\ln L_R$  values obtained of the regression equations in (a,b), and their corresponding  $b_R$  values, to an animal of 21.65 g WM, which is the approximate mid-size value of the mass range reported.

In epipelagic cephalopods, sustained rapid growth is likely related to semelparity and short lifespans (less than 2 years) [3,21,29,31], whereas many fish species tend to have longer adult lifespans and are iteroparous [33]. For instance, the largest epipelagic cephalopod in our study, *D. gigas*, lives up to 2 years [46]. In stark contrast, relatively small clupeiformes (e.g. anchovies, herrings and sardines) mature at approximately 2 years old and live for a total of approximately 8 years, on average [33]. High predation in the pelagic environment may also favour continuously high levels of activity and thus locomotor energetic costs [21,29,47] that scale steeply with body mass (e.g.  $M^{0.8}$ , [29]). Hence, growing in size results in active squids receiving smaller mass-specific savings in locomotor costs than do fish, whose locomotor costs scale less steeply as  $M^{0.7}$  [48]. Consequently, squids may require high  $b_R$  and  $L_R$  to support high activity at all sizes and to sustain near constant mass-specific growth rates throughout life [11,21]. Higher resting or routine metabolic rates (and  $b_R$ ) may reflect higher growth rates even if short-term experimental conditions

during respiration measurements include starvation. Thus, in sunlit waters, differences in adult lifespan and reproductive intensity favouring different growth trajectories (exponential versus asymptotic), along with different scaling of locomotor costs, may influence the size scaling of metabolic demands and account for contrasting metabolic scaling between cephalopods and teleost fish (figure 6).

Moreover, we have shown that relatively steep metabolic scaling in the more active cephalopods is associated with enhanced body-shape shifting that permits greater surface area enlargement for cutaneous resource uptake and waste elimination. Further, we argue that this interpretation of our findings is not contradicted by the observed negligible contribution to respiration from the outer mantle surface in restrained adults of two squid species [27], as those experiments did not account for how body-shape shifting would still increase the respiratory surface area directly in contact with seawater within the mantle and potentially permit elongation of gills [27]. Lack of ventilation in the experimentally restrained adults may also reduce cutaneous respiration.



**Figure 6.** A proposed scheme to account for contrasting metabolic scaling across species of teleost fishes (a) and cephalopods (b). Red (dashed) lines depict metabolism in the sunlit pelagic and bathypelagic, and blue (solid) lines represent bathypelagic and benthic. Thick lines represent allometric relationships between standard or routine metabolic rates and body mass; thin lines represent maintenance metabolism (i.e. excluding overhead costs of growth and, for routine metabolism, excluding costs of locomotion). Although maintenance is assumed to scale approximately isometrically with body mass, contributions from growth overheads and locomotion may vary in amount and slope. In sunlit waters, with high predation risks favouring high locomotor activity and rapid growth, cephalopods have steeper metabolic scaling associated with steeper scaling of locomotor costs and exponential growth, which is favoured when adult life is very short and reproduction is semelparous. Body-shape shifting enables sustained cutaneous intake of resources, hence metabolism, in these active species. Although teleost fish also typically grow fast in sunlit water, their growth declines during ontogeny, resulting in lower metabolic demands of growth. This is likely associated with a longer adult life and typically iteroparous reproduction. Shallower scaling of locomotor costs and the low energetic costs of maintaining buoyancy owing to swim bladders may also contribute to their lower metabolic scaling exponent. At greater depths, growth in cephalopods is slower, and growth overheads contribute less to metabolic scaling. Shallower scaling exponents could also be associated with reduced shape shifting. (Online version in colour.)

Furthermore, it is unclear whether low cutaneous respiration would apply to active juveniles because juveniles often show more cutaneous respiration than adults in various aquatic animals [49,50]. Therefore, body-shape flattening or elongation during growth may enable species with more active lifestyles to overcome geometric constraints associated with isomorphic growth, and hence  $2/3$ -power scaling of body surface area and associated cutaneous and branchial material exchange rates. As a result, higher  $b_A$  ( $>2/3$ ) may permit higher  $b_R$  ( $>2/3$ ) [8,10,25,51].

Euclidean predictions of  $b_A$  using  $b_L$  ignore increases in surface convolutions or fractal dimension during ontogeny (e.g. convolutions from gill development) and can therefore underestimate surface area increase [10,22,24]. This underprediction of surface area enlargement may partially explain why most species in this study have  $b_R$  values above the upper limits of the  $b_A$  prediction envelope (figure 3). A better estimation of actual exchange surface areas, including the relative importance of gill versus cuticle exchange over ontogeny, would be beneficial for understanding  $b_R$  variation. Alternatively, under-prediction of  $b_R$  based on  $b_A$  predictions could also be owing to the metabolic demands of growth [11,21,22] and possibly locomotion, which raises

the question about the extent to which metabolic scaling is influenced by metabolic demand relative to resource supply (the growth-scaling hypothesis). Is shape change a response to high metabolic demands, or does shape change permit or drive the steep scaling of metabolic rates? As natural selection may favour a matching of resource supply capacity with demand, refuting either statement is likely to be difficult [42]. Nonetheless, understanding the importance of various factors influencing energy flow and assimilation in an organism will be crucial for improving our knowledge on how and why metabolic rate varies with size.

### (b) Metabolic scaling in the benthos and at greater depths

Bathypelagic cephalopods have significantly lower  $\ln L_R$  values than species with other lifestyles (figure 4a). Lower metabolic levels could result from reduced visual predation at greater depths [19], which could relax selection on maintaining high locomotor activity. This may also include a switch to sit-and-wait predatory behaviour, which has lower energetic costs [8,19,52]. A reduced requirement for high locomotor activity could also favour the use of



buoyancy mechanisms [53], which include reduced amounts of metabolically active musculature, and accumulation of relatively high amounts of buoyancy-enhancing, low-density, metabolically inactive, ammonium or gelatinous body materials, as found in many bathypelagic cephalopod species [19,53,54]. Although research on the growth of deep-sea cephalopods is scarce, growth rates tend to be slower at greater depths [55] and mass-specific growth may decline with size in deeper-living and benthic species [55,56].

Benthic cephalopods have temperature-corrected  $\ln L_R$  values that are significantly lower than those of pelagic species ( $p = 0.005$ ). For benthic cephalopods, bottom structures may provide refuge from predation, while also enabling ambush foraging [19]. Therefore, reduced active prey pursuit and predator avoidance in benthic octopods could decrease selection for high swimming speeds and the greater metabolic levels needed to sustain them. Hence, both benthic and deep-water species have lower predation risks and metabolic levels and are subsequently considered together in figure 6.

As growth [55] and locomotion [19] tend to be reduced in deeper water and benthic-living species, supporting energy costs will also decrease. In contrast to cephalopods, metabolic scaling is steep in bathypelagic and benthic-living teleosts. Within the least active bathypelagic cephalopods and fish, cephalopods ( $b_R = 0.76 \pm 0.04$ ) have significantly lower metabolic scaling exponents than do fish ( $b_R = 0.94 \pm 0.04$ ;  $t = -3.059$ , d.f. = 9.596,  $p = 0.013$ ). This difference may relate to growth, as tentative evidence suggests that bathypelagic fish have steeper scaling exponents for growth with body mass in these habitats [57] in comparison to cephalopods (figure 6 and [56]).

### (c) General relationship between metabolic scaling and metabolic level

Shape shifting may have facilitated the significant positive relationship that we observed between  $b_R$  and  $L_R$  in cephalopods (figure 2), as indicated by the positive relationship between  $b_R$  and  $1/b_L$  (figure 3). Hence, the more metabolically active squids had greater shape change during ontogeny, thus allowing them to maintain high relative surface area for exchange of resources and wastes. The positive relationship between  $b_R$  and  $1/b_L$  parallels the significant relationship found in the phylum Mollusca [10]. However, the molluscan relationship appeared to result largely from marked differences in the degree of shape shifting and metabolic scaling observed between cephalopod and pteropod species, whereas our analysis still finds a significant correlation between  $b_R$  and  $1/b_L$  within a more complete cephalopod dataset (i.e. even when the strong influence of pteropods is excluded).

Our results provide some support for the MLBH, in that scaling of surface area for exchange of resources or wastes correlates positively with routine  $b_R$ , across species, which

correlates positively with  $L_R$ . Shape shifting, hence non-isometric scaling of body surface (including the inner mantle cavity) may allow for steeper  $b_R$  in the most active (high  $L_R$ ) cephalopods. However, steeper ontogenetic scaling of growth in the most active species and its greater contribution to whole-body metabolism may also contribute to such non-negative associations between  $b_R$  and  $L_R$ , as proposed by the growth-scaling hypothesis.

Hence, we suggest that the observed positive correlation between  $b_R$  and  $L_R$  among cephalopod species occurs because of coadaptive changes in several behavioural, life-history, morphological and metabolic traits that affect both resource supply and metabolic demand. Higher levels and steeper scaling of growth and locomotor activity in some (especially epipelagic) species likely involve sustained mass-specific metabolic demands throughout life, resulting in both higher metabolic levels ( $L_R$ ) and steeper metabolic scaling ( $b_R$ ). Steeper metabolic scaling could, in turn, be accommodated by steeper scaling of respiratory surface area ( $b_A$ ) made possible by shape shifting, which is supported by the correlation between  $b_R$  and  $b_A$ . As supply capacity and metabolic demand are likely coadjusted and thus convergent, metabolic scaling in cephalopods is likely a result of both resource demand and supply [58].

In conclusion, we present support for the importance of a meta-mechanistic approach to metabolic scaling [11,35]. In doing so, we have proposed an explanation for how and why cephalopods have metabolic scaling slopes that increase with increasing metabolic levels. We suggest that sustained metabolic demands of growth and potentially locomotion may explain near isometric metabolic rate scaling in those cephalopods with the highest metabolic levels. Such isometric scaling of metabolic rates may be supported by surface area enlargement through shape shifting. The combination of body-shape shifting with costs and size scaling of growth and locomotion, adapted to different mortality and energetic pressures, may explain the contrasting metabolic scaling of cephalopods and teleost fishes. Thus, even for similar-sized coexisting animals, differences in water depth, lifestyle, growth and body shape can cause striking differences in metabolic scaling.

**Data accessibility.** The data supporting this article have been uploaded as part of the electronic supplementary material.

**Authors' contributions.** H.T., A.G.H. and D.A. designed the study; H.T. and A.G.H. collected the data, H.T. performed the metaanalysis and phylogenetic analyses. H.T., A.G.H., D.A. and D.S.G. all contributed to the writing of the paper. All authors gave final approval for publication.

**Competing interests.** We declare we have no competing interests.

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