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# Life in the unthinking depths: energetic constraints on encephalization in marine fishes

T. L. IGLESIAS\*, A. DORNBURG†, M. C. BRANDLEY‡, M. E. ALFARO§ & D. L. WARREN\*

\*Department of Biological Sciences, Macquarie University, North Ryde, Sydney, NSW, Australia

†Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA

\$School of Biological Sciences, University of Sydney, Sydney, NSW, Australia

\$Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

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# Abstract

Several hypotheses have been proposed to explain the limitation of brain size in vertebrates. Here, we test three hypotheses of brain size evolution using marine teleost fishes: the direct metabolic constraints hypothesis (DMCH), the expensive tissue hypothesis and the temperature-dependent hypothesis. Our analyses indicate that there is a robust positive correlation between encephalization and basal metabolic rate (BMR) that spans the full range of depths occupied by teleosts from the epipelagic (< 200 m), mesopelagic (200-1000 m) and bathypelagic (> 4000 m). Our results disentangle the effects of temperature and metabolic rate on teleost brain size evolution, supporting the DMCH. Our results agree with previous findings that teleost brain size decreases with depth; however, we also recover a negative correlation between trophic level and encephalization within the mesopelagic zone, a result that runs counter to the expectations of the expensive tissue hypothesis. We hypothesize that mesopelagic fishes at lower trophic levels may be investing more in neural tissue related to the detection of small prey items in a low-light environment. We recommend that comparative encephalization studies control for BMR in addition to controlling for body size and phylogeny.

# Introduction

Understanding what factors have influenced the diversity of vertebrate brain sizes has long been of interest to evolutionary biologists. Heritability of brain size has been demonstrated across a wide range of taxa such as primates, mice, birds and fish (Cheverud *et al.*, 1990; Airey *et al.*, 2000; Rogers *et al.*, 2007; Kolb *et al.*, 2013; Kotrschal *et al.*, 2013). However, it is unknown to what extent brain size is influenced by independent and synergistic effects of developmental and ecological environments, and selection on genes and plasticity. Body size (Harvey & Pagel, 1988) and phylogenetic relatedness (Felsenstein, 1985) can be confounding factors; current studies therefore typically control for these in interand intraspecific analyses examining brain size. However, there are other potential limitations on brain size that may not necessarily be informative for understanding the evolutionary drivers of encephalization. One of the most widely accepted hypotheses for limits to brain size is the direct metabolic constraints hypothesis (DMCH). The DMCH focuses on the high metabolic cost of developing and maintaining large brains (Mink et al., 1981; Armstrong, 1983; Hofman, 1983) and suggests that basal metabolic rate (BMR) could limit brain size. The DMCH has been supported by positive correlations between brain size and BMR (Armstrong, 1983; Hofman, 1983). While this hypothesis has been called into question (McNab & Eisenberg, 1989), recent work has renewed interest in this line of enquiry by demonstrating a positive correlation between BMR and brain size in mammals (Isler & van Schaik, 2006b).

However, there is a growing body of evidence suggesting that vertebrate brain size evolution may be constrained by additional factors. Some groups of primates show a negative correlation between brain size and gut mass (Aiello & Wheeler, 1995). This observation

*Correspondence*: Teresa L. Iglesias, Department of Biological Sciences, Macquarie University, North Ryde, Sydney, NSW 2109, Australia. Tel.: +61 2 9850 8179; fax: +61 2 9850 8245; e-mail: teresa.l.iglesias@ gmail.com

resulted in the establishment of the expensive tissue hypothesis, which posits a diet-facilitated trade-off between the metabolic demands of large brains and gut tissues, which also have high metabolic costs (Aiello & Wheeler, 1995). Additionally, brain size shows a negative correlation with pectoral musculature (but not BMR) in birds (Isler & van Schaik, 2006a). Evidence that brain tissue trades off with tissues other than gut led to the formation of the energy trade-off hypothesis. This hypothesis extends the expensive tissue hypothesis to predict that brain size can trade off not only with other energetically expensive tissues, but also with energetically costly functions such as digestion, locomotion and reproduction (Isler & van Schaik, 2009). However, there is not enough information available to test the energy trade-off hypothesis at this time.

Although there is a growing body of evidence supporting a linkage between biotic factors (such as BMR or energetic trade-offs) and brain size, investigations of brain size evolution are hindered by the complex influence of biotic and abiotic factors on BMR itself (Lovegrove, 2003; Anderson & Jetz, 2005; Careau et al., 2007). Temperature regimes experienced by an organism represent an oft-overlooked potential constraint in the evolution of vertebrate brain size (Gillooly et al., 2001; Gillooly & McCoy, 2014). This has led to the proposal of the temperature-dependent hypothesis, which predicts a positive correlation between brain size and temperature. Ectothermy reduces the complexity of the mechanisms needed for thermal homoeostasis (Lovegrove, 2003; Anderson & Jetz, 2005; Careau et al., 2007) suggesting that large-scale investigations of primarily ectothermic clades could be particularly fruitful for further investigation of major biotic and abiotic drivers in brain size evolution. However, ectotherms are typically under-represented in comparative studies of vertebrate brain size.

Marine teleost fishes, which comprise over 25% of living vertebrate species (Eschmeyer & Fricke, 2012), are an exemplary system for macroevolutionary studies of encephalization. Marine teleosts span a broad range of habitats from tropical coral reefs to some of the most extreme environments on earth, including deep-sea trenches and high-latitude polar environments (Nelson, 2006; Tittensor et al., 2010), and span a correspondingly wide range of biotic and abiotic factors that might affect encephalization. A number of recent studies have produced large, well-resolved teleost phylogenies (Miya et al., 2003; Alfaro et al., 2009; Near et al., 2012, 2013; Wainwright et al., 2012; Rabosky et al., 2013; Santini et al., 2013; Betancur-R et al., 2014). Likewise, encephalization data are available for more than a thousand species in over two hundred families, resulting in a broad taxonomic coverage for phylogenetic studies.

Comparative anatomical surveys of teleost brains suggest a trend towards smaller brains at extreme (> 1000 m) depths (Kotrschal *et al.*, 1998). While BMR decreases with lower temperatures in teleost fishes, at greater ocean depths, the decrease in BMR is too large to be due to the effects of temperature alone (Torres *et al.*, 1979). Light availability can also affect diet and sensory biology, which in turn can affect brain size (Garamszegi *et al.*, 2002; Pearce & Dunbar, 2012). Understanding what underlies the systematic reduction of teleost brains at depth therefore requires the inclusion of biotic factors such as BMR and energy trade-offs as well as the variation in temperature and light regimes in different strata of the world's oceans (Lalli & Parsons, 1997; Pinet, 2011).

Here, we test three hypotheses of brain size evolution using ecological, phylogenetic and encephalization data in marine teleosts: the DMCH, the expensive tissue hypothesis and the temperature-dependent hypothesis. We use information criterion-based model selection to compare models built using phylogenetic generalized least squares (PGLS) to examine the effects of latitude, depth and trophic level on encephalization across marine fishes. Each hypothesis makes different predictions about the expected relationship between ocean depth, ocean latitude, trophic level and brain size. For example, the DMCH predicts a negative relationship between ocean depth and brain size, the temperature-dependent hypothesis predicts a negative relationship between latitude and brain size, and the expensive tissue hypothesis predicts a positive relationship between trophic level and brain size. Our aim was to determine whether future encephalization studies should control for BMR, ambient temperature and/or trophic level to better understand the evolution of brain size.

# **Materials and methods**

#### Data set assembly

We obtained body and brain mass measurements in the field from samples collected during September 2011 in Curaçao and August 2013 in Guam. In total, we collected 322 individuals representing 159 species (vouchers deposited in the Yale Peabody Museum of Natural History; Table S1). Fish were caught using dip nets, barrier nets and clove oil. Fish were euthanized using MS-222 in sea water. Brains were dissected from freshly euthanized fish or from specimens that had been frozen for less than a week. Following dissection, brains were washed in clean 10% PBS under a dissecting microscope, blotted dry and then weighed. Only portions of the brainstem housed inside the skull of the fish were allowed to contribute to measures of mass. To these data, we added brain and body mass data from published sources (Bauchot et al., 1979, 1989; Bauchot & Bauchot, 1986; Chin, 1996; Albert et al., 1999; Froese & Pauly, 2014). Of the species we collected, 51 were not present in these published encephalization data sets.

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To control for allometric scaling in our statistical tests, we calculated encephalization quotients as the species average residual from a log–log regression of brain mass on body mass for all individuals with available data (3407 individuals in 1137 species, slope = 0.617, intercept = -4.327,  $R^2 = 0.851$ ). Interspecific variance in residuals was considerably greater than intraspecific variance for almost all species (Fig. S1), supporting that brain size measures used here are not likely due to intraspecific phenotypic plasticity in body or brain size.

To establish that our field data collection was comparable with existing data sets, we conducted a two-tailed paired-samples *t*-test to calculate differences between encephalization estimates for species that occurred in both data sets. We found no significant differences (P = 0.944, n = 108 species). For all species with encephalization data (n = 1137), we compiled data from FishBase (Froese & Pauly, 2014) on trophic level (range = 2-4.5; a lower number corresponds to a lower trophic level), maximum recorded depth (range = 1-5998 m) and maximum absolute latitude (distance from the equator) (range =  $11-87^{\circ}$ ). Maximum recorded depth was used to assign species to one of three ocean photic zones: epipelagic (< 200 m), mesopelagic (200–1000 m) and bathypelagic (> 1000 m). We also conducted a separate set of analyses using the mid-point of the depth distribution for each species instead of the maximum.

#### **Comparative analyses**

We used PGLS to test predictions for three hypotheses regarding the evolution of encephalization (Table 1). As

**Table 1** Predictions for hypotheses tested in this study. Arrows indicate whether encephalization is predicted to decrease  $(\downarrow)$  or increase  $(\uparrow)$  with higher latitude, greater depth and higher trophic level according to each hypothesis. 'No effect' indicates that no correlation should be detected between the explanatory variable and encephalization. Pale grey areas indicate where predictions are uninformative for hypotheses.

		Explanatory variables			
Hypotheses	Depth zones	Latitude	Depth	Trophic level	
Temperature -dependent hypothesis Direct metabolic constraints	Epipelagic Mesopelagic Bathypelagic All Epipelagic Mesopelagic	↓ ↓ No effect ↓	↓ ↓ ↓ ↓ ↓		
hypothesis	Bathypelagic All	No effect ↓	' ↓ ↓		
Expensive tissue hypothesis	Epipelagic Mesopelagic Bathypelagic All			↑ ↑ ↑	

PGLS models are dependent upon a model of character evolution, we began by fitting Brownian motion and Ornstein–Uhlenbeck (OU) models to the data (brain size, depth, latitude and trophic level) using the cor-Brownian and corMartins function in the ape R package (Paradis *et al.*, 2004). For all tests, the alpha parameter used for the OU model-based regressions was estimated using the fitContinuous function in the Geiger package for R (Harmon *et al.*, 2008).

Visual inspection of data indicated possible heteroscedasticity in variables. Rather than log-transforming the data, we fit all subsets of data used in our analyses to models specifying different variance structures using the nlme R package (Pinheiro *et al.*, 2011). We then used Akaike information criterion scores for small sample sizes (AICc) to select the most appropriate variance structure (Zuur *et al.*, 2009). We found that models constructed with data from the epipelagic zone or with data across all three zones combined performed better when the constant plus power of the variance covariate function (var-ConstPower) was applied to trophic level. Models with data from mesopelagic and bathypelagic zones did not perform better when a variance structure was applied.

All comparative analyses were conducted using the phylogeny of Rabosky et al. (2013). This is a time-calibrated 7822 taxon tree inferred from a 13-gene supermatrix constructed using a 'mega-phylogeny' approach (Smith et al., 2009). All data matrices and the tree topology were pruned to only the subset of taxa sampled in the phylogeny for which we had data for all variables (brain size, depth, latitude and trophic level). The final data sets comprised 489 species, including 17 species from our field collections that were not previously sampled (Table S2). We reconstructed ancestral states using parsimony-based optimizations in Mesquite (Maddison & Maddison, 2001) to visually assess the evolution of depth, latitude, trophic level and brain size across marine teleosts. This allowed us to insure multiple independent transitions between the extremes of all trait values (e.g. no single clade comprises all high encephalization values).

To control for the availability of light and temperature and the potential effect this may have on brain size (Kotrschal et al., 1998), we partitioned data into three subsets based on species' maximum depth and analysed these subsets separately. The partitions consisted of the epipelagic zone (< 200 m, 369 species), the mesopelagic zone (200-1000 m, 75 species) and the bathypelagic zone (> 1000 m, 45 species). The epipelagic zone receives enough sunlight to support photosynthesis. Temperatures in the epipelagic are approximately 18 °C on average and range from 36 to -2 °C, with temperatures decreasing at greater depths and higher latitudes. The mesopelagic zone receives enough light to distinguish day from night, but not enough to support photosynthesis. Mesopelagic zone temperatures are approximately 9 °C on average and

© 2015 EUROPEAN SOCIETY FOR EVOLUTIONARY BIOLOGY. J. EVOL. BIOL. 28 (2015) 1080-1090 JOURNAL OF EVOLUTIONARY BIOLOGY © 2015 EUROPEAN SOCIETY FOR EVOLUTIONARY BIOLOGY range from 20 to -2 °C with increasing depth and latitude. Light does not penetrate the bathypelagic zone, where the approximate average temperature is 4 °C with a range from 5 to -2°C with depth and across latitudes (Lalli & Parsons, 1997; Pinet, 2011).

Each of the three hypotheses makes different predictions about the expected relationship between depth, latitude, trophic level and brain size when depth zones are considered independently (Table 1). For example, the temperature-dependent hypothesis predicts that brain size will decrease with latitude and depth across epipelagic and mesopelagic zones, but not bathypelagic, as temperatures in this zone are confined to a very narrow range regardless of depth or latitude. This hypothesis would also predict that the effect of latitude in the epipelagic zone would have a significant negative effect on brain size (Table 1), because latitudinal temperatures within the epipelagic zone span the widest range (36 to -2 °C). Alternatively, the DMCH predicts a negative effect of depth [proxy for BMR (Torres et al., 1979; Torres & Somero, 1988b)] on brain size in each zone, and that the effects of depth will be stronger than any effect of latitude within the mesopelagic and bathypelagic zones. The expensive tissue hypothesis predicts that trophic level positively affects brain size within each zone and across zones combined, reflecting the effects of higher energy intake (Clutton-Brock & Harvey, 1980; Crawford, 1992; Carlson & Kingston, 2007) or gut mass trade-offs (Aiello & Wheeler, 1995; Fish & Lockwood, 2003) as higher quality diets are shown to correlate with shorter guts in fishes (Kramer & Bryant, 1995; Elliott & Bellwood, 2003; Wagner et al., 2009).

We conducted an additional analysis combining all depth zones. Although results from this analysis do not allow us to distinguish between support for the temperature-dependent hypothesis and the DMCH, we can nonetheless assess the relative effect of depth and latitude on brain size across the entire range of depth and temperature and to determine whether trophic level affects brain size (Table 1).

We constructed four sets of models (one for each of the three zones and one for all zones combined) where each set was composed of seven competing models. Models were constructed using trophic level, depth, latitude and intercept-only (null model) as predictors, with brain size as the response variable. We built generalized least-squares models using the R package nlme (Pinheiro et al., 2011), specifying OU as the model of character evolution with alpha parameters calculated for data subsets independently. We used the R package arm (Gelman & Su, 2014) to rescale and centre data to allow comparison of effect size between predictors. We used the R package bbmle (Bolker, 2014) to calculate AICc, and AICcmodavg (Mazerolle, 2014) to calculate model-averaged coefficients and unconditional SE with 95% confidence intervals (CI) using all models in the set. We considered coefficient magnitudes, unconditional SE and 95% CI calculated from the averaged models to assess the relevance of predictors for brain size.

## Results

Visualization of the relationship between depth, trophic level and encephalization suggests a decline in encephalization at greater depths (Fig. 1). The highest diversity of trophic levels occurs in the epipelagic zone, as this is the only zone in which photosynthesis occurs, resulting in an absence of herbivores at greater depths (Fig. 1). Ancestral state reconstructions of the evolution of these traits across marine teleosts support multiple independent transitions to the extremes of each trait with no extreme trait values (e.g. high or low trophic level) represented in only a single clade (Fig. 2).

When all depth zones were combined in a PGLS analysis, we found support for the DMCH and temperature-dependent hypothesis as greater depth and distance from the equator correlated with smaller brains (Tables 2 and 3). Model-averaged estimates (effect size) indicated that depth exerts a stronger constraint on brain size than latitude (Table 2). There was no evidence that trophic level affected brain size (Tables 2 and 3).

Models built within the epipelagic zone (depth < 200 m) revealed a negative relationship between brain size and depth, supporting the DMCH (Tables 2 and 3). However, we find no support for the temperature-dependent hypothesis or the expensive tissue hypothesis, as there is no effect of latitude or trophic level within the epipelagic zone (Tables 2 and 3). Within the mesopelagic zone (depth = 200–1000 m), model results indicate a negative relationship between brain size and depth, and between brain size and trophic level (Table 2). These findings further support the DMCH and run counter to predictions of the expensive tissue hypothesis. Within the bathypelagic zone (depth > 1000 m), model results indicate a negative relationship between brain size and depth (Table 2), which supports the DMCH.

Analyses using the mid-point of depth ranges did not differ from those obtained using maximum depth, so we do not discuss them further. We found no effect of an interaction between depth and latitude in any analysis, and therefore, models with this interaction were removed from the set to simplify interpretation of the main effects. This resulted in model sets composed of six models instead of seven (Table 3).

#### Discussion

This first broad comparative study of environmental effects on encephalization within marine teleost fishes supports the prediction that encephalization correlates positively with BMR (using depth as a proxy) and hence the DMCH. However, we find little support for



**Fig. 1** Encephalization and trophic level as a function of maximum depth in metres (top panel) and maximum absolute latitude in degrees from the equator (bottom panel). Encephalization values below zero (dashed line) indicate species that have smaller brains than expected given their body mass, as determined by a log–log regression (see text). Points are coloured by trophic level, with lower values indicating more herbivorous diets.

the hypothesis proposed by Gillooly *et al.* (2001) that a decrease in temperature, here indicated by latitude, correlates with smaller brains. We find no support for the hypothesis that increased energy intake due to higher trophic level increases encephalization, and therefore no support for the expensive tissue hypothesis, which predicts that increased investment in neural tissue correlates with diet-mediated decreases in gut mass. The only significant association between encephalization and trophic level was confined to species in the mesopelagic zone, and that correlation was opposite to the direction predicted. We discuss the implications of these results below.

#### The influence of latitude on encephalization

Our results indicate that fishes at higher latitudes, and hence lower temperatures, are less encephalized. However, this relationship is only detected when all zones are analysed together. This suggests that the effect of lower ambient temperature on brain size, if it exists, may be too weak to be detected within smaller subsets of the data. Alternatively, the lack of an effect of latitude when depth zones are analysed separately may suggest either that cold compensation in higher latitude fishes (Torres & Somero, 1988a; van Dijk *et al.*, 1998; Hardewig *et al.*, 1998; Brodeur *et al.*, 2003; Portner *et al.*, 2005) releases temperature constraints on encephalization or that temperature itself does not directly affect encephalization, but correlates with other factors that are responsible (Clarke, 1993; Clarke & Fraser, 2004).

The influence of temperature on the evolution of fish neural anatomy is poorly understood, although studies of Antarctic fishes suggest that the influence of temperature on brain metabolic activity may be mitigated by



**Fig. 2** Phylogenetic reconstructions of the evolutionary pathways that gave rise to present-day patterns of encephalization, depth, geographic distribution and trophic level. Following the colour legends, the clade highlighted by the dashed box would indicate (working from right to left) species at a low trophic level, inhabiting moderate latitudes at shallow depth, have moderately sized brains compared to body size.

some combination of high concentrations of mitochondria, increased enzyme efficiency and/or increased enzyme concentrations (Hardewig et al., 1999; Kawall et al., 2002; Somero, 2004). Comparative analyses of Antarctic fish brains have revealed these to be more similar to other temperate teleosts than deep-sea fishes (Eastman & Lannoo, 1995), and given, even partial adaptation to permanently cold conditions such as those suggested above could provide an explanation for the lack of a strong trend between brain size and latitude in our analyses. However, the latitudinal temperature range within the epipelagic zone (36 to -2 °C) mirrors the temperature range for depth across all zones. If temperature were the main driver of encephalization, latitude should correlate with encephalization within the epipelagic zone. As we do not detect this pattern, we conclude that temperature does not directly affect encephalization.

#### The influence of feeding ecology on encephalization

There is a general correlation between shorter guts and higher quality diets in fishes (Kramer & Bryant, 1995; Elliott & Bellwood, 2003; Wagner et al., 2009), although there are exceptions (Day et al., 2011; Pogoreutz & Ahnelt, 2014). The expensive tissue hypothesis predicts that there is a trade-off between investing in guts and brains (Aiello & Wheeler, 1995); therefore, we would expect to detect an effect of trophic level on encephalization in our analyses. Although an intraspecific study in a marine fish did not show trade-offs between expensive tissues such as testes, liver and brain (Warren & Iglesias, 2012), we considered it possible that an indirect measure of a trade-off between gut length and brain mass across almost 500 species of fish would reveal such a pattern if it existed. However, our results offer no evidence that the expensive tissue

**Table 2** Model-averaged coefficient estimates for all predictors in the models with unconditional SE and 95% confidence interval calculated by averaging across all models in the set for individual zones or all zones combined. Predictors indicated in bold [95% confidence intervals (CI) does not include zero] are good model predictors for brain size in fish. All variables have been rescaled and centred to allow meaningful comparisons of effect size between predictors within model sets.

Depth zone	Model predictors	Model-averaged estimate	Unconditional se	Unconditional 95% Cl
All	Depth	-0.21	0.05	-0.32, -0.10
	Latitude	-0.13	0.06	-0.24, -0.02
	Trophic level	-0.02	0.05	-0.13, 0.09
Epipelagic	Depth	-0.09	0.04	-0.16, -0.01
	Latitude	-0.06	0.05	-0.15, 0.03
	Trophic level	0.07	0.07	-0.06, 0.20
Mesopelagic	Depth	-0.27	0.07	-0.42, -0.13
	Latitude	-0.18	0.13	-0.43, 0.07
	Trophic level	-0.33	0.10	-0.52, -0.14
Bathypelagic	Depth	-0.40	0.21	-0.81, -0.02
	Latitude	-0.08	0.16	-0.39, 0.24
	Trophic level	-0.23	0.20	-0.62, 0.16

hypothesis holds across marine fishes. The lack of any effect of trophic level on encephalization in the epipelagic zone is particularly striking, given that epipelagic zone species show the most variation in trophic level and composed over seventy per cent of the species in our data set.

Although encephalization in marine fishes of the mesopelagic was partially explained by trophic level (Tables 2 and 3), this finding disagrees with expectations under the expensive tissue hypothesis. Rather than finding an increase in encephalization at higher trophic positions, our analysis supported an inverse relationship. This trend of increased brain size relative to body size at lower trophic positions may be partially explained by the increased sensory needs of planktonic feeders at depths below 200 m. Upper mesopelagic fishes and mesopelagic fishes undergoing vertical migrations are characterized by extreme visual modifications that allow for detecting slight contrasts of light and making use of bioluminescence (Kotrschal et al., 1998). Plankton feeders in particular tend to have greater eye and lateral line modifications in order to detect more minute prey quantities (Bleckmann, 1986; Coombs et al., 1988). While changes in brain morphology have been associated with epipelagic fishes living in turbid water (Huber & Rylander, 1992; Kotrschal et al., 1998), it is unclear whether there are also systematic trends in the reduction or enlargement of specific brain regions in mesopelagic fishes at different trophic levels. Our analyses highlight this as a particularly fruitful area of future research.

A caveat to these results is that the accuracy of trophic level calculated by FishBase (Froese & Pauly,

**Table 3** AICc comparison of generalized least squares models for fishes of the epipelagic (depth < 200 m), mesopelagic (depth = 200 -1000 m), bathypelagic zone (depth > 1000 m) and across all three ocean depth zones (depth = 1-6000 m). All models compared are shown along with degrees of freedom (d.f.), the difference in AICc model likelihood scores ( $\Delta$  AICc) and the relative AICc weights for models within each set. Models are listed in order of rank (best performing) from the top for each model set.

Depth zone	Model predictors	d.f.	Δ AICc	AICc weight
All zones	Depth + latitude	7	0.00	0.62
	Depth + latitude + trophic level	8	1.90	0.24
	Depth	6	3.00	0.14
	Latitude	6	11.60	0.002
	Intercept-only	5	20.70	< 0.001
	Trophic level	6	22.60	< 0.001
Epipelagic	Depth	6	0.00	0.37
	Depth + latitude	7	0.70	0.26
	Depth + latitude + trophic level	8	1.40	0.18
	Latitude	6	3.00	0.08
	Intercept-only	5	3.20	0.08
	Trophic level	6	4.60	0.04
Mesopelagic	Depth + latitude + trophic level	6	0.00	0.95
	Depth	4	6.70	0.03
	Depth + latitude	5	8.80	0.01
	Trophic level	4	12.30	0.002
	Intercept-only	3	16.20	< 0.001
	Latitude	4	17.00	< 0.001
Bathypelagic	Depth	4	0.00	0.35
	Intercept-only	3	0.07	0.25
	Trophic level	4	1.70	0.15
	Depth + latitude	5	2.30	0.11
	Latitude	4	2.80	0.09
	Depth + latitude + trophic level	6	3.60	0.06

2014) is unclear. Fish species on FishBase for which diet data are lacking can still be assigned a trophic level calculated based on what is known about the closest relative in the database with available diet information (Froese & Pauly, 2000). This is an assumption that has unknown reliability, as patterns of trophic disparity and missing data will vary nonrandomly among taxa. Several studies have attempted to verify FishBase's assignment of trophic level, with some showing good agreement between empirically derived measures and FishBase trophic levels (Kline & Pauly, 1998; Mancinelli et al., 2013) and others showing weak or variable agreement (Faye et al., 2011; Carscallen et al., 2012). It is unknown how many of the species included in our analyses had trophic levels that were calculated from other species' data, a caveat that emphasizes the need for natural history studies to aid our understanding of macroevolutionary trends (McCallum & McCallum, 2006). Given this, and that we tested the expensive tissue hypothesis indirectly, our conclusions regarding the validity of the expensive tissue hypothesis should be interpreted with caution.

#### The influence of depth on encephalization

Our analyses support a strong correlation between depth and encephalization across marine teleosts (Tables 2 and 3). Basal metabolic rate is known to decrease significantly with depth, and temperature only accounts for approximately 2% of that change (Torres *et al.*, 1979). Further, the decrease in BMR experienced by deep-water fishes surpasses that experienced by high-latitude fishes at the same temperature (Torres & Somero, 1988a). Therefore, our results support the DMCH, which states that BMR is a primary physiological factor limiting encephalization.

The DMCH is supported by patterns we detect across depth zones analysed together and independently. The transition from the mesopelagic to the bathypelagic zone has been linked with an abrupt shift towards brain size reduction in teleosts (Fine *et al.*, 1987; Kotrschal *et al.*, 1998; Lannoo & Eastman, 2000), and there is also evidence of a similar large-scale pattern of brain reduction in sharks (Yopak & Montgomery, 2008; Yopak, 2012). Our results are consistent with these observed shifts (Tables 2 and 3), but it is possible this trend may be explained by greater depths promoting the evolution of alternate sensory systems that are more suited to conditions at depth (Deng *et al.*, 2013), which require less brain mass and are therefore less costly to maintain.

Basal metabolic rate is predicted to continue to decrease in bathypelagic teleosts with increasing depth. As brain size is tightly correlated to BMR, the DMCH predicts that encephalization should also continue to decrease with depth. However, is there a lower limit to encephalization in fishes? There is an abundance of slow-moving ambush predators at extreme depths (Koslow, 1996), which suggests the possibility that energetic trade-offs might reduce activity levels instead of tissue mass. Further analysis of the relationship between BMR, encephalization and energetic budget trade-offs is currently not possible, as studies of brain morphology and metabolic rates have only been conducted on a few species of deep-sea fishes. As we continue investigating the ecology and evolution of deepsea fishes, understanding the drivers of brain size reduction and the factors limiting this reduction will significantly increase our understanding of sensory biology.

Broad comparative studies show that encephalization correlates with higher BMR in primates and bats, but not rodents and carnivores (Isler & van Schaik, 2006b). Avian studies also report a lack of correlation between BMR and encephalization; instead, there appears to be a trade-off between pectoral muscle mass and brain mass (Isler & van Schaik, 2006a). Taken together, these results emphasize that, regardless of the energetic budget, allocation to encephalization is not the only successful strategy towards maximizing fitness (Isler & van Schaik, 2009). Given the breadth of ecologies and life histories of the epipelagic fishes in our data, it is possible that life history differences may be counteracting the influence of depth, latitude and trophic level in a variety of ways; habitat (reef versus pelagic), feeding mode (ram suction versus sweeping) and social systems have all been linked to brain size (Bauchot et al., 1988; van Staaden et al., 1995; Huber et al., 1997; Dunbar, 1998; Kotrschal et al., 1998). This suggests that a broader hypothesis, such as the energy trade-off hypothesis, may generate more specific predictions that can facilitate identification of common trade-offs that must be controlled for when testing encephalization hypotheses within a group of interest. Finally, given our results, we propose that in addition to controlling for body size and phylogeny, comparative encephalization studies examining functional explanations for encephalization should control for BMR where appropriate.

# Conclusion

Our goal in this study was to determine the relative contribution of ocean depth, latitude and trophic level on marine fish encephalization and to interpret the resulting patterns in the light of what has been shown for other taxa. This study is the first broad comparative study within fish to assess different environmental effects on encephalization. We find several trends that are unique among vertebrates. First, we demonstrate that ocean depth, a proxy for BMR, is the strongest predictor of encephalization across all fishes, thereby supporting the DMCH. Second, our analyses also support the evolution of increased encephalization at lower trophic positions in mesopelagic fishes, a statistically robust result that runs counter to expectations and to predictions of the expensive tissue hypothesis. Finally, our results also confirm the well-documented shift towards extreme brain size reduction in bathypelagic fishes (Fine et al., 1987; Kotrschal et al., 1998; Lannoo & Eastman, 2000). As we continue to strive towards a general understanding of the biology of deep-sea fishes, our results highlight that increased sampling of mesopelagic and bathypelagic fishes in detailed comparative phylogenetic analyses could promote a more general understanding of the evolution of vertebrate brains in one of the most extreme environments on earth.

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# **Supporting information**

Additional Supporting Information may be found in the online version of this article:

Figure S1 Intraspecific variance for the 489 species included in our analyses.

**Table S1** Locality and Yale Peabody Museum identifi-<br/>cation number of newly collected specimens used in<br/>this study.

**Table S2** Species included in all analyses, data source, and calculated encephalization value.

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