

Large and expensive brain comes with a short lifespan: The relationship between brain size and longevity among fish taxa

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Abstract

Vertebrates show substantial interspecific variation in brain size in relation to body mass. It has long been recognized that the evolution of large brains is associated with both costs and benefits, and it is their net benefit which should be favoured by natural selection. On one hand, the substantial energetic cost imposed by the maintenance of neural tissue is expected to compromise the energetic budget of organisms with large brains and their investment in other critical organs (expensive brain framework, EBF) or important physiological process, such as somatic maintenance and repair, thus accelerating ageing that shortens lifespan, as predicted by the disposable soma theory (DST). However, selection towards larger brain size can provide cognitive benefits (e.g., high behavioural flexibility) that may mitigate extrinsic mortality pressures, and thus may indirectly select for slower ageing that prolongs lifespan, as predicted by the cognitive buffer hypothesis (CBH). The relationship between longevity and brain size has been investigated to date only among terrestrial vertebrates, although the same selective forces acting on those species may also affect vertebrates living in aquatic habitats, such as fish. Thus, whether this evolutionary trade-off for brain size and longevity exists on a large scale among fish clades remains to be addressed. In this study, using a global dataset of 407 fish species, I undertook the first phylogenetic test of the brain size/longevity relationship in aquatic vertebrate species. The study revealed a negative relationship between brain size and longevity among cartilaginous fish confirming EBF and DST. However, no pattern emerged among bony fish species. Among sharks and rays, the high metabolic cost of producing neural tissue transcends the cognitive benefits of evolving a larger brain. Consequently, my findings suggest that the cost of maintaining brain tissue is relatively higher in ectothermic species than in endothermic ones.

KEYWORDS

aquatic, brain mass, cognition, life history, ray-finned fishes, sharks

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1 | INTRODUCTION

Variation in relative brain size is extensive at all taxonomic levels and across all vertebrates (Striedter, 2005). This relatively large and complex organ is one of the most characteristic features of this lineage, and is related to various fundamental aspects of vertebrate behaviour and ecology (Amiel *et al.*, 2011). Highly flexible cognitive abilities are central to the success of many vertebrate taxa and may have imposed powerful selection for increase in relative brain size (Benson-Amram *et al.*, 2016; Martin, 1981; Sol *et al.*, 2008). In contrast, maintaining a large brain is energetically expensive: the metabolic cost of brain function is among the highest of any organ (the proportion of metabolic energy allocated to the brain in the resting state for both endotherms and ectotherms is on average >5% of the total energetic budget; Mink *et al.*, 1981). We thus might expect the benefits of increased cognition to be balanced against metabolic costs, with relative brain size in any given species reflecting this trade-off (Gillooly & McCoy, 2014; Martin, 1981).

A number of hypotheses aiming to explain the evolution of brain size variation among and within different vertebrate taxa have been formulated (Isler & van Schaik, 2009; Kotrschal *et al.*, 2019; Sol, 2009). On one side the cognitive buffer hypothesis (CBH; Sol, 2009) predicts that large relative brain masses (to body size) are associated with increased cognitive abilities with the potential to enhance the efficiency of behavioural responses to novel socio-ecological challenges (González-Lagos *et al.*, 2010; Sol, 2009; Vonk, 2016), such as rapid reactions to unexpected threats (*e.g.*, avoiding predation), finding new food sources or obtaining a mate (Allman *et al.*, 1993; Benson-Amram *et al.*, 2016; Holekamp & Benson-Amram, 2017; Striedter, 2005). On the other side, however, the metabolic costs associated with the development of larger brains have to be met by either increasing the total energy budget (*e.g.*, by increasing foraging time) or compensating for changes through energy allocation to other maintenance or developmental functions, as predicted by the expensive brain framework (EBF; Isler & van Schaik, 2009). Moreover, evolving a larger brain could also divert energy away from somatic maintenance and repair, risking the rapid decline of physiological process and the rapid accumulation of harmful mutations, which can accelerate ageing rates (Kirkwood, 1992). In this context, the disposable soma theory (DST) suggests that organisms adjust their investment of energy and resources into somatic maintenance or other costly functions, such as reproduction (Kirkwood, 2017). Thus, investment in the development of a larger brain could compromise energy allocation into somatic maintenance, consequently accelerating ageing and reducing lifespan overall (Kotrschal *et al.*, 2019).

These hypotheses consistently recognize that beyond its key role in cognitive advantages that can influence survival (Striedter, 2005), the brain influences a range of crucial fitness-relevant processes, such as the rate of ageing, by means of its regulatory function in the maintenance of physiological and hormonal processes (Hofman, 1983). Provided that these regulatory, as well as cognitive, benefits of large brain size outbalance the metabolic cost of its development, a positive correlation between brain size and lifespan would be expected and *vice versa*.

Evidence for the relationships between brain size and longevity has exclusively been focused on large-scale studies examining tetrapod species (*e.g.*, González-Lagos *et al.*, 2010; Jiménez-Ortega *et al.*, 2020; Minias & Podlaszczuk, 2017; Sol *et al.*, 2007, 2016; Stark & Pincheira-Donoso, 2022; Yu *et al.*, 2018) and has revealed mixed results with support for both the CBH and EBF/DST. Surprisingly, the evidence for any link between brain size and longevity remains lacking for fish, *i.e.*, broadly across species, clades and regions. Interestingly, a major experimental study using guppies (*Poecilia reticulata*) artificially selected for divergence in brain size found that increased brain size led to accompanying reduction in fecundity, gut size and lifespan (Kotrschal *et al.*, 2013, 2019). This suggests that the evolutionary implications of energetic constraints could be similar for both tetrapod and fish species. If, as hypothesized, brain tissue is relatively more costly to generate and maintain in fish, this could facilitate the proposed macroevolutionary relationship between brain size and life span. However, without formally testing this pattern among fish clades, we cannot be confident that the important relationship between brain size and lifespan is a common feature of all vertebrates.

This paper presents the first large-scale study investigating the association between brain size and lifespan among the Osteichthyes (bony fish) and Chondrichthyes (cartilaginous fish), while controlling for a set of possible confounding effects, such as body size, sampling size and life-history traits. The two alternative predictions proposed above are addressed: (1) larger relative brain size prolongs lifespan among fish clades (in line with the CBH) and (2) the metabolic cost imposed by large brains reduces somatic maintenance, and consequently also lifespan, by accelerating ageing, leading to a trade-off whereby smaller brains are associated with longer lifespans (in line with the EBF and DST).

2 | MATERIALS AND METHODS

2.1 | Data collection

A dataset on whole brain sizes for 407 fish species encompassing 36 orders (~60% of all fish orders) and 120 families (~25% of all fish families) of Osteichthyes and Chondrichthyes was compiled. In these comparative analyses, the whole brain mass was used because it has been consistently shown that whole-brain size positively correlates with several measures of behavioural flexibility and the ability to survive in novel ecological conditions (Lefebvre & Sol, 2008; Striedter, 2005). Data on brain mass (and the other variables, see below) were primarily collected from Mull *et al.* (2020) for sharks and rays, and from Tsuboi *et al.* (2018) for teleost species. The primary literature is available together with the full database and metadata in Supporting Information Appendix S1.

Fish body size was represented by mass in grams and was collected from the same source of brain-size data for each species. Following recommendations by Sol *et al.* (2007), the residuals of brain size against body mass were extracted using log-log least-square

linear regression ($R^2 = 0.88$, $P < 0.0001$), which is one of the most popular methods in comparative studies on brain size evolution and has the advantage of eliminating problems of collinearity (while using brain and body size as covariates), while effectively removing body size effects (Sol *et al.*, 2007; González-Lagos *et al.*, 2010; Galván & Møller, 2011; Abelson, 2016; Minias & Podlasczuk, 2017; Yu *et al.*, 2018). Brain size residuals were calculated with phylogenetic corrected least-square regression using the Analysis of Phylogenetics and Evolution (APE) package (Paradis *et al.*, 2004).

Longevity data of bony and cartilaginous species were taken primarily from the AnAge database (De Magalhães & Costa, 2009), with the rest of the longevity data retrieved from multiple literature sources (for the full reference list see Supporting Information Appendix S1.2). The data values for longevity reflect the maximum lifespan for each species, which is the most commonly reported measure in the literature (Magalhães *et al.*, 2007; Scharf *et al.*, 2015; Stark *et al.*, 2020a; Wilkinson & Adams, 2019).

2.2 | Confounding variables

Records for maximum longevity may provide information on lifespan only if adjusted for sample size, as the probability of recording extremely old individuals increases with sample size (Stark & Meiri, 2018). Furthermore, there are some drawbacks in using maximum values as estimates of longevity given that the maximum age of an individual may not be representative of the species as a whole (Carey, 2003) or that estimates could be based on unequal numbers of individuals for different species (Stark *et al.*, 2018). Therefore, the sample sizes for which longevity is estimated for each species were used to correct for these potential biases inherent in the use of maxima. Following Stark *et al.* (2020b), data on sample sizes from AnAge and classified small sample as species with one individual, medium samples as having 11 specimens per species, and large samples as having 101 individuals sampled were used. Moreover, it was noted whether maximum longevity was measured in captivity or in the wild due to the possible bias of using only captive specimens that are not exposed to extrinsic mortality factors (in captivity there are no predators and animals receive ample food and veterinary care) and thus may have higher values (Stark & Meiri, 2018). Accordingly, data obtained from the wild or from captivity may not be equivalent. Thus, the source of longevity data was also included (as well as sample size) as a fixed factor in all the models.

Most life-history traits may covary with life span and brain size (Healy *et al.*, 2019; Tsuboi *et al.*, 2018), therefore it is important to examine their correlative relationship with brain size and longevity. Covariation of life-history traits is common across species (Bakewell *et al.*, 2020; Bielby *et al.*, 2007; Healy *et al.*, 2019), therefore data on life-history traits that are typically correlated with life span from previous studies on fish taxa was extracted (Mull *et al.*, 2020; Rochet *et al.*, 2000), including indicators of parental investment such as age at sexual maturity, clutch and egg size, and reproduction mode.

2.3 | Phylogenetic and statistical analyses

Prior to analyses, continuous variables were checked for normality using the Shapiro–Wilk test and log transformed to reduce heteroscedasticity. In comparative studies, closely related species are more likely to demonstrate similar life-history strategies and phenotypes due to shared ancestry (Healy *et al.*, 2019). Thus, to control for the shared evolutionary history, phylogenetic generalized least squares (PGLS) regression (Freckleton *et al.*, 2002) was conducted using the most recent phylogeny for the Osteichthyes and Chondrichthyes groups. Rabosky *et al.* (2013) phylogeny was used for >30,000 living species of ray-finned fishes, while for sharks, rays and chimaeras, the tree from Stein *et al.* (2018) was used, which includes 610 species. The ‘caper’ package in R (Orme *et al.*, 2013) was used to estimate the maximum likelihood value of Pagel’s λ , a statistically powerful index for measuring whether data exhibit phylogenetic dependence and its strength (Freckleton *et al.*, 2002). The scaling parameter λ represents the magnitude of the phylogenetic signal in the data and model residuals (Freckleton *et al.*, 2002), with λ values covering a scale ranging from 0 (phylogenetic nonindependence) to 1 (complete phylogenetic dependence; Freckleton *et al.*, 2002).

To determine whether multicollinearity existed in the data among the predictor variables, the variance inflation factors (VIF; O’Brien, 2007) were calculated. In all the analyses none of the predictors had a VIF value higher than 5 and the analyses are thus not biased by multicollinearity (O’Brien, 2007). A phylogenetic ANCOVA test was conducted starting from a full model and using a backwards stepwise elimination procedure, sequentially deleting factors with P values >0.05 until a minimum adequate model was obtained in which all predictors were significant (at $\alpha < 0.05$). There were two main models: the first was for body size (predictor) and brain size (response), and the second, the PGLS model, included maximum longevity (years) as the dependent variable. Relative brain size (extracted residuals from a brain mass in grams against body mass in grams log–log least-square linear regression), log age at sexual maturity (years), log clutch (number of eggs of per batch) and egg size (mm) and reproductive mode (oviparous, ovoviviparous and viviparous) were included as covariates, while sampling size and the source of longevity data were entered as fixed factors. Each major fish group was analysed separately (Osteichthyes and Chondrichthyes) to determine whether the basic division of the Tree of Life among these groups influences the life-history traits (following Stark *et al.*, 2020b), which may in turn affect the relationship between brain size and longevity. All statistical analyses in this study were performed in R 4.1.2 (R Core Team, Vienna, Austria) using the RStudio 1.4.1106 (RStudio Inc., Boston, MA, USA) interface.

3 | RESULTS

3.1 | Brain size and longevity patterns

Brain size varied significantly among both Osteichthyes ($n = 329$) and Chondrichthyes ($n = 79$) species, and spanned several orders of magnitude among both groups (Figure 1a,b). Brain sizes in the database varied from 3 mg (banded pipefish *Doryrhamphus dactyliophorus*; Tsuboi *et al.*, 2017) to

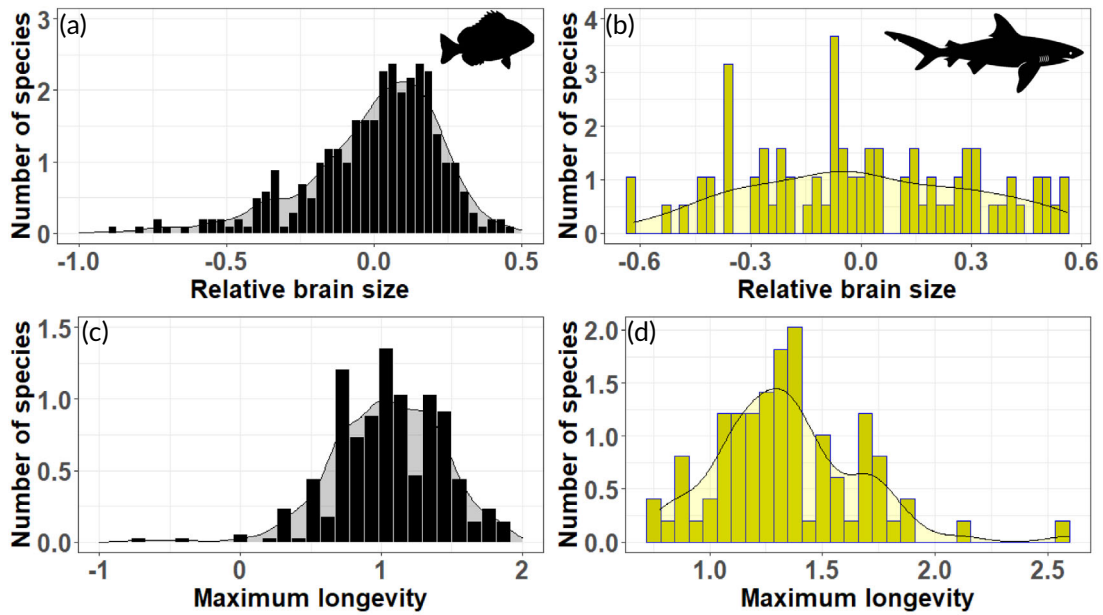


FIGURE 1 Distribution of the relative brain size (extracted residuals from a brain mass in grams against body mass in grams log–log least-square linear regression) and maximum longevity (years in log transformed) of (a) and (c) bony fish (Osteichthyes, black columns) and (b) and (d) cartilaginous fish (Chondrichthyes, yellow columns)

TABLE 1 Brain size as a function of body mass for bony and cartilaginous fishes using phylogenetic analysis

Factor	Estimate	Standard error	t	P
Intercept (Osteichthyes)	-1.889	0.186	-10.1	<0.0001
Body mass	0.506	0.010	47.4	<0.0001
$\lambda = 0.97, R^2 = 0.88, n = 316, P < 0.0001$				
Intercept (Chondrichthyes)	-0.895	0.152	-5.8	<0.0001
Body mass	0.411	0.029	13.8	<0.0001

Note: $\lambda = 0.93, R^2 = 0.80, n = 51, P < 0.0001$.

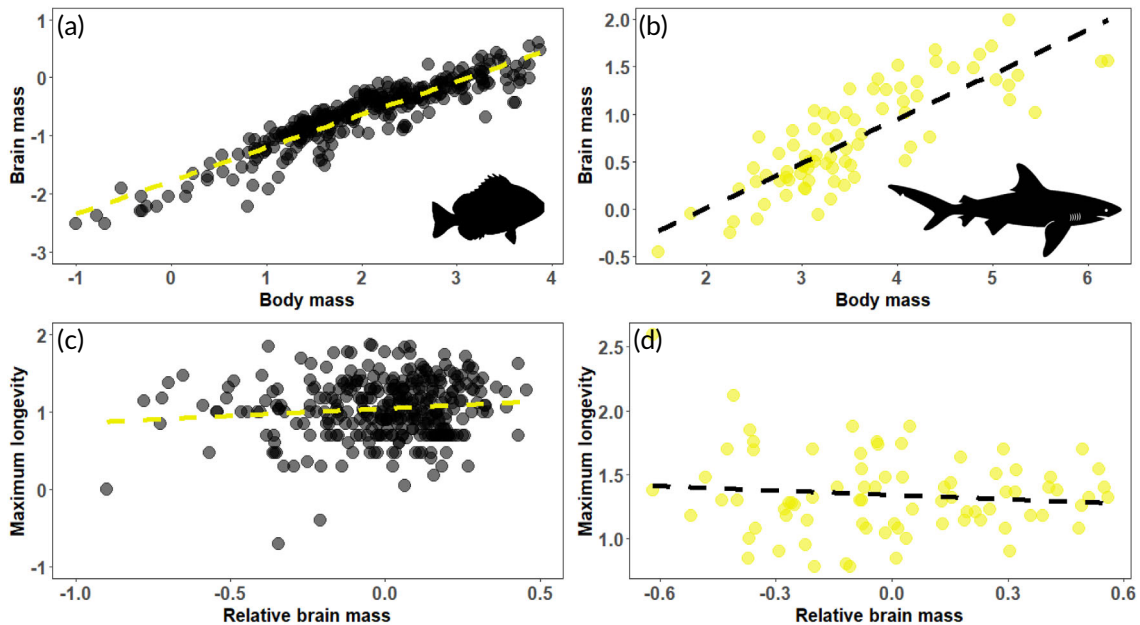


FIGURE 2 Top panels: the relationship between brain mass and body mass (both grams in log transformed) among (a) bony fish (Osteichthyes, black points, yellow dashed line) and (b) cartilaginous fish (Chondrichthyes, yellow points, black dashed line). Bottom panels: the relationship between relative brain size (extracted residuals from a brain mass in grams against body mass in grams log–log least-square linear regression) and maximum longevity (years in log transformed) among (c) bony fish and (d) cartilaginous fish

almost 4 g (yellowfin tuna *Thunnus albacares*; Tsuboi *et al.*, 2018) among bony fish, and from 355 mg (shortnose sawshark *Pristiophorus nudipinnis*; Mull *et al.*, 2020) to around 100 g (great hammerhead *Sphyrna mokarran*; Mull *et al.*, 2020) among cartilaginous fish. Maximum lifespan also varied extensively across bony fish species, from that of the blue sprat (*Spratelloides delicatulus*; Milton *et al.*, 1993), which lives only 5 months, to 104 years for the white sturgeon (*Acipenser transmontanus*; Cailliet *et al.*, 2001; Figure 1c). For cartilaginous fish, one of the shortest lifespan species in the dataset was the spadenose shark (*Scoliodon laticaudus*; Fowler & Cavanagh, 2005), which lives about 6 years, while the longest-living species (and also the longest-lived vertebrate known) was the Greenland shark (*Somniosus microcephalus*; Nielsen *et al.*, 2016), which can live up to a maximum of 392 years (Figure 1d).

3.2 | Body and brain mass among fish

The phylogenetic analyses (PGLS) performed between brain size and body size showed that brain mass increased with larger body mass (Table 1) for bony fish (Figure 2a) and cartilaginous fish (Figure 2b). In general, body size explained a major part of the variance in brain size among fish species (80%–88% for Chondrichthyes and Osteichthyes, respectively).

3.3 | Brain size and longevity

When the full PGLS models for the relationship between relative brain size and lifespan were analysed, while correcting for the confounding variables (*i.e.*, life-history traits and biasing factors, *e.g.*, origin of data

TABLE 2 Minimal adequate model for the analysis among fish classes

Factor	Estimate ^a	SE	t	P
Osteichthyes				
Intercept	0.693	0.225	3.0	0.002
Residual brain size	−0.064	0.118	−0.5	0.59
Age at sexual maturity	0.553	0.070	7.9	<0.0001
Clutch size	0.044	0.021	2.0	0.04
Sample size	0.046	0.028	1.6	0.11
Origin of data (wild)	−0.006	0.135	−0.1	0.96
Chondrichthyes				
Intercept	0.322	0.461	0.7	0.49
Residual brain size	−0.473	0.225	−2.1	0.04
Age at sexual maturity	0.717	0.093	7.6	<0.0001
Pup/egg size	0.480	0.178	2.6	0.01
Sample size	−0.057	0.066	−0.8	0.39
Origin of data (wild)	−0.391	0.294	−1.3	0.19

Note: Osteichthyes (bony fish) full model results: $\lambda = 0.615$, $R^2 = 0.35$, $n = 156$, $P < 0.0001$. Chondrichthyes (cartilaginous fish) full model results: $\lambda = 0.99$, $R^2 = 0.26$, $n = 35$, $P < 0.0001$. Model predictors shown below the intercept. SE, standard error.

^aEstimates for predictors in each model are slopes.

and sample size), no pattern emerged among bony fish (Table 2 and Figure 2). In contrast, the PGLS analysis on cartilaginous fish only found a negative relationship between relative brain size and maximum lifespan (slope = -0.473 ± 0.225 , $P = 0.04$). When bony fish species only were analysed, the PGLS model found an effect of some of the life-history traits on longevity, while others did not affect longevity (reproduction mode and egg size). Among cartilaginous fish species, a similar (positive) effect of age at maturity on longevity was found, as well as a positive effect of pup size on cartilaginous lifespans. Surprisingly, almost no effect of the fixed factors (sample size or origin of data) on maximum longevity among bony or cartilaginous fish was found (Table 2).

4 | DISCUSSION

This study presents the first large-scale analysis aimed at expanding our understanding of the relationship between lifespan and brain size across all vertebrate classes by contributing comparative evidence for fish clades that complements the existing evidence for tetrapods. Although the current study demonstrates considerable variations in relative brain size and maximum lifespans across bony and cartilaginous fish species, no evidence was found for any association between these two variables after controlling for several potential confounding factors, such as age at maturity, for bony fish clades (Osteichthyes). However, for sharks and rays (Chondrichthyes) a pattern did emerge. This finding (for Chondrichthyes species only) aligns with recent experimental evidence in guppies (*Poecilia reticulata*), in which lifespan decreases with larger brains (Kotrschal *et al.*, 2019). Thus, this research suggests that evolving a larger brain can increase the metabolic cost and divert energy from more life-extending processes (*e.g.*, somatic maintenance), which may promote the evolution of a shorter lifespan.

Evolutionary selective forces shaping brain size variation among vertebrates are constrained by the trade-offs between the cognitive advantages that are attained with a larger brain and the high energetic costs allocated towards its maintenance (Dunbar & Shultz, 2007; González-Lagos *et al.*, 2010; Harraan, 1955; Jiménez-Ortega *et al.*, 2020; Lefebvre *et al.*, 1997; Minias & Podlaszczuk, 2017; Mink *et al.*, 1981; Sol, 2009; Yu *et al.*, 2018). As a result, natural selection can favour either one strategy or the other depending on the extent to which a given increment in brain mass is accompanied by certain cognitive advantages that increase lifetime fitness despite its energetic costs. The pattern that seems to emerge among endotherms was a positive relationship between brain size and longevity, while a negative relationship emerged across terrestrial ectotherms (Barrickman *et al.*, 2008; Barton & Capellini, 2011; González-Lagos *et al.*, 2010; Isler & van Schaik, 2009; Jiménez-Ortega *et al.*, 2020; Kotrschal *et al.*, 2019; Minias & Podlaszczuk, 2017; Sol *et al.*, 2007, 2016; Stark & Pincheira-Donoso, 2022). Although the relative brain mass of birds and mammals can be up to 10-fold heavier than in amphibians and reptiles (Font *et al.*, 2019), this positive relationship between brain size and longevity is not observed in both fish classes.

The correlational results presented here may suggest a trade-off between brain-size and longevity across the Chondrichthyes class, but no such relationship was observed among Osteichthyes species. Consequently, it is suggested that the increment in cognitive faculties contributed by a larger brain mass remains below the threshold at which the fitness benefits of behavioural flexibility outweigh the energetic cost. Indeed, this study's findings are consistent with previous evidence that the cost of maintaining brain tissue is relatively higher in ectothermic species than in endothermic ones (Stark & Pincheira-Donoso, 2022).

There are several well-known differences between endotherms and ectotherms regarding brain metabolism: (1) ectotherms have a 10-fold lower whole-body resting metabolic rate (Mink *et al.*, 1981), (2) metabolic oxygen consumption of the central nervous system and the metabolic cost of ectothermic brain tissue are as high as those of birds and mammals (Stark *et al.*, 2020b), and (3) there is strong support for negative trade-offs between brain size and other traits (as proposed by the EBF; Isler & van Schaik, 2009), observed from studies on ectothermic groups such as fishes (Kotrschal *et al.*, 2013; Tsuboi *et al.*, 2014) and amphibians (Liao *et al.*, 2016). Overall, these differences reinforce the assumption that brain tissue may be relatively more costly to generate and maintain in ectotherms, which could lead to the negative relationship between brain size and lifespan observed in cartilaginous species.

The inconsistency observed in the brain size/lifespan relationship among fish classes is difficult to explain. It may be that these patterns emerged from the fundamental differences in the major life-history and phylogenetic discrepancies between the two classes, which are likely to lead to internal differences in how key traits trade off the allocation of energetic budgets as a function of their contribution to lifetime fitness. Reproduction investment is critical for management of energy allocation, with both groups differing considerably in their reproductive activities and outputs. For example, bony fish generally engage in energetically demanding reproductive output, with females tending to have much larger numbers of offspring than do sharks or rays (*e.g.*, the Atlantic sturgeon *Acipenser oxyrinchus* can produce up to 2.5 million eggs, while the ocean sunfish *Mola mola* can release 300 million eggs over the course of one spawning season; Van Eenennaam *et al.*, 1996; Forsgren *et al.*, 2020). To support this reasoning, it may be essential to look into further biometric parameters such as the gonadosomatic index (GSI), which can act as a good indicator of reproductive activity in fish while also helping to evaluate the way the species get resources from the habitat. This kind of parameter should be incorporated in future studies that investigate reproductive differences among fish clades.

Furthermore, bony fishes may make use of the extra computing power a larger brain confers, with better cognitive flexibility or similar. This may outweigh the energetic costs of such a brain and so conceal the relationship between brain size and longevity. In cartilaginous fishes a relatively larger brain may not be useful as it may not transfer into any cognitive advantage that may increase survival. However, the specific explanation for these observed discrepancies remains difficult to establish at present without risking much speculation.

In conclusion, the results of this study indicate that the link between brain size and longevity may only be contingent on the mechanism of mortality, as was found experimentally in fish (Kotrschal *et al.*, 2019). It is shown that the evolutionary patterns of an animal's life history are not consistent across vertebrate taxa, and that differences between bony and cartilaginous fish species should be accounted for when examining the relationship of brain size and lifespan among classes of the same taxa. Thus, this research suggests that across macroecological scales the high metabolic cost of producing neural tissue may surpass the cognitive benefits of evolving a larger brain, resulting in a negative pattern among cartilaginous fish.

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CONFLICT OF INTEREST

There are no competing interests for the author of this manuscript.

DATA ACCESSIBILITY STATEMENT

All data used in the analyses and the associated metadata are available in Supporting Information Appendix S1. All codes used in the analyses are available in Supporting Information Appendix S2.

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