INTRODUCTION

Brain size varies considerably across the animal kingdom, both in absolute and in relative terms (Isler & van Schaik, 2012; Gonda et al., 2013; Sayol et al., 2016; Mai & Liao, 2019). The development and maintenance of a large brain are costly (Martin, 1981; Pagel & Harvey, 1988; Niven & Laughlin, 2008), and we thus require evolutionary explanations for why some organisms invest more heavily into their brains than others. A wide range of hypotheses have been proposed in this regard, and these fall into two broad categories: first, there are hypotheses concerning the costs of and constraints on brain size increases, with a focus on identifying those conditions...
under which these limitations are relaxed, as in the ‘expensive brain/tissue hypothesis’ (Aiello & Wheeler, 1995; Isler & van Schaik, 2009). Second, there are hypotheses concerning the potential benefits of enlarged brains. Among these, the ‘social brain hypothesis’ (Dunbar & Shultz, 2007) and the ‘cognitive buffer hypothesis’ (Sol, 2009) have attracted considerable interest and inspired large bodies of work. An underlying assumption of these ideas is that enlarged brains enhance cognitive ability and/or behavioural flexibility, which in turn convey adaptive benefits. The two sets of hypotheses are not mutually exclusive, but put different emphasis on the two sides of the fundamental trade-offs between brains and other ecological and physiological processes. In other words, where larger brains evolve, these must either confer greater benefits or incur reduced costs compared to those situations where brains remain small.

Across vertebrates, evolutionary costs of enlarged brains have been documented in a variety of systems. Fecundity is reduced as brains get bigger in birds (Jiménez-Ortega et al., 2020) and mammals (Weisbecker & Goswami, 2010), likely because larger brains necessitate the production of fewer but larger offspring (Isler & van Schaik, 2009). As a consequence, large brains are proposed to only evolve where post-zygotic parental care allows for extended developmental times and increased resource availability (Barton & Capellini, 2011; Tsuboi et al., 2018). Accordingly, investment into digestive tracts decreases with increasing brain size in anurans (Liao et al., 2016), guppies (Kotschal et al., 2013) and cichlids (Tsuboi et al., 2015), likely because of energetic and developmental trade-offs between these different organs. The costs incurred from large brains can even reduce immune function (Kotschal et al., 2016) and ultimately lifespan (guppies (Kotschal et al., 2019); wasps (van der Woude et al., 2019)). In addition, migration (Winkler et al., 2004; Sol et al., 2010), hibernation (Heldstab et al., 2018), diet (DeCasien et al., 2017), reproduction (Tsuboi et al., 2015), and morphology and development (Koyabu et al., 2014) have been proposed as constraining brain sizes. These findings are interpreted as support for the ‘expensive tissue hypothesis’ (Aiello & Wheeler, 1995; Isler & van Schaik, 2009), showing how the energetic costs of building, maintaining and carrying a large brain as measured at the individual-level influence evolutionary patterns (Kuzawa et al., 2014).

Benefits of larger brains have also been identified across taxa and traits, likely because larger brains typically afford individuals with greater numbers of neurons and inter-neuronal connections, which in turn allow for increased information storage, behavioural flexibility and overall cognitive ability (Gonda et al., 2013). A key advantage suggested in this regard is the ability to reap greater benefits from increased sociality (‘social brain hypothesis’ (Dunbar & Shultz, 2007)). Monogamy, for example, has been shown to co-occur with increased brain size in primates (Schillaci, 2006), carnivores and ungulates (Shultz & Dunbar, 2007) and across birds (Shultz & Dunbar, 2010; West, 2014), with researchers arguing that this pattern emerges because stable social interactions between monogamously paired partners have increased cognitive demands, but in turn enhance reproductive success. A similar argument concerns the co-evolution of parental care and brain size: because caring for young is cognitively demanding, it necessitates the evolution of larger brains (carnivores (Gittleman, 1994); cichlids (Gonzalez-Voyer et al., 2009)), but also greatly improves offspring survival. Indeed, there appears to be positive feedback between increases in brain size and longevity in several taxa (birds (Minias & Podlaszczuk, 2017; Jiménez-Ortega et al., 2020); mammals (González-Lagos et al., 2010)), either because larger brains favour reduced senescence (e.g. by reducing mortality via increased sociality (Isler & van Schaik, 2012) and/or decreased predation (Kondoh, 2010)), or because longer lives increase the payoffs of large brains (e.g. by increasing the scope for social learning (Street et al., 2017) and/or social bonds (Shultz & Dunbar, 2010)). Further, success in novel environments is increased for species with larger brains among mammals (Sol et al., 2008) and birds (Sol et al., 2005), and larger brains also occur in mammalian species that experience increased variability in food resources (primates (van Woerden et al., 2014)) or use different habitat types (ungulates (Shultz & Dunbar, 2006)). In birds, larger-brained species also do better in urban environments (Maklakov et al., 2011) and under variable environmental conditions (Schuck-Paim et al., 2008; Fristoe et al., 2017). These findings are taken as support that enlarged brains help animals to deal with environmental variability and complexity (‘cognitive buffer hypothesis’ (Sol, 2009)), a view in line with other proposed adaptive benefits of larger brains (e.g. reduced predation risk (Kotschal et al., 2015), increased attractiveness to mates (Boogert et al., 2011), or enhanced tool use (Lefebvre et al., 2002)).

Much of the work on brain size evolution has focused on birds and mammals (Figure 1), with comparably few studies looking at other vertebrates (particularly when correcting for total species

![FIGURE 1](cumulative_number_of_articles.png)

**FIGURE 1** Cumulative number of publications on brain size evolution (y-axis) over time (x-axis) by taxonomic group (see legend; green line and squares: birds; brown line and triangles: mammals; blue line and circles: fishes). We performed a literature search using the online database ‘Web of Science’ using the keywords ‘brain size’ and ‘evolution’ AND ‘mammal’, OR ‘fish’ OR ‘birds’. Afterwards, we manually scanned the titles of all papers and removed cases which clearly did not investigate questions related to brain size evolution in any of the three taxa. In total, this search revealed 720 publications (364 mammal, 296 bird and 97 fish studies) from 1977 to 2020.
numbers (Wiens, 2015). Although all of this work is highly valuable, it brings with it some limitations, namely the fact that birds and mammals may not be representative of vertebrates as a whole (let alone all animals), particularly with regard to brain evolution. This is because Aves and Mammalia are evolutionarily young Classes (Irisarri et al., 2017), they are determinate growers (Hariharan et al., 2016), and they all perform post-zygotic parental care (Reynolds et al., 2002), with the exception of some brood parasites, they have much larger relative brain sizes than most other animals (Tsuboi et al., 2018), and their brain morphologies are very distinct from those of other groups (Butler & Hodos, 2005). In addition, various aspects of brain evolution claimed to be of general relevance due to their support from data on birds and mammals remain contentious in specialist fields (e.g. the role of sociality in primate brain evolution (Dunbar & Shultz, 2007; DeCasien et al., 2017)). It thus appears necessary to test some of these hypotheses also in other taxa. To this end, we compiled a dataset of brain sizes and relevant ecological and behavioural variables for several classes of ‘fishes’, using this term in a general, not explicitly taxonomic sense (see below). Our source is a publicly available database known as FishBase (www.fishbase.se; Froese & Pauly, 2000). As such, FishBase contains information on Actinopteri (the majority of ray-finned fishes), Cladistii (bichirs and polypterids), Coelacanths (coelacanths), Dipneusti (lungfishes), Elasmobranchii (sharks and rays), Holocephali (chimaeras), Myxini (hagfishes) and Petromyzonti (lampreys). Although being polyphyletic, these taxonomically diverse groups have traditionally been referred to as ‘fishes’, highlighting their ecological and morphological similarities, and their close association with aquatic habitats (Helfman et al., 2009). Our dataset thus allows to probe findings from studies of brain evolution in birds and mammals in a range of taxa that share some key traits (they are aquatic indeterminate growers) while being phylogenetically distinct, evolutionarily old, within each group ecologically diverse (including a wide range of sizes, trophic adaptations, [parental] behaviours and reproductive modes), and of central importance in evolutionary sciences and neurobiology (Mank et al., 2005; Helfman et al., 2009; Kaluuff et al., 2014; Vila Pouca & Brown, 2017; Maruska & Fernald, 2018).

Specifically, we wanted to investigate the support from fishes for the ‘expensive tissue hypothesis’ (Isler & van Schaik, 2009), the ‘social brain hypothesis’ (Dunbar & Shultz, 2007) and the ‘cognitive buffer hypothesis’ (Sol, 2009), in order to unravel whether the costs and benefits of enlarged brains are similar between birds, mammals and fishes. This is of particular interest, because fish brains continue to show high levels of neurogenesis also in adulthood, in stark contrast to the very limited cellular development and regeneration of adult avian and mammalian brains (Zupanc & Horschke, 1995; Ganz & Brand, 2016). By extending the potential timeframe for brain growth, this may alter the costs and benefits of large brains in fishes (Tsuboi, 2021), despite the allometric relationships between body mass and brain mass in adults being similar for all vertebrate classes (Tsuboi et al., 2018). After initial examination of the data, we thus selected six ecological/phenotypic traits relevant to the above hypotheses, and devised three principal models to correlate these traits with brain weight, the most widely available measure of brain size, in a phylogenetically controlled way. Each of these models contained two of the selected traits that are biologically related and also had a large overlap in data availability in our dataset. As such, the first model included information on life history characteristics: fecundity and lifespan. We predicted that larger brains would co-occur with reduced fecundity and increased longevity. The second model included breeding system traits: mating system and parental care behaviour. We predicted a positive association between brain size and monogamy and parental care. The third model included habitat features: whether species occupy less complex pelagic or more complex benthic environments (Axelrod et al., 2018) and whether species migrate between marine and freshwater environments or not (McDowall, 1992). We predicted a positive correlation between brain size and habitat complexity and a trade-off-between costly migratory behaviour and brain size.

2 | MATERIALS AND METHODS

2.1 | Data acquisition and organization

Using the R package rfishbase (version 3.1.6 (Boettiger et al., 2021)), we downloaded information from FishBase (www.fishbase.se; Froese & Pauly, 2000) using the package’s default commands and functions (all data initially downloaded during the second half of March 2021). FishBase is a publicly available database and analysis tool with the aim ‘to provide key information on fishes of the world, that is both global and deep’ (Froese & Pauly, 2000). For more than three decades, FishBase has pursued this goal by extracting data from the primary and secondary literature on fishes and collating it in a searchable digital repository. As such, a lot of information has been manually transcribed from scientific articles, books and other forms of publishing into FishBase’s data structure, with the respective source being referenced in FishBase. It should thus be noted that the data found on FishBase is imperfect, either because existing information has not (yet) been included, information was included inaccurately (e.g. typos), or the information in the source material was already wrong (Froese & Pauly, 2000). There are ongoing efforts to make FishBase as error-free as possible, and by being an openly available database in which only already published information is included, at least two lines of checks exist: first, data need to pass reviewing processes during their initial publication. Second, once data enter FishBase, they are subject to the scrutiny of its users, which has repeatedly led to updates and corrections (Froese & Pauly, 2000). FishBase is thus the most reliable and comprehensive source of information for the greatest number of fish species currently available (Froese & Pauly, 2000). Our aim here was to collate a comprehensive dataset of brain sizes and corresponding variables of interest that relate to our questions about (i) associations between brain size and certain life history parameters; (ii) co-evolutionary links between breeding systems and brain size; (iii) and potential influences of habitat features on brain size evolution. To this end, we pre-screened
all data available on FishBase for relevant information and selected those variables that we deemed most biologically meaningful. We did not trace entries on FishBase back to their sources. We selected two life history parameters (longevity and fecundity), two aspects of breeding systems (mating system and post-zygotic parental care) and two habitat features (a pelagic or demersal lifestyle and the presence or absence of migrations between marine and freshwater habitats) for our analyses. Specifically, we first extracted data for each species from FishBase’s ‘Species Table’ using the rfishbase function ‘species’ (see Froese & Pauly, 2000) for descriptions of each of the FishBase-specific terms indicated by quotation marks). For each species, we included the scientific name (column name in the table: ‘Species’), habitat information (‘DemersPelas’ (indicating whether the species follows a demersal or pelagic lifestyle), ‘AnaCat’ (indicating whether the species migrates between marine and freshwater habitats or not), life history information (‘LongevityWild’, ‘LongevityCap’ (indicating lifespan estimates in years in the wild or in captivity, respectively), and body size information (‘Length’ (length measurements in centimetres), ‘LengthTypeMaxM’ (indicating the type of length measurement provided; see Appendix S1) and ‘Weight’ (weight measurements in grams). This yielded a total of 34,299 species entries. As FishBase’s ‘Orders Table’ is currently not available via rfishbase, we manually added information on higher taxonomic classifications from FishBase’s ‘Classification List’ (https://www.fishbase.se/tools/Classification/ClassificationList.php), yielding an entry for Genus, Family, Order and Class for each of the 34,299 species. Every species was classified as pelagic or demersal, and 4,025 were classified as migratory between marine and freshwater habitats or as non-migratory. For 117 species, longevity data in years from both captivity and the wild were available, whereas at least one of these estimates was provided for 212 (captive) and 1,341 (wild) species, respectively. We elected to use the larger of these two measurements wherever both were provided. A length measurement in centimetres was given for 30,180 cases (see Appendix S1). Weight data in grams could be retrieved for 2,184 species. Both length and weight data were provided as maximum values recorded for a given species. We then downloaded fecundity data using the rfishbase function ‘fecundity’ and including the columns ‘Species’, ‘FecundityMin’ (2,300 entries for 1,374 species), ‘FecundityMax’ (2,607 entries for 1,570 species) and ‘FecundityMean’ (112 entries for 88 species), where fecundity is given as the number of eggs/oocytes found in a single ripe female. We elected to use the maximum value provided in any of the fecundity data for each species, resulting in a total sample size of 1,763 species. We downloaded information on the breeding system of each species using the rfishbase function ‘reproduction’ and including ‘Species’, ‘MatingSystem’ (995 species), ‘RepGuild1’ (10,645 species), ‘RepGuild2’ (8,218 species) and ‘ParentalCare’ (6,761 species). We classified species as either monogamous or polygamous (pooling all species classified as polyandrous or promiscuous), and as either showing post-zygotic parental care (pooling all species that do not just scatter their eggs upon mating, see Froese & Pauly, 2000) for detailed descriptions of categories) or not performing care. This yielded a total of 995 species for which we had mating system information and 10,655 species with information on post-zygotic parental care (also referred to as ‘parental care’ throughout the manuscript). Subsequently, we used the rfishbase function ‘brains’ to download a total of 5,744 brain weights (‘BrainWeight’ in milligrams) and the weight of the corresponding donor individual (‘BodyWeight’ in grams) from FishBase, representing 1,436 species (as above, we included ‘Species’ for later merging of information). Information on a donor individual’s sex was only available for 36 species, and we thus omitted ‘Sex’ in our analyses. For each species for which multiple brain and donor weights were available, we chose to include in our species comparisons only the data of the heaviest individual measured, making it more comparable to our other phenotypic information (maximum length, weight, lifespan and fecundity). Notably, relative brain weight (brain weight divided by donor weight, referred to as ‘EncCoeff’ in FishBase) declines with body weight (and body length) both within and across species (Kotrschal et al., 1998; Appendix S2). By considering only the data of the largest individual available, we minimize potential biases stemming from greater proportions of juveniles measured for some species.

We elected to perform all analyses separately for each class, due to their distant taxonomic relatedness (Meyer & Zardoya, 2003), the lack of a fully resolved and dated phylogeny for all of our focal species, and the clear differences in brain evolution between the included classes (Figures S1.1, S2.3, S3.11; Butler & Hodos, 2005; Lisney & Collin, 2006). In line with previously published data (Salas et al., 2017; Tsuboi et al., 2018), we found the following allometric regression slopes (±SE) between body mass and brain mass: Actinopteri: 0.48±0.01 (n=1,267 species; r2=0.72); Elasmobranchii: 0.43±0.02 (n=140 species; r2=0.7); and Petromyzonti: 0.28±0.05 (n=15; r2=0.72). Due to sample size limitations and highly skewed data distributions, analyses of breeding systems and habitat features were only performed for Actinopteri (see Appendix S4 and Appendix S5 for details). As such, we divided our complete dataset into five subsets: one each for Elasmobranchii and Petromyzontii in the analysis of the potential costs of large brains (see below), and three for Actinopteri (one each for the analysis of the potential costs of large brains, the analysis of potential links between breeding systems and brain size, and the analysis of potential links between habitat features and brain size). Each analytical step, that is taxonomic reconstructions, estimates of phylogenetic signal and statistical analyses, was performed separately for each of these datasets. We thus use 5 phylogenetic hypotheses, 20 estimates of phylogenetic influence and 5 statistical models throughout this manuscript.

### 2.2 Taxonomic reconstructions

We reconstructed taxonomic relationships for all species in a given analysis. Each tree (phylogenetic hypothesis) was devised in the same principal manner: using ape’s (version 5.5; Paradis et al., 2004; Paradis, 2012) ‘as.phylo’ function, we aligned species according to
their Order, Family and Genus and subsequently computed branch lengths using the ‘compute.brlen’ function with Method set to ‘Grafen’ (Grafen, 1989). The resulting trees are necessarily unrooted (we include no outgroup) and non-binary (nodes can have > 2 daughter nodes), and branch lengths are arbitrary (we include no estimates of divergence times).

2.3 Estimates of phylogenetic signal

For each variable of interest, we estimated the influence of the underlying phylogeny on the variable’s distribution in a given dataset by Moran’s autocorrelation index (Moran’s I), using ape’s ‘correlogram.formula’ function (Paradis, 2012). Moran’s I was chosen over other estimates of phylogenetic signal (Münkemüller et al., 2012) because it quickly afforded us with a graphical representation of whether the use of phylogenetically corrected analyses was necessary, doing so in a fairly conservative way (Münkemüller et al., 2012; Paradis, 2012). Given the limitations of our taxonomic reconstructions (see above), we deemed this the most reasonable approach (see (Symonds & Blomberg, 2014), for a brief discussion of the need to statistically correct for phylogenetic correlations in comparative data). We estimated Moran’s I at each taxonomic level available, that is for the influence of Order, Family and Genus. However, this was not possible in the analysis of potential costs of large brains among Petromyzonti and we estimated Moran’s I only at that level at which variation in the dataset was observed, Genus (all species in the dataset being assigned to the same Order and Family).

2.4 Statistical analyses

Phylogenetically controlled generalized least squares models (pGLS; Symonds & Blomberg, 2014) were fitted by residual maximum likelihood (REML) methods using nime’s (version 3.1–152; Pinheiro & Bates, 2021) ‘gls’ function. In total, we fitted 5 models (see above). We assumed a Brownian mode of evolution and thus used ape’s ‘corBrownian’ function (Paradis, 2012) to create the respective correlation structure for each model. Prior to running the models, continuous variables were natural logarithm (ln) transformed. Each model included brain weights as response variable and, to control for the strong impact of allometric scaling on relationships between brain size and body size (Appendix S2), maximum body weight (ln transformed) as an explanatory variable. For analyses of the potential associations of large brains with certain life history traits, we fitted models that included a species’ maximum lifespan and fecundity as additional explanatory variables (both ln transformed; a total of three models, one each for Actinopteri, Elasmobranchii and Petromyzonti). To investigate potential links between breeding systems and brain size, we fitted a model that instead included a species’ mating system and whether it shows post-zygotic parental care as additional explanatory variables (both binary and thus untransformed; one model for Actinopteri). The model scrutinizing the effect of habitat features on brain evolution instead included whether a species is pelagic or not and whether it migrates between marine and freshwater habitats or not as additional explanatory variables (both binary and thus untransformed; one model for Actinopteri). We fitted each model with the (ln transformed) absolute values as downloaded from FishBase, and with Z values derived for each dataset ($Z_i = (x_i - \bar{x}) / S$, where $Z_i$ is the Z score of species $i$ for a given variable of interest $x$; $x_i$ is the absolute value of variable $x$ for species $i$; $\bar{x}$ is the mean value of variable $x$ across all species in the respective dataset; and $S$ is the standard deviation of variable $x$ across all species in the respective dataset). As expected, t-values and p-values did not differ between models using Z transformed or absolute values, but estimates and standard errors necessarily did (see Appendix). Following recommendations for unbiased representation of phylogenetically controlled analyses (Mundry, 2014), we only include findings from Z values in the main manuscript, but present all results on absolute data in the Appendix to show that Z transformation itself did not impact our conclusions. We used ‘summary’ to extract model estimates and subsequently created various diagnostic plots to probe each model’s fit (see Appendix). All work was carried out in R (version 4.1.0; R Development Core Team, 2013). We divide our results into those that are ‘significant’ (i.e. $p \leq 0.05$) and those that are ‘not significant’ (i.e. $p > 0.05$; see (Wasserstein et al., 2019) for a discussion on the use of such strict cut-off values), and we provide estimates of effect and sample sizes to help with the interpretation of results.

3 RESULTS

3.1 Is increased brain size associated with certain life history traits?

Information on brain weight, body weight, fecundity and lifespan was available for 162 species. We computed Class-specific pGLSs for Actinopteri (111 species; Figure S3.1), Elasmobranchii (40 species; Figure S3.2) and Petromyzonti (8 species; Figure S3.3), but not for Coelacanthi (1 species) or Dipneusti (2 species; see Appendix S3 for additional details). We found a strong phylogenetic signal in each dataset, warranting the use of statistical approaches that aim to control for phylogeny (for more details see Figure S3.4; Paradis, 2012). Fecundity significantly decreased with increasing brain weight among Elasmobranchii ($t = -4.751$, $p < 0.001$; Appendix S3.7, Appendix S3.8; Figure 2c), but not among Actinopteri ($t = 0.065$, $p = 0.948$; Appendix S3.5, Appendix S3.6; Figure 2a) or Petromyzonti ($t = -2.563$, $p = 0.063$; Appendix S3.9, Appendix S3.10; Figure 2e). Lifespan significantly decreased with increasing brain weight among Petromyzonti ($t = -3.187$, $p = 0.033$; Appendix S3.9, Appendix S3.10; Figure 2f), but not among Actinopteri ($t = 0.777$, $p = 0.439$; Appendix S3.5, Appendix S3.6; Figure 2b) or Elasmobranchii ($t = -2.014$, $p = 0.052$; Appendix S3.7, Appendix S3.8; Figure 2d). Body weight was a significant predictor of brain weight in all analyses (Actinopteri: $t = 7.18$, $p < 0.001$; Elasmobranchii: $t = 7.29$, $p < 0.001$; Petromyzonti: $t = 7.03$, $p < 0.001$).
Are there co-evolutionary links between breeding systems and brain size?

Potential co-evolutionary links between brain weight and breeding systems could be investigated in 148 species of Actinopteri (Figure S4.1) where information on brain weight, body weight, mating system and parental care behaviour was available (see Appendix S4 for additional details). Again, we found a strong phylogenetic signal, warranting the use of statistical approaches that aim to control for phylogeny (for more details, see Appendix S4.2). Monogamous species had heavier brains than polygamous ones ($t = 2.23, p = 0.027$), but the size of this effect was small (Figure 3a). Parental care was not significantly associated with changes in brain weight ($t = -1.943, p = 0.054$), despite seemingly clear differences between caring and non-caring species (Figure 3b). Again, body weight was a significant predictor of brain weight ($t = 18.381, p < 0.001$; Appendix S4.3, S4.4).

Do habitat features influence brain size evolution?

Patterns of co-evolution between brain weight and habitat features could be investigated for 435 species of Actinopteri (Figure S5.1). Although data on brain weight, body weight, migratory behaviour and habitat type were available for several species of other Classes, distributions of trait values were heavily skewed in these (see Appendix S5 for additional information; for example, all Petromyzonti classified as demersal). In Actinopteri, we found a strong phylogenetic
**FIGURE 3** The potential co-evolutionary links between brain size and breeding systems in Actinopteri, represented as the relationship between brain size (y-axes; \(Z\) values of ln transformed absolute brain weights in mg) and (a) mating system (x-axis; species either classified as monogamous (‘yes’; dark pink) or not (‘no’; light pink)) or (b) parental care behaviour (x-axis; species either classified as showing post-zygotic parental care (‘yes’; dark blue) or not (‘no’; light blue)). See Methods for details of categorizations. Numbers below boxes give sample sizes as numbers of species (total \(n = 148\) Actinopteri in both plots). (a) Monogamous species had heavier brains than polygamous ones (\(p = 0.027\)). (b) Parental care was not significantly associated with changes in brain weight (\(p = 0.054\)). See Results for details of analyses.

**FIGURE 4** The potential co-evolutionary links between brain size and habitat features in Actinopteri, represented as the relationship between brain size (y-axes; \(Z\) values of ln transformed absolute brain weights in mg) and (a) migratory behaviour (x-axis; species either classified as migratory (‘yes’; dark yellow) or not (‘no’; light yellow)) or (b) habitat type (x-axis; species either classified as pelagic (‘yes’; dark green) or not (‘no’; demersal lifestyle; light green)). See Methods for details of categorizations. Numbers below boxes give sample sizes as numbers of species (total \(n = 435\) Actinopteri in both plots). (a) Brain weight did not differ between migratory and non-migratory species (\(p = 0.267\)), (b) nor between pelagic and demersal species (\(p = 0.19\)). See Results for details of analyses.
signal, warranting the use of statistical approaches that aim to control for phylogeny (for more details see Appendix S5.2). Brain weight did not differ between migratory and non-migratory species ($t = -1.113, p = 0.267$; Figure 4a), nor between pelagic and demersal species ($t = 1.313, p = 0.19$; Figure 4b), but body weight was a significant predictor of brain weight ($t = 30.822, p < 0.001$; Appendix S5.3, S5.4).

**4 | DISCUSSION**

Our results show that large brains incur costs to fecundity and longevity in at least some Classes of fishes (Figure 2), and that breeding system traits indeed co-evolve with brain size in Actinopteri (Figure 3), whereas proxies of habitat variability and complexity do not (Figure 4). As such, our findings do support some of the hypotheses about costs and benefits in brain size evolution as derived predominantly from birds and mammals and outlined in the Introduction, namely that large brains co-occur with reduced fecundity (indicating a cost (Isler & van Schaik, 2009)) and increased sociality (indicating a benefit (Shultz & Dunbar, 2007)). Interestingly, we did not find support for the often reported positive correlation between brain size and lifespan (González-Lagos et al., 2010; Minias & Podlaszcuk, 2017; Jiménez-Ortega et al., 2020) among Elasmobranchii and Petromyzonti this relationship was negative (albeit not significantly so in Elasmobranchii), and there was no strong effect for Actinopteri (Figure 2). Similarly, the proposed positive link between post-zygotic parental investment and brain size (Gittleman, 1994; Gonzalez-Voyer et al., 2009; Shultz & Dunbar, 2010; Tsuboi et al., 2015) was reversed in our data: caring Actinopteri species had smaller brains (albeit not significantly so; Figure 3b).

If we assume that those cases where our findings in fishes match those from birds and mammals are the result of similar selective forces, exerted by similar costs and benefits of enlarged brains, two aspects of brain evolution appear near universal in vertebrates: first, large brains necessitate shifts in reproduction towards higher per-capita investment and thus reduced fecundity (Figure 2; (Isler & van Schaik, 2009)). Indeed, increased maternal investment is associated with larger brains among sharks and rays (Mull et al., 2020), and selection for increased brain size reduces fecundity in guppies (Kotrschal et al., 2013). Second, increased sociality requires increased investment into cognitive skills and thus larger brains (Figure 3a; Dunbar & Shultz, 2007)). In the special case of that measure of a more social lifestyle which we use in this study, monogamy, an additional factor may be at play: monogamy likely frees up resources for brain growth that might otherwise be directed towards sexually selected traits in polygamous species (Pitnick et al., 2006; Schillaci, 2006). However, some previous works have failed to find similar support for links between brain size and fecundity (Drake, 2007) or sociality (Reddon et al., 2016), particularly in Actinopteri. We thus need additional data and analyses to draw firmer conclusions. This is also true in those cases where our results diverge from our expectations. In several regards, our data reveal aspects of brain evolution that seemingly do not universally apply to all vertebrates.

First, why is there no appreciable reduction in fecundity as brain size increases among Actinopteri (Figure 2a)? In several groups of fishes, a negative relationship between fecundity and brain size has been shown: across sharks, rays and chimaeras, increased maternal investment per offspring (and thus necessarily reduced offspring numbers for the same amount of maternal investment) is related to larger brain size (Mull et al., 2011; Mull et al., 2020), equivalent to our own findings for Elasmobranchii and Petromyzonti (Figure 2c,e). Even more strikingly, among Actinopteri at least some taxa appear to also follow this pattern, with increased egg sizes (and thus necessarily fewer eggs produced for the same amount of maternal investment) co-occurring with enlarged brains (cichlids: (Tsuboi et al., 2015)). However, no clear support for a trade-off between brain size and reproduction is found in other Actinopteri (Drake, 2007; Rowiński et al., 2020). It may thus be that across Actinopteri, with their great diversity in reproductive strategies and ecological adaptations (Helfman et al., 2009), this trade-off is masked, for example, by concurrent reductions in egg size as brain size increases (Closs et al., 2013; Jonsson & Jonsson, 2014). Unfortunately, information on such potential effects was too limited in our dataset to allow us to confidently explore this further.

Second, why does lifespan not increase with increasing brain size in Actinopteri, Elasmobranchii, or Petromyzonti (Figure 2)? The most drastic difference between our results on fishes and previously published results on birds and mammals (and anurans: (Mai & Liao, 2019)) is the non-existent or even negative (in Petromyzonti) relationship between brain size and longevity in our data. That being said, works on links between lifespan and brain size in taxonomically more narrow sets of fish groups had already hinted in this direction (Kotrschal et al., 2019; Sowersby et al., 2021). It thus appears that those factors that likely result in the concerted increases in longevity and brain size observed in other vertebrates, namely increases in sociality and reductions in mortality (Kondoh, 2010; Shultz & Dunbar, 2010; Isler & van Schaik, 2012; Street et al., 2017), do not apply to fishes (Reddon et al., 2016). Additionally, fishes are exceptional among vertebrates for their longevity (Reznick et al., 2002; Nielsen et al., 2016) and neurogenesis (Ganz & Brand, 2016). They are indeterminate growers (including their brain (Zupanc & Horschke, 1995)) and fecundity typically increases with age, which is in stark contrast to mammals or birds, which show constant fecundity across age classes or a decline with increasing age (i.e. reproductive senescence (Reznick et al., 2002)). As such, selection pressures in life history evolution may be different among at least some species of fish compared to mammals and birds (Reznick et al., 2002), with resulting changes in genomic traits and ecological adaptations (Kolora et al., 2021). These factors might create different senescence patterns in fish compared to mammals and birds, which may overshadow any other benefits of a larger brain that impacts lifespan.

Third, why do Actinopteri that provide post-zygotic parental care have smaller brains than those that do not (Figure 3b)? The other unexpected relationship in our data was that between parental care
and brain size in Actinopteri, which ran exactly contrary to published results on birds and mammals. What is more, there is evidence from smaller subsets of fishes that parental care can co-evolve with brain size increases (Gonzalez-Voyer et al., 2009; Tsuboi et al., 2015). However, contrasting evidence comes from other studies (Samuk et al., 2014; Reddon et al., 2016). In our dataset, parental care was very unevenly distributed across the phylogeny (Appendix S4.6), with the majority of cases found in only five Orders (Cichiliformes, Gobiformes, Ovalentaria, Syngnathiformes and Tetraodontiformes), which also introduces biases with regard to body size distributions into the data (with their concomitant impact on brain sizes, see Appendix S2). This likely explains why the phylogenetically corrected analysis was non-significant, despite the seemingly strong effect of parental care on brain size (Figure 3b). Nevertheless, the relationship between parental care and brain size in fishes may yet fundamentally differ from that in other vertebrates, because most care involves the defence of eggs and juveniles (Mank et al., 2005), the costs of which likely scale much less with numbers of offspring compared to, for example, feeding or teaching. In turn, the benefits of enlarged brains with regard to the cognitive demands of parental care in most fishes may be lower than in other vertebrates. Moreover, previous studies investigating the relationship between brain size and parental care found a clear positive correlation between the duration of parental care and increases in brain size (Barton & Capellini, 2011; Tsuboi et al., 2018). This indicates that our dataset might not have been detailed enough as we only used the mere presence (lumping all types of post-zygotic parental investment together) or absence of parental care. Future investigations using more detailed datasets that also include a proxy of the investment into parental care for different fish species would be required to resolve this discrepancy. Although further confirmation is required, smaller brain sizes in caring species might hint to a potential trade-off between parental care and other activities, such as feeding, which is particularly pronounced in several fish species. For example, many mouthbrooding species starve while caring for embryos and fry inside their mouth (Oppenheimer, 1970). Thus, parental care in fishes might incur high energetic costs, which mask or even reverse potential benefits of extended developmental times and increased resource availability that appear to be involved in the evolution of larger brains in caring avian and mammalian species (Tsuboi et al., 2018).

Fourth, why does neither migratory behaviour nor habitat type correlate with brain size in Actinopteri (Figure 4)? Given the amount of work pointing towards links between habitat features and brain evolution in fishes, it is somewhat surprising that there was no detectable correlation in our dataset. For example, effects of habitat complexity on brain size and/or organization have been shown for cichlids (Shumway, 2010), gobies (White & Brown, 2015), mosquito fish (Jenkins et al., 2021), salmon (Kithslinger & Nevitt, 2006), sunfish (Axelrod et al., 2018) and sticklebacks (Gonda et al., 2009). That being said, a previous analysis on a smaller dataset did not find evidence for an influence of brain size on invasion success in fishes (Drake, 2007), one of the key arguments for the ‘cognitive buffer hypothesis’ (Sol, 2009). Much less attention has been paid to connections between brain size (or brain morphology) and migratory behaviour of fishes, but also here at least some evidence suggests that such an evolutionary link exists (Kolm et al., 2009). This seems intuitive, given the challenges migration and orientation impose on a fish’s brain (Odling-Smee et al., 2011; Podgornik et al., 2015). Seeing that fish are less constrained by migration with regard to brain growth compared to birds (additional brain weight likely being less of an issue during aquatic compared to aerial migrations), it may thus be less surprising that migrating species had slightly larger brains than non-migrating ones in our sample (Figure 4a). With this effect being so weak, however, more detailed work is needed to draw real conclusions. Alternatively (or additionally), certain brain areas linked to habitat features might have been increased at the expense of other areas, resulting in similar overall brain sizes. For example, a comparative and a developmental study using cichlid fishes showed that individuals experiencing a more complex habitat, or a more complex social environment, have larger cerebellum sizes without a significant overall increase in total brain size (Pollen et al., 2007; Fischer et al., 2015). Whether selection acts on single brain areas (the ‘mosaic brain evolution hypothesis’ (De Winter & Oxnard, 2001)) or on overall brain size (the ‘concerted evolution hypothesis’ (Finlay & Darlington, 1995)) is a long-standing question in evolutionary biology. Recent evidence from a controlled experiment using guppies selected for larger telencephalon sizes showed unequivocal support for the mosaic brain evolution hypothesis (Fong et al., 2021), and thus for the idea that selection may also act on individual brain areas and not just on overall brain size alone (De Winter & Oxnard, 2001). This, in turn, may obscure patterns of brain evolution when brain morphologies differ vastly (Kotrschal et al., 1998; Butler & Hodos, 2005) and/or only gross brain size is considered (Logan et al., 2018), both of which are true in our current study.

Taken together, these unexpected results highlight one thing clearly: there is much scope for additional work on comparative brain evolution in fishes, and our analyses have in many ways only scratched the surface. There are a few explicit caveats that readers should be aware of when interpreting our study. First, drawing comparisons across such wide ranges of taxa as we do here may mask effects observed at narrower scales. For example, even such a fundamental trait as brain-body allometry may vary considerably, depending on the taxonomic level at which it is investigated (Tsuboi et al., 2018; Burger et al., 2019; Smaers et al., 2021). Lumping together distantly related species may thus result in analyses that include both ‘apples’ and ‘oranges’. This may at least partly explain why some of the patterns observed for smaller sets of fish species were not replicated in our large dataset. Indeed, one might argue that it is more surprising that we find any associations between brain size and other ecological traits at all, given the great diversity of organisms included, especially among the Actinopteri and Elasmobranchii. Once better data are available (see ‘third’ below), it will be interesting to search for those levels of biological organization that are most meaningful in the co-evolution between brains and other traits; analysing effects within species, families and clades in parallel will identify patterns that hold across taxonomic
levels and those that are more taxon specific. For example, among Percomorpha some groups are obligate carers (e.g. cichlids), some do not care (e.g. flatfish), and others include carers and non-carers (e.g. wrasses). This allows to ask questions like ‘do correlations between brain size and a given trait in caring wrasses more closely resemble those of cichlids, those of non-caring wrasses, or those of Percomorpha in general?’ We would thus gain insights into the respective patterns at each taxonomic level, as well as into the presence or absence of confounding effects of parental care on the relationships between brains and other traits (Gonda et al., 2013).

Second, both gross brain size as a measure of cognitive ability and a narrow focus on a few select ecological or behavioural traits in comparative studies of brain evolution have been criticized in the past (Healy & Rowe, 2007; Dechmann & Safi, 2009; Logan et al., 2018). However, as high-quality behavioural and ecological (experimental) data are often missing and as direct comparisons of brain morphologies across wider phylogenetic ranges are difficult (Butler & Hodos, 2005), we are often still confined to such coarse comparisons when first probing potential drivers of brain evolution outside of narrowly defined and experimentally tractable taxa. Third, our dataset itself is limited both with regard to taxonomic resolution and available data. The unrooted, non-binary trees we derived from taxonomic classifications available on FishBase are clearly inferior to fully resolved and dated phylogenies (Dubois, 2007), and missing information for key traits limits sample sizes or completely prohibits certain analyses, for example, of sex effects. This ties in with the first two limitations: to maximize sample sizes, we derived a single estimate of each variable of interest for each species. As a result, a lot of potentially interesting and/or confounding information is lost, particularly with regard to developmental effects on brain growth (Kuzawa et al., 2014) and sex differences in brain size (Samuk et al., 2014). This is exacerbated in cases where we reduced a multi-level variable to a binary state, as for example in the case of mating systems and forms of parental care. Nevertheless, our study highlights evolutionary similarities between mammals, birds and fishes with regard to links between brain size and patterns of reproduction and sociality. Perhaps more importantly, our results also point towards fundamental differences between the (mostly) terrestrial determinate growers that have traditionally received the most attention (Figure 1) and the aquatic indeterminate growers we investigate here. Although it is beyond the scope of this study to further characterize the potential reasons for the observed differences between the aforementioned groups of vertebrates, we believe that the following points will provide fruitful avenues for future research: first, the differences in adult neurogenesis (Ganz & Brand, 2016); second, the limitations terrestrial life, and especially flight, sets for growth of brains and bodies (Smaers et al., 2021); third, the different degrees to which reproduction and parenting vary in each group (Tsuboi et al., 2018).

In summary, we have shown here that analyses of brain size evolution in fishes corroborate some of the hypotheses already supported by data on birds and mammals, but that fishes differ from such patterns in other regards. Specifically, we show that large brains co-occur with reduced fecundity (Figure 2) and increased rates of monogamy (Figure 3a) in fishes, as they do in birds and mammals. Lifespan (Figure 2) and the propensity to provide post-zygotic care (Figure 3b), however, decrease as brains become larger in fishes, opposite to what has been observed in Aves and Mammalia. As the availability of the respective phylogenetic, ecological and phenotypic data increases, it will be interesting to see whether these results stand the test of time, or whether our current understanding of brain size evolution across vertebrates was impacted by biases in the distribution of knowledge in the tree of life (Burger et al., 2019).

To this end, we believe that comprehensive datasets like the one we provide here will help to shed light on taxa that have thus far been underrepresented in the discussions about brain evolution. Our work clearly shows that it is necessary to test even supposedly well-established hypotheses in groups where this has not previously been done—life is always more diverse and fascinating than our theories give it credit for.

**AUTHOR CONTRIBUTIONS**

SF and AJ conceived of the study. AJ analysed the data and wrote the first draft of the manuscript. SF and AJ contributed equally to revisions and approve of the final manuscript.

**ACKNOWLEDGEMENTS**

We thank Joachim Frommen and Dieter Lukas for helpful comments that greatly improved the manuscript. SF is supported by the Vienna Science and Technology Fund (awarded to Sabine Tebbich, CS18-042).

**CONFLICT OF INTEREST**

The authors have no conflict of interest to declare.

**PEER REVIEW**

The peer review history for this article is available at https://publo ns.com/publon/10.1111/jeb.14026.

**DATA AVAILABILITY STATEMENT**

The data that support the findings of this study are openly available in dryad at https://doi.org/10.5061/dryad.sxksn035q

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