





RESEARCH ARTICLE

Ecological and behavioural drivers of offspring size in marine teleost fishes

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Abstract

Aim: Our aim was to evaluate the role of ecological and life-history factors in shaping global variation in offspring size in a marine clade with a diverse range of parental care behaviours.

Location: Global.

Time period: Data sourced from literature published from 1953 until 2019.

Major taxa studied: Marine teleost fishes.

Methods: We compiled a species-level dataset of egg and hatch size for 1,639 species of marine fish across 45 orders. We used Bayesian phylogenetic mixed models to evaluate the relationship between offspring size and environmental factors (i.e., mean temperature, chlorophyll-*a* and dissolved oxygen content together with their annual variation), as well as latitude, reproductive strategy, parental body size and fecundity. We also tested long-standing hypotheses about the co-evolution of offspring size and the presence of parental care in BAYESTRAITS.

Results: After controlling for parental body size and phylogenetic history, we find that increased egg size is associated with colder and oxygen-rich waters, while hatch size further depends on food supply and the reproductive strategy exhibited by the species. Irrespective of the initial investment in egg size, species with parental care or demersal egg development yield larger hatchlings compared to pelagic spawners. We also demonstrate that hatch size has co-evolved with advanced forms of care in association with parental body but fail to find a relationship with other types of care.

Main conclusions: Our study shows that parental care behaviours, together with environmental context, influence the evolution of classic life-history trade-offs on a global scale. While the initial investment in eggs is driven primarily by temperature and oxygen content, hatch size also reflects the impact of care an offspring has received throughout development. In support of the 'offspring-first' hypothesis, we find that an increase in hatch size drives the evolution of advanced care provision.

KEYWORDS

marine fishes, marine life histories, offspring size, parental investment, trait biogeography, trait co-evolution

1 | INTRODUCTION

Across the tree of life, species employ a variety of strategies to maximize reproductive success (Clutton-Brock, 1991). The 'fast-slow' continuum of life-history traits (Stearns, 1992), for example, describes a trade-off between number and size of offspring, but many other factors can influence the extent to which parents invest energy in offspring development (D. J. Marshall et al., 2018). In particular, parental care can decrease the risk of predation on young, modulating the correlation between offspring size and mortality (Nussbaum, 1987; Sargent et al., 1987; Summers et al., 2006). These relationships, however, are also highly dependent on the environmental context (Anderson & Gillooly, 2020; Barneche et al., 2018; Duarte & Alcaraz, 1989; D. J. Marshall et al., 2018; Winemiller & Rose, 1992), as well as parental body size (Jorgensen et al., 2011; Rollinson et al., 2019; Sargent et al., 1987; Stoddard et al., 2017) and the developmental stage at which investment in young is considered (Klug & Bonsall, 2010). The relative roles of each of these factors in determining offspring size is not yet fully understood.

Many comparative studies of the evolution of parental care come from birds and mammals, which display a relatively limited set of care behaviours (Clutton-Brock, 1991; Cooney et al., 2020; Remeš et al., 2015; West & Capellini, 2016). Other clades, such as amphibians or fish, encompass a wider variety of parental care strategies (Furness & Capellini, 2019; Mank et al., 2005; Vági et al., 2019), but due in part to the difficulty of broad-scale data collection efforts in these groups, less attention has been paid to the relationship between care and life-history trade-offs. The availability of fish life-history information from resources such as FishBase (Froese & Pauly, 2019), however, combined with a recent phylogeny of ray-finned fishes (Rabosky et al., 2018) and species range data (IUCN, 2020; Kaschner et al., 2019), allows detailed investigation into the many inter-related factors driving variation in fish offspring size.

There are two main causal explanations for the evolution of a link between offspring size and parental care in fish. The first, the 'safe harbour' hypothesis, proposed by Shine (1978) and later modified by Sargent et al. (1987), predicts that the presence of care drives the evolution of larger egg sizes by lengthening the time offspring can develop in the relative safety of an egg. The second is Nussbaum's (1985, 1987) suggestion that an initial increase in egg size – due to higher survival rates of offspring that hatch from larger eggs – could facilitate the subsequent evolution of parental care behaviours by increasing susceptibility to predation or requiring additional oxygenation, that is, an 'offspring-first' hypothesis for the purposes of this article. Of course, these two explanations are not mutually exclusive; one of these mechanisms could trigger a co-evolutionary feedback loop (Nussbaum & Schultz, 1989), or a third unrelated factor could be independently driving the evolution of both egg size and parental care (Shine, 1989). A positive association between parental care and egg size has been found in taxa with aquatic eggs including amphibians (Summers et al., 2006), some fish families (Carcupino et al., 2002; Sargent et al., 1987) and reef fishes in general (Kasimatis & Riginos, 2016). By contrast, among

terrestrial organisms, longer care is associated with smaller eggs in birds (Stoddard et al., 2017), and no relationship has been found in insects (Gilbert & Manica, 2010), emphasizing the importance of ecological context when selecting a clade for broad-scale life-history analyses.

In addition to evolutionary drivers related to care behaviours, variation in fish offspring size could be a response to the external environment. An early survey showed that egg sizes in polar and deep-sea species are larger compared to sister taxa from warmer waters (N. B. Marshall, 1953), an example of the Thorson–Rass rule (Laptikhovskiy, 2006), with an inverse size–temperature correlation as one of many metabolic relationships known to vary with a temperature gradient (Brown et al., 2004). A recent modelling study pinpointed egg survival rate as the main driver for this pattern as egg survivorship decreases with both increasing temperatures and larger egg sizes (Anderson & Gillooly, 2020). Elevated temperatures can also affect offspring development indirectly by reducing the supply of dissolved oxygen in the spawning habitat (Breitburg et al., 2018; Rombough, 1988). A comparative analysis of 288 marine fish species found that, congruent with earlier findings in marine invertebrates (D. J. Marshall & Burgess, 2015; D. J. Marshall et al., 2012), egg size decreases with increasing temperature and chlorophyll-*a* levels (i.e., a proxy for food regime) while environments characterized by greater temperature seasonality or unpredictable food supply select for fewer – but larger – offspring (Barneche et al., 2018). By contrast, however, the southern pygmy perch (*Nannoperca australis*) produces a greater number of smaller eggs in harsher streams with more physical disturbance (Morrongiello et al., 2012), suggesting that different measures of environmental uncertainty can have contrasting effects.

Few studies to date have evaluated potential environmental and parental behaviour drivers of offspring size simultaneously, with most instead focused either on extrinsic or on intrinsic effects. Furthermore, few studies make an explicit contrast between offspring size at hatching (or leaving parental body) and egg size, even though the former encompasses survival benefits of care after spawning while the latter primarily represents maternal investment. Here we assemble a large species-level dataset to test the relative effects of parental care and environmental factors on offspring size in marine teleost fishes. Within a phylogenetic context, and controlling for latitude (Kasimatis & Riginos, 2016), parental body size (Jorgensen et al., 2011; Rollinson et al., 2019; Sargent et al., 1987) and fecundity (Duarte & Alcaraz, 1989), we expect offspring size to increase in response to low temperatures and poor food regime. We also anticipate a positive relationship between parental care and offspring size, with a stronger relationship between parental body size and offspring size in species that provide care than those that do not. We furthermore set out to determine whether there is evidence that offspring size has co-evolved with parental care in line with either the 'safe harbour' or the 'offspring-first' hypothesis. Taken together, our analyses evaluate the evolutionary forces driving parental investment at two different developmental stages in marine teleost fishes.

2 | MATERIALS AND METHODS

2.1 | Data collection

We collated mean values of fish egg size and larval size at hatching or upon leaving parental body, total adult body length and fecundity per species using global and regional datasets, larval guides, FishBase (Froese & Pauly, 2019) and family-level reviews; all sources are provided as part of Supplementary Data. All species with at least one proxy for offspring size were then classified as exhibiting one of seven reproductive strategies based on Eugene Balon's categorization of reproductive guilds (Balon, 1975; see Figure 1). Each strategy was assigned to three main categories with respect to where egg development takes place: (a) 'pelagic' or floating in the water column (including eggs that are free-floating or developing within pelagic structures); (b) 'demersal' or developing on the sea floor (including demersal scatterers and guarders); (c) developing in close association with 'parental body' (including external bearers, pouch brooders and livebearers). Where available, we recorded the primary caregiver in species with care (i.e., 'male', 'female', 'biparental', 'live invertebrate'). We distinguished between two categories of certainty with regards to the reproductive behaviour: A, reproductive strategy determined by direct observations as part of an experimental or a field study

and/or listed as 'species-specific' in a secondary source; B, reproductive strategy listed as 'presumed' in the literature or inferred from that of other species within the genus with a known strategy or from the family-level description in FishBase (Froese & Pauly, 2019). Further details on data collection and categorization of reproductive strategies are available in Supporting Information Methods S1.

Overall, our finalized dataset contained 1,639 species with body length measurements and at least one proxy for offspring size (1,347 and 292 species were in category A and B of certainty with regards to their reproductive strategy, respectively; see Supplementary Data for the full dataset). We recorded 1,187 species with egg size (A = 1,014; B = 173) and hatch size (A = 1,017, B = 170) values, with both variables available for a subset of 735 species (A = 684, B = 51). The absolute fecundity values were available for 648 species (A = 546, B = 102).

2.2 | Environmental variables

A set of six GIS raster layers was obtained from the global marine environmental dataset Bio-ORACLE 2.0 (Assis et al., 2018) at 0.08° resolution. To encompass environmental variation most likely related to offspring size, we selected the following variables: mean

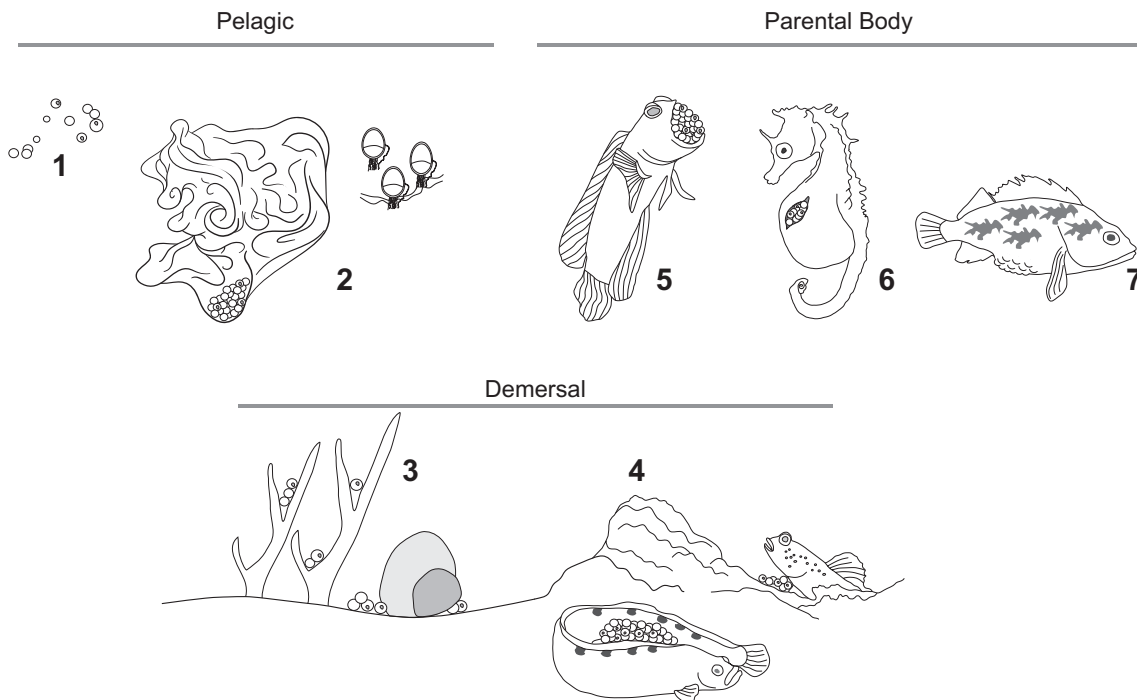


FIGURE 1 An overview of reproductive strategies in marine fishes; the place of egg development is indicated above the grey line. 1 = 'open water', free-floating eggs; 2 = 'structures', eggs develop in floating structures (left: goosefish egg rafts, Lophiidae family; right: saury eggs with attaching filaments, Scomberesocidae family); 3 = 'scatterers', eggs develop in or under substrate/vegetation on the sea floor with no further care; 4 = 'nesters', eggs are cared for by the parent(s) after spawning (left: gunnels, Pholidae family, are clutch tenders that care for eggs without modifying their nesting habitat; right: gobies, Gobiidae family, are nest-builders that place eggs in specially constructed burrows); 5 = 'external bearers', eggs are brooded in close contact with parental body as exemplified by a mouthbrooding male jawfish, Opistognathidae family; 6 = 'pouch brooders', eggs develop within a pouch-like structure as exemplified by a brooding male seahorse, Syngnathidae family; 7 = 'livebearers', eggs develop within the reproductive tract of the mother as exemplified by a gestating female rockfish, Sebastidae family. See Supporting Information Methods S1 for further information

temperature, chlorophyll-*a* and dissolved oxygen content, together with their ranges. In line with Barneche et al. (2018), we used environmental data exclusively from the sea surface layers because the preferred spawning depth was unknown for the majority of species in our dataset. The mean values represented monthly averages from 2000 until 2014, while the range values reflected the average of the absolute difference between the minimum and maximum records per year throughout this time period. These values were then intersected with species range polygons from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2020) and AquaMaps (Kaschner et al., 2019) in R Project v3.6.1 (R Core Team, 2019) to provide a mean value for each species, with additional details available in Supporting Information Methods S1. Principal component analysis (PCA) was used to reduce the dimensionality of the set of six environmental variables per species because they were moderately to highly correlated with each other (Dormann et al., 2013; Supporting Information Table S1). All variables were mean centred and expressed in units of standard deviation before PCA. The first three principal components (PCs) captured c. 98% of all variance in environmental data (Supporting Information Table S2). In order to improve the interpretability of the results, a varimax rotation (Kaiser, 1958) was applied to each component to reduce the number of variables exhibiting high factor loadings. As the datasets of egg size and hatch size contained a different combination of species, we ran separate PCAs on each set of environmental variables, with qualitatively similar results in both A and A + B datasets (Supporting Information Table S2), in a subset of species with both egg size and hatch size values available and in subsets with fecundity values available (Supporting Information Table S3).

2.3 | Bayesian phylogenetic mixed models

To test the relationship between offspring size (i.e., egg size or hatch size), parental care, and the environment, we ran Bayesian phylogenetic mixed models (BPMs) in R package 'mulTree' (Guillaume & Healy, 2014), which runs Markov chain Monte Carlo (MCMC) generalized linear mixed models (Hadfield, 2010) across a distribution of phylogenetic trees. Offspring size and body size variables were log-transformed and latitude was square-root transformed before the analysis. All continuous variables were mean centred and expressed in units of standard deviation. We used three different sets of categorical variables relating to reproduction: (a) place of egg development; (b) post-spawning care; (c) seven reproductive strategies. The variance inflation factor (VIF) of all non-interaction variables in all models was less than 5, demonstrating that multicollinearity was not a concern in our analyses (Dormann et al., 2013). In order to account for non-independence of traits in species that share common ancestry, a phylogenetic tree structure was included in the model as a random effect. We used a distribution of 100 all-taxon assembled, time-calibrated phylogenetic trees of ray-finned fishes (Rabosky et al., 2018). In advance of running the BPMs, we mapped the variation in offspring size and in the seven reproductive strategies on

a single tree extracted from this distribution in R package 'ggtree' (Yu et al., 2017). We also visualized evolutionary change in offspring size using the *fastAnc* function in R package 'phytools' (Revell, 2012).

Following the recommendations in Hadfield (2010), we used inverse-Wishart priors for the phylogenetic and residual variance ($V = 1, \nu = 0.002$) and diffuse normal priors for fixed effects (mean 0, $V = 10^{10}$). For each of the 100 tree topologies in our sample, we ran three MCMC chains for 2.4×10^5 iterations, discarded the first 4×10^4 iterations as burnin and sampled every 100 iterations, which resulted in effective sample sizes of $> 1,500$ for all parameters tested per phylogenetic tree. The model outputs were then summarized across all trees following Karagicheva et al. (2018). Chain convergence was assessed using the Gelman–Rubin statistic (Gelman & Rubin, 1992), with potential-scale reduction values less than 1.1 for all model outputs. The autocorrelation was determined using function *acf*, with 0.1 used as a target threshold.

2.4 | BAYESTRAITS analysis of trait co-evolution

We assessed the potential causal relationship between the presence of parental care and offspring size using Pagel's discrete algorithm (Pagel, 1994) implemented in BAYESTRAITS v3.0.1 (Pagel & Meade, 2017). The discrete algorithm compares the marginal likelihood of a dependent model where two binary traits co-evolve with each other to a model where these traits evolve independently. The output from the BPMs indicated that the presence of post-spawning care was significantly correlated with size at hatching, with the strongest positive effect in species that develop in association with parental body. As the method required the use of binary discrete traits, we dichotomized the hatch size variable by the (a) median value and (b) third quartile (Q3) values (i.e., by very large sizes at hatching versus the rest). We also dichotomized the parental care variable in three different ways: (a) post-spawning care presence/absence, $n = 1,187$; (b) post-spawning care in association with parental body (i.e., external and internal egg-bearing) presence/absence, $n = 1,187$; (c) post-spawning care presence/absence in a subset of species with external egg development only (i.e., egg-bearing species had been excluded), $n = 1,084$. The median value was 3 mm in both datasets; the Q3 cut-point values were 4.7 and 4.29 mm in the full (a,b) and external (c) datasets, respectively. We used the same distribution of phylogenetic trees (Rabosky et al., 2018) as for BPMs; all trees were scaled by a constant using the default setting of a mean branch length of 0.1 as per the BAYESTRAITS manual. Each BAYESTRAITS model was run for 1.1×10^7 iterations with an initial burn-in of 10^6 and was sampled at every 10^5 iterations, which resulted in a posterior distribution of 100 samples per tree. We forced Markov chains to spend equal time on each tree using the *EqualTrees* command, and we ran two independent chains per model to assess convergence. In all cases, we used a hyper-prior of an exponential distribution (seeding from a uniform distribution on the interval 0–100) for a reversible-jump MCMC procedure (Pagel & Meade, 2006). The marginal likelihood was then estimated for each tree using a

stepping stone sampler (Xie et al., 2011) where 50 stones were distributed according to a beta distribution ($\alpha = 0.4$, $\beta = 1.0$) and each stone was run for 5×10^4 iterations. For each model, we compared the first chain's median likelihoods, across the distribution of trees, using the log Bayes factor. The inspection of all traces of parameter estimates in TRACER v1.7.1 (Rambaut et al., 2018) confirmed adequate mixing and effective sample sizes greater than 2,000, with one exception. The dependent (co-evolutionary) model for the subset of species with external egg development using Q3 as the cut-point exhibited substantial chain mixing problems due to the small sample size and high phylogenetic signal in the data; we thus only use the median as the cut-point for this subsample.

3 | RESULTS

3.1 | General trends in offspring size

We deployed two proxies for offspring size – egg size and larval size at hatching/leaving parental body. Both the smallest and the largest eggs are found among external bearers, ranging from 0.24 mm in two cardinalfish species to 20 mm in the sea catfish *Sciades couma*. The smallest size at hatching (0.94 mm) is exhibited by two Antennariidae species, where eggs develop in floating rafts of mucus, while the offspring of the mouthbrooding sea catfish *Arius latiscutatus* become independent at 10 cm. The distribution of raw data indicates that both egg and hatch size vary with parental care strategy (Supporting Information Figures S1–S3). The phylogenetic distribution of offspring size (Figure 2), however, does not suggest a clear link between the presence of parental care and larger offspring sizes. While some families with care behaviour do produce larger eggs (e.g., Ariidae, Nototheniidae and Zoarcidae in Figure 2a) or sizes at hatching (e.g., Syngnathidae in Figure 2b) compared to families with no care, other clades dominated by caregiving species such as Gobiidae, Pomacentridae and Apogonidae are not associated with an increase in offspring size.

We observe a latitudinal gradient in the mean offspring size, with the highest values consistently found in polar regions, that is, in the Southern Ocean and in the seas bordering the Arctic Ocean (Figure 3a,b). The prevalence of species with parental care after spawning is also somewhat higher in polar and temperate areas (e.g., in the Bering Sea and the Gulf of Alaska, see Figure 3c). Fish species richness in our sample, by contrast, is highest in the coastal areas and exhibits a latitudinal gradient with more species found in tropical waters (Figure 3d).

Males are the sole care providers in 76% of species with available information ($n = 403$) while maternal care is present in 19% of caregiving species (Supporting Information Figure S4). Biparental care (3%) and egg development in live invertebrates, for example, in gills of crabs, (2%) are the rarest types of care among marine fishes. The sex of caregiver is also closely linked to the reproductive strategy. While nesters, external bearers and pouch brooders are characterized predominantly by male care, all livebearing species exhibit maternal care.

3.2 | Drivers of variation in egg size

A decrease in temperature together with an increase in dissolved oxygen content – corresponding to the PC1 – is the strongest extrinsic predictor of an increase in egg size, with larger eggs generally found in colder and oxygen-rich waters (Figure 4a–c; see Supporting Information Tables S1–S3 for further details on environmental variables and Supporting Information Tables S4–S6 for full phylogenetic mixed model outputs). This is consistent with the observed geographical pattern of offspring size increasing towards the polar regions (Figure 3a,b). Other extrinsic factors such as latitude, seasonality in temperature and oxygen levels (PC2) and mean chlorophyll-*a* concentration and its annual range (PC3), however, are not significant predictors of egg size at an interspecific level.

The body size of the parent is the strongest intrinsic predictor found to correlate with egg size, with large-bodied species generally producing larger eggs. Place of egg development is not a significant predictor after we control for covariation with the environmental conditions, body size and phylogeny (Figure 4a, Supporting Information Table S4) and, contrary to our predictions, we do not find evidence that provision of parental care after spawning is associated with an increase in egg size (Figure 4b, Supporting Information Table S5). A further breakdown by reproductive strategy indicates that both livebearers and species spawning in pelagic structures exhibit smaller eggs compared to the 'open water' spawners (Figure 4c, Supporting Information Table S6). The maternal investment in the egg itself in these cases might be limited by the resources required to produce the structures surrounding the egg or to provide further care throughout internal development. The rerun of these models in the subset of high-quality data (A , $n = 1,014$) broadly corroborates these results, but we additionally find larger eggs in environments with abundant but variable food supply (PC3), and the negative association with spawning in pelagic structures is no longer significant (Supporting Information Tables S7–S9). We also show that the interaction between parental body size and reproductive behaviour is not a significant predictor of egg size. There is a weak negative relationship between egg size and body size in demersal scatterers, meaning that eggs in this category are smaller than would be expected given the size of the parent (Supporting Information Tables S10–S12). When we test the association between the absolute fecundity and egg size, we find that the production of larger offspring does come at the cost of reduced number of eggs ($n = 577$, Supporting Information Tables S13–S16). In accordance with the main analysis, neither the place of egg development nor the presence of parental care is a significant predictor of egg size.

3.3 | Drivers of variation in hatch size

We also identify the combination of low temperatures and high dissolved oxygen content as the main extrinsic driver of large sizes at hatching or leaving the parent, followed by plentiful but variable food regime (Figure 4d–f; Supporting Information Tables S17–S19).

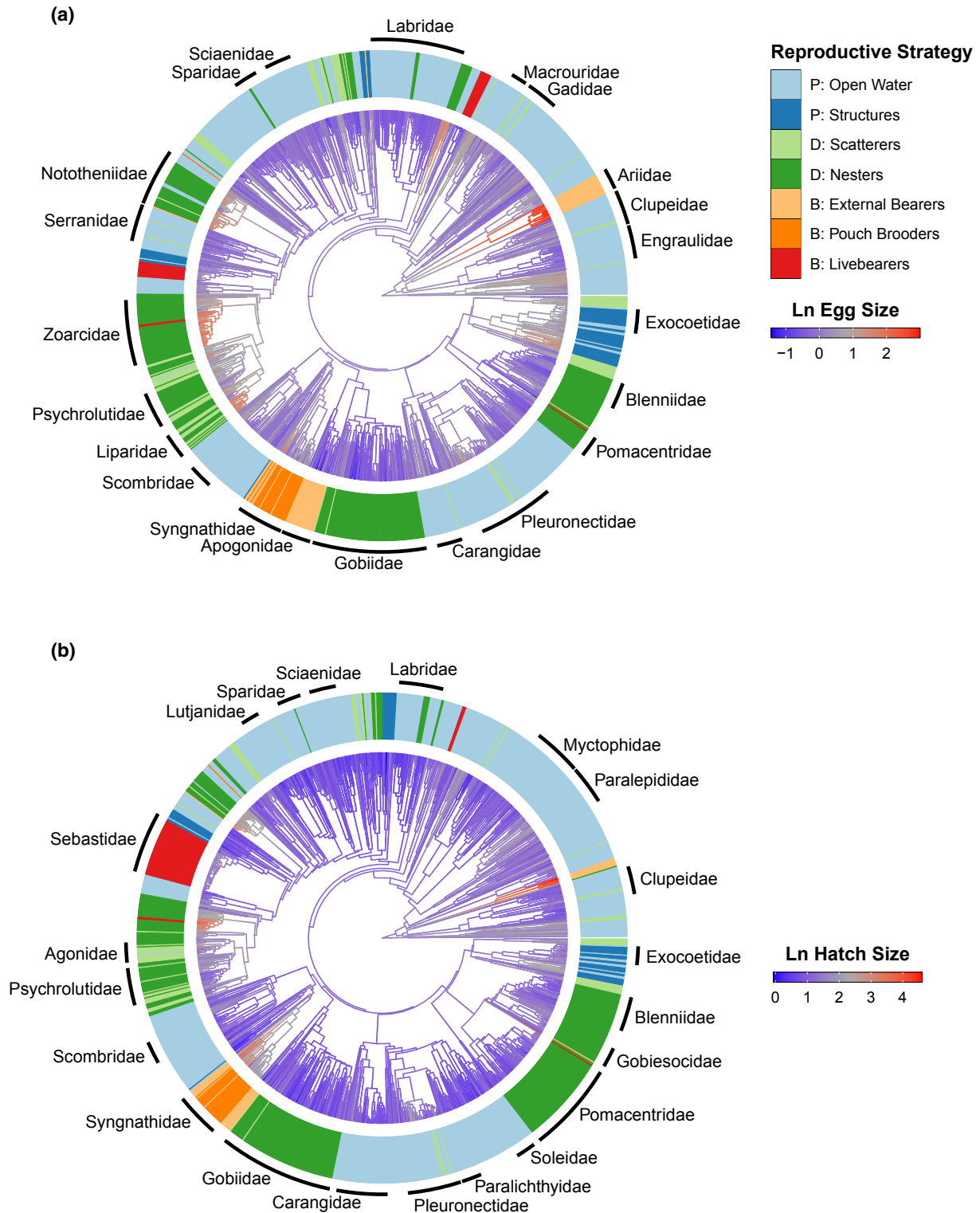


FIGURE 2 Distribution of (a) egg size and (b) hatch size ($n = 1,187$ for each proxy) in marine fishes across a single topology extracted from 100 phylogenetic trees provided in Rabosky et al. (2018). The ancestral state reconstructions of offspring size using the *fastAnc* function in 'phytools' (Revell, 2012) are visualized on the tree structure. The outer circle depicts seven reproductive strategies at branch tips (see Figure 1 and Supporting Information Methods S1 for more information). For ease of interpretation, only the names of families with records for 15 species or more have been displayed. P = pelagic; D = demersal; B = parental body

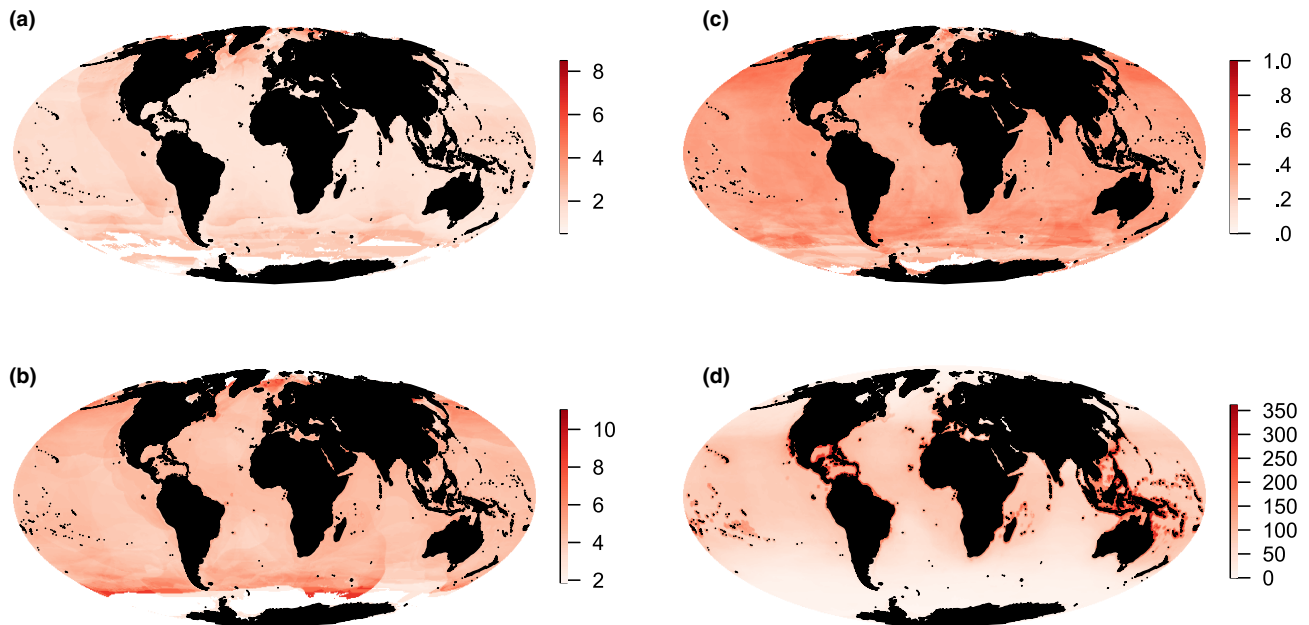


FIGURE 3 Geographical distribution of (a) mean egg size ($n = 1,187$), (b) mean hatch size ($n = 1,187$), (c) proportion of species exhibiting post-spawning care ($n = 1,639$, species with at least one proxy for offspring size), where 1 = all species exhibit care, 0 = no species exhibit care, (d) species richness ($n = 1,639$), per 0.5° grid cell. Grid cells with fewer than three species have been removed from the visualizations and therefore appear blank

As with egg size, larger-bodied species hatch at larger sizes compared to smaller-bodied species. While species where eggs develop demersally or in association with parental body do not exhibit larger eggs compared to pelagic spawners, they do yield markedly larger hatchlings (Figure 4d, Supporting Information Table S17). The presence of parental care after spawning is also associated with significantly larger sizes at hatching, which highlights the contribution the caring parent makes in addition to the initial maternal investment in eggs (Figure 4e, Supporting Information Table S18). A further breakdown by reproductive strategy (Figure 4f, Supporting Information Table S19) shows that all strategies with demersal eggs or egg-bearing within/on the body exhibit increased size at hatching compared to pelagic spawners – with the strongest positive association in external bearers, pouch brooders and livebearers. Unexpectedly, demersal scatterers with no care after spawning exhibit a larger positive shift from 0 compared to nesters that provide care for eggs. This is corroborated with the results from the high-quality data (A, $n = 1,017$, Supporting Information Tables S20–S22). The interaction between body size and the presence of parental care is positively associated with hatch size, meaning that, for a given increase in parental body size, the hatch size in species with care increases significantly more compared to non-caring species. The relationship between parental body size and hatch size also varies depending on the reproductive strategy, with external bearers and pouch brooders exhibiting a positive interaction between body size and size at hatching. By contrast, we observe a negative association in livebearing species, which indicates that the hatch size of livebearers increases significantly less with parental body size than that of species with no care (Supporting Information Tables S23–S25). The output from

models with fecundity as one of the predictors ($n = 439$, Supporting Information Tables S26–S29) shows that this variable does remove the significant association between hatch size and care after spawning – but eggs developing demersally or in association with parental body still yield larger hatchlings compared to pelagic eggs.

As hatch size is expected to be strongly correlated with egg size (Duarte & Alcaraz, 1989), we also ran a set of models where egg size was included as a predictor of hatch size in order to evaluate the correlates of deviation from this relationship ($n = 735$; Supporting Information Tables S30–S33). The results were similar to the outputs obtained from the hatch size analysis using the full dataset. Even after accounting for the correlation between these two size proxies, there is a significant positive association between hatch size and lower temperature/higher oxygen levels, indicating that species that hatch at higher-than-expected sizes are more likely to be found in cooler/more oxygenated environments irrespective of egg size. Though accounting for egg size in the hatch size model removes the strong positive association with body size, hatching at larger sizes is still more likely in species with demersal or within/on body development than in pelagic spawners. The positive relationship between hatch size and the presence of parental care also remains significant.

3.4 | Co-evolution of hatch size and parental care

While we find a strong present-day positive association between post-spawning care and size at hatching, there is no evidence that these two traits have co-evolved over macroevolutionary time [log Bayes factors (BF) -13.54 and -6.68 at median and third quartile

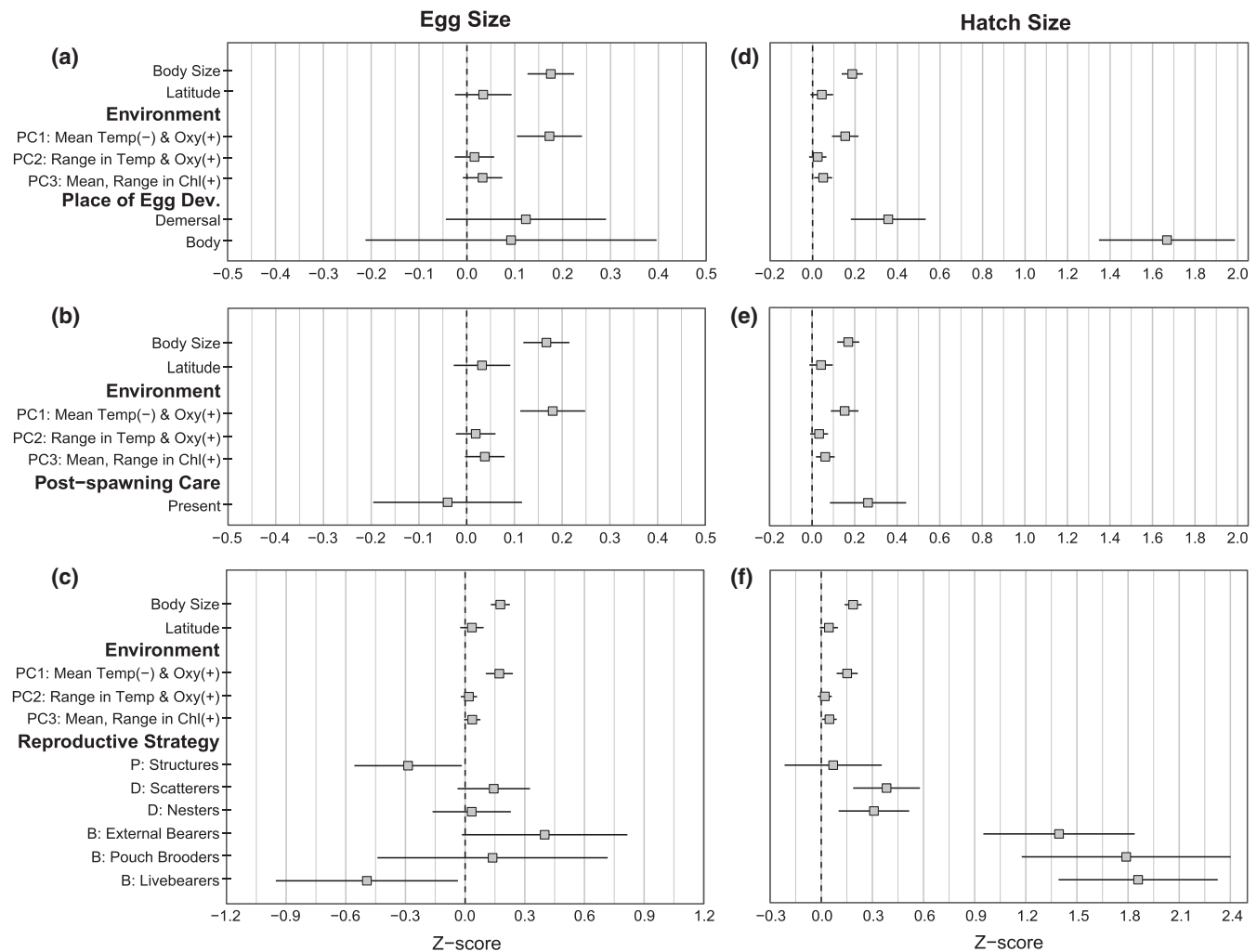


FIGURE 4 Predictors of (a–c) egg size and (d–f) hatch size ($n = 1,187$ species in each dataset) calculated with a Bayesian phylogenetic mixed model including (a,d) place of egg development ('pelagic' as reference), (b,e) presence of parental care ('absent' as reference) and (c,f) reproductive strategies ('open water' as reference). Significant predictors can be identified by a substantial shift from 0. Temp = temperature; Oxy = oxygen; Chl = chlorophyll- a ; (-) = decrease; (+) = increase; P = pelagic; D = demersal; B = parental body. See Supporting Information Tables S4–S6, S17–S19 for further information

(Q3) cut-points, respectively; a log BF > 2 is interpreted as positive evidence for trait co-evolution (Kass & Raftery, 1995)]. We obtain the same result in a dataset that only includes species with external egg development (log BF -5.54 at median cut-point). We do, however, find support for the co-evolution of size at hatching and development in association with parental body, that is, in external bearers, pouch brooders and livebearers, with log BF 3.35 at the median cut-point and 37.62 at Q3 (Figure 5; Supporting Information Tables S34–S35). Overall, large hatch size is more likely to evolve from smaller hatch size in egg-bearing species, rather than in species with external development (median $q_{24} = 8.85$, median $q_{13} = 0.31$ at Q3 cut-point), while transitions from external development to body development are found only in species with large hatch size (median $q_{12} = 0.00$, $q_{34} = 0.30$ at Q3 cut-point). The external development of large hatchlings is identified as the most likely ancestral state in the analysis with Q3 as cut-point (median $p = .99$).

4 | DISCUSSION

Our analyses of global drivers of marine teleost fish offspring size suggest that both environmental and behavioural factors mediate the evolution of this key life-history trait. We demonstrate that increases in both size at hatching and egg size are associated with lower temperatures and higher oxygen content as well as lower fecundity and larger parental body size. Furthermore, hatching size – but not egg size – is positively correlated with abundant but variable food regime and reproductive strategies where eggs develop on the sea floor or in association with parental body, with the strongest effect in advanced forms of parental care, that is, external and internal egg-bearing. While we find no evidence that size at hatching co-evolves with post-spawning care in general, we show that external development of large hatchlings acts as the first step towards the evolution of egg-bearing. This finding lends support for the 'offspring-first' hypothesis, which posits that an increase in offspring size drives the

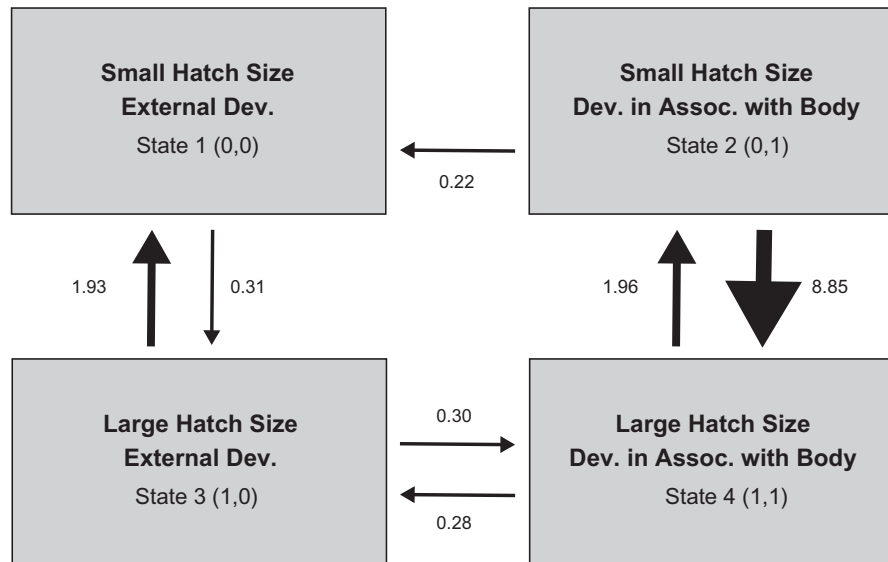


FIGURE 5 Results from the BAYESTRAITS reversible-jump Markov chain Monte Carlo (MCMC) discrete dependent analysis testing the co-evolution of hatch size and the place of egg development. Grey boxes illustrate four possible evolutionary states (1–4), with the transition paths between them indicated by arrows. The continuous value of size at hatching has been dichotomized by the third quartile value ('0' if hatch size ≤ 4.7 mm; '1' if hatch size > 4.7 mm). An increase in arrow thickness corresponds to an increase in transition rates with median transition rates across the distribution of 100 phylogenetic trees provided above each arrow. The median transition rate from State 1 to State 2 is 0.00. State 3 was identified as the most likely ancestral state. Dev. = development; Assoc. = association. See Supporting Information Table S35 for further information

subsequent evolution of care behaviours (Nussbaum, 1987), above the 'safe harbour' hypothesis (Sargent et al., 1987; Shine, 1978). Our analysis emphasizes the importance of incorporating phylogenetic history, environmental factors and different developmental stages in the study of life-history trade-offs.

We find that size at hatching increases with the level of care provision – and that the trade-off between offspring number and size can account for only some of this increase. By contrast, egg size correlates primarily with environmental factors, suggesting that the presence of care behaviours does not determine the initial maternal investment in young. Our finding also reflects fundamental differences in life-history strategies associated with the 'fast-slow' continuum (Stearns, 1992). Within this framework, pelagic spawners align closer to 'fast' strategists with large numbers of small offspring and no parental care while non-pelagic spawners cluster with 'slow' strategists that exhibit the opposite reproductive traits. Hatching at large sizes is advantageous in demersal habitats because larger offspring are better at exploiting limited resources, that is, their mortality is size-dependent. This contrasts with the production of many small offspring in the stochastic surface environments where survival is more affected by chance (Duarte & Alcaraz, 1989; Winemiller & Rose, 1992, 1993).

Our results indicate that the increased hatch size among demersal spawners remains significant even after controlling for differences in fecundity and egg size, suggesting a slowdown in the rate of egg development on the sea floor. Modelling approaches identify slow egg development rate as one of the key conditions necessary for the evolution of parental care, as it increases the time developing embryos are at risk from predators and harsh environmental

conditions (e.g., hypoxia in aquatic habitats; Klug & Bonsall, 2010). Most reports of a positive correlation between egg size and parental care arise from clades with aquatic eggs (Kasimatis & Riginos, 2016; Sargent et al., 1987; Summers et al., 2006), while animals with terrestrial development exhibit no such relationship (Gilbert & Manica, 2010; Stoddard et al., 2017), which suggests that oxygen availability represents a unique constraint on the evolution of offspring size in water. Furthermore, brood defence and provision of oxygen via fanning or mouthing – provided almost exclusively by males in this group – are the most common types of care among fish species with demersal eggs (Green & McCormick, 2005; Wootton & Smith, 2014). In co-evolutionary analyses that include such external care behaviours, however, we find that care does not co-evolve with hatch size. These results are consistent with a recent meta-analysis showing that male care is not associated with higher offspring survival (Goldberg et al., 2020), and our analyses further highlight other factors that might drive the evolution of external care, such as territoriality and a polygynous mating system (Ah-King et al., 2004; Mank & Avise, 2006). Territoriality promotes parent-offspring association as the two generations frequently encounter each other (Lion & van Baalen, 2007); moreover, brood defence comes at little energetic cost to the territorial male (Goldberg et al., 2020; Smith & Wootton, 1995). In addition, female preference for more 'caring' males that, for example, fan their eggs more frequently (Östlund & Ahnesjö, 1998) or provision broods from previous matings (Unger & Sargent, 1988) further amplifies selection for external care among demersal spawners (Alonzo, 2012; Goldberg et al., 2020).

We show that species where eggs develop in close association with parental body exhibit the largest sizes when leaving care

compared to other reproductive strategies. This reflects the extensive parental investment by egg-bearing parents throughout development, which includes provisioning their young with nutrients and oxygen as well as waste removal and osmoregulation (Carcupino et al., 2002; Schürch & Taborsky, 2005; Wourms, 1981; Wourms & Lombardi, 1992). We also find that size at hatching does co-evolve with external and internal egg-bearing and that the external development of large offspring precedes the evolution of egg-bearing in line with the 'offspring-first' hypothesis (Nussbaum, 1987). While the high transition rate from small to large hatchlings observed in egg-bearing species gives some support to the 'safe harbour' hypothesis (Shine, 1978), meaning that the presence of this parental behaviour contributes to the evolution of large offspring, it is not the most likely evolutionary pathway from the ancestral state of a large hatchling that develops externally. In support of the prediction that offspring mortality in species with parental care depends on the survival of the parent (Jorgensen et al., 2011), we find significant interactions between size at hatching and parental body size in all categories of egg-bearers – but not in demersal guarders (Supporting Information Table S25). This might be due to size differences between the offspring and the guarding adult as most brood predators are not large enough to pose a threat to the caregiver (Perrone & Zaret, 1979) – while species that prey on egg-bearers target the adult rather than the brood.

Our results add to the large number of studies that report an inverse relationship between offspring size and ambient temperature in aquatic species, or the Thorson–Rass rule (Barneche et al., 2018; D. J. Marshall & Keough, 2007; N. B. Marshall, 1953). Importantly, we show that both proxies for offspring size are sensitive to changes in temperature and oxygen levels, which are highly correlated in surface waters. This implies that the ongoing trend of global warming and the accompanying decline in oxygen levels in the world's oceans have the potential to change the species composition of marine fish communities via effects on reproductive output and dispersal over the next decades (Breitburg et al., 2018; Feary et al., 2014). The strong link between offspring size and temperature has potential implications for our finding that demersal habitats are associated with larger hatchlings compared to surface waters. While we interpret this as evidence for size-dependent mortality, our result could also reflect the impact of a temperature–depth gradient (Laptikhovskiy, 2006) on the developmental rate of demersal hatchlings. Future studies that incorporate the preferred spawning depth for each species would help clarify whether demersal eggs in general are exposed to a different set of environmental conditions compared to pelagic eggs. Our analysis using a subset of high-quality data also indicates that, contrary to previous studies (Barneche et al., 2018; Robertson & Collin, 2015), low food regimes are associated with smaller, rather than larger, eggs – but we also note that in our dataset high chlorophyll content is strongly correlated with large annual variation in this variable. If annual peaks in food supply do not coincide with the reproductive season or are unpredictable, mothers might invest relatively more in each offspring as part of a conservative 'bet-hedging' strategy (Einum & Fleming, 2004).

5 | CONCLUSION

Overall, our study provides a broad-scale insight into the distribution of offspring size in a diverse marine clade. Even though parental investment has been subject to decades of theoretical research, we provide a rare comparative assessment of environmental and behavioural factors that contribute to the global variation in this key life-history trait. We demonstrate fundamental trade-offs between offspring size and number across a broad spectrum of reproductive strategies. Our study highlights that, while parental investment in eggs is driven primarily by environmental factors, size at hatching also reflects the impact of total parental care an offspring receives, which suggests that exploring alternative proxies for reproductive traits could be a fruitful avenue for future studies in aquatic and terrestrial clades.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

CS and KV designed the study. AP, BM and KV collected the data. KV performed the analyses with feedback from CS. KV wrote the manuscript and all authors contributed to revisions.

DATA AVAILABILITY STATEMENT

The dataset of offspring size, life-history traits, latitude and environmental variables that forms the basis of this study, together with a reference list and a key, is available from the Dryad repository at <https://doi.org/10.5061/dryad.mw6m905x9>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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