

1 **Ecological and behavioural drivers of offspring size in marine**
2 **teleost fishes**

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17 data. KV performed the analyses with feedback from CS. KV wrote the manuscript and all
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30 **Biosketch:** Karina Vanadzina is a PhD candidate at the University of St Andrews (UK). Her
31 research focuses on the evolution of parental care and associated life-history traits in ray-
32 finned fishes and passerine birds.

33 **Running title:** Global variation in fish offspring size

34 **Key words:** parental investment, marine life histories, offspring size, marine fishes, trait co-
35 evolution, trait biogeography

36

37

38 **Abstract**

39 **Aim**

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

42 **Location**

43 Global.

44 **Time period**

45 Data sourced from literature published from 1953 until 2019.

46 **Major taxa studied**

47 Marine teleost fishes.

48 **Methods**

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

56 **Results**

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

64 **Main conclusions**

65 Our study shows that parental care behaviours, together with environmental context,
66 influence the evolution of classic life-history trade-offs on a global scale. While the initial
67 investment in eggs is driven primarily by temperature and oxygen content, hatchling size

68 also reflects the impact of care an offspring has received throughout development. In
69 support of the 'offspring-first' hypothesis, we find that an increase in hatch size drives the
70 evolution of advanced care provision.

71 **1. INTRODUCTION**

72 Across the tree of life, species employ a variety of strategies to maximise reproductive
73 success (Clutton-Brock, 1991). The ‘fast-slow’ continuum of life-history traits (Stearns,
74 1992), for example, describes a trade-off between number and size of offspring, but many
75 other factors can influence the extent to which parents invest energy in offspring
76 development (Marshall et al., 2018). In particular, parental care can decrease the risk of
77 predation on young, modulating the correlation between offspring size and mortality
78 (Nussbaum, 1987; Sargent et al., 1987; Summers et al., 2006). These relationships,
79 however, are also highly dependent on the environmental context (Duarte & Alcaraz, 1989;
80 Winemiller & Rose, 1992; Barneche et al., 2018; Marshall et al., 2018; Anderson & Gillooly,
81 2020), as well as parental body size (Sargent et al., 1987; Jorgensen et al., 2011; Stoddard
82 et al., 2017; Rollinson et al., 2019) and the developmental stage at which investment in
83 young is considered (Klug & Bonsall, 2010). The relative roles of each of these factors in
84 determining offspring size is not yet fully understood.

85

86 Many comparative studies of the evolution of parental care come from birds and mammals,
87 which display a relatively limited set of care behaviours (Clutton-Brock, 1991; Remeš et al.,
88 2015; West & Capellini, 2016; Cooney et al., 2020). Other clades, such as amphibians or
89 fish, encompass a wider variety of parental care strategies (Mank et al., 2005; Furness &
90 Capellini, 2019; Vági et al., 2019), but due in part to the difficulty of broad-scale data
91 collection efforts in these groups, less attention has been paid to the relationship between
92 care and life history trade-offs. The availability of fish life-history information from resources
93 such as FishBase (Froese & Pauly, 2019), however, combined with a recent phylogeny of
94 ray-finned fishes (Rabosky et al., 2018) and species range data (Kaschner et al., 2019;
95 IUCN, 2020), allows detailed investigation into the many inter-related factors driving variation
96 in fish offspring size.

97

98 There are two main causal explanations for the evolution of a link between offspring size and
99 parental care in fish. The first, the ‘safe harbour’ hypothesis, proposed by Shine (1978) and
100 later modified by Sargent et al. (1987), predicts that the presence of care drives the evolution
101 of larger egg sizes by lengthening the time offspring can develop in the relative safety of an
102 egg. The second is Nussbaum’s (1985, 1987) suggestion that an initial increase in egg size
103 – due to higher survival rates of offspring that hatch from larger eggs – could facilitate the
104 subsequent evolution of parental care behaviours by increasing susceptibility to predation or

105 requiring additional oxygenation, i.e., an 'offspring-first' hypothesis for the purposes of this
106 article. Of course, these two explanations are not mutually exclusive; one of these
107 mechanisms could trigger a co-evolutionary feedback loop (Nussbaum & Schultz, 1989), or
108 a third unrelated factor could be independently driving the evolution of both egg size and
109 parental care (Shine, 1989). A positive association between parental care and egg size has
110 been found in taxa with aquatic eggs including amphibians (Summers et al., 2006), some
111 fish families (Sargent et al., 1987; Carcupino et al., 2002) and reef fishes in general
112 (Kasimatis & Riginos, 2016). By contrast, among terrestrial organisms, longer care is
113 associated with smaller eggs in birds (Stoddard et al., 2017), and no relationship has been
114 found in insects (Gilbert & Manica, 2010), emphasising the importance of ecological context
115 when selecting a clade for broad-scale life history analyses.

116

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

135

136 Few studies to date have evaluated potential environmental and parental behaviour drivers
137 of offspring size simultaneously, with most instead focused either on extrinsic or on intrinsic
138 effects. Furthermore, few studies make an explicit contrast between offspring size at
139 hatching (or leaving the parental body) and egg size, even though the former encompasses

140 survival benefits of care after spawning while the latter primarily represents maternal
141 investment. Here we assemble a large species-level dataset to test the relative effects of
142 parental care and environmental factors on offspring size in marine teleost fishes. Within a
143 phylogenetic context, and controlling for latitude (Kasimatis & Riginos, 2016), parental body
144 size (Sargent et al., 1987; Jorgensen et al., 2011; Rollinson et al., 2019) and fecundity
145 (Duarte & Alcaraz, 1989), we expect offspring size to increase in response to low
146 temperatures and poor food regime. We also anticipate a positive relationship between
147 parental care and offspring size, with a stronger relationship between parental body size and
148 offspring size in species that provide care than those that do not. We furthermore set out to
149 determine whether there is evidence that offspring size has co-evolved with parental care in
150 line with either the 'safe harbour' or the 'offspring-first' hypothesis. Taken together, our
151 analyses evaluate the evolutionary forces driving parental investment at two different
152 developmental stages in marine teleost fishes.

153

154 **2. MATERIALS AND METHODS**

155 **2.1 Data collection**

156 We collated mean values of fish egg size and larval size at hatching or upon leaving parent's
157 body, total adult body length and fecundity per species using global and regional datasets,
158 larval guides, FishBase (Froese & Pauly, 2019) and family-level reviews; all sources are
159 provided as part of the Supporting Data. All species with at least one proxy for offspring size
160 were then classified as exhibiting one of seven reproductive strategies based on Eugene
161 Balon's categorisation of reproductive guilds (Balon, 1975), see Figure 1. Each strategy was
162 assigned to three main categories with respect to where egg development takes place: (1)
163 'pelagic' or floating in the water column (including eggs that are free-floating or developing
164 within pelagic structures); (2) 'demersal' or developing on the sea floor (including demersal
165 scatterers and guarders); (3) developing in close association with 'parental body' (including
166 external bearers, pouch brooders and livebearers). Where available, we recorded the
167 primary caregiver in species with care (i.e., 'male', 'female', 'biparental', 'live invertebrate').
168 We distinguished between two categories of certainty with regards to the reproductive
169 behaviour: A, reproductive strategy determined by direct observations as part of an
170 experimental or a field study and/or listed as 'species-specific' in a secondary source; B,
171 reproductive strategy listed as 'presumed' in the literature or inferred from that of other
172 species within the genus with known strategy or from the family-level description in FishBase

173 (Froese & Pauly, 2019). Further details on data collection and categorisation of reproductive
174 strategies are available in Supporting Information Methods S1.

175 Overall, our finalised dataset contained 1,639 species with body length measurements and
176 at least one proxy for offspring size (1,347 and 292 species were in category A and B of
177 certainty with regards to their reproductive strategy, respectively; see Supporting Data for
178 the full dataset). We recorded 1,187 species with egg size (A = 1,014; B = 173) and hatch
179 size (A = 1,017, B = 170) values, with both variables available for a subset of 735 species (A
180 = 684, B = 51). The absolute fecundity values were available for 648 species (A = 546, B =
181 102).

182

183 **2.2 Environmental variables**

184 A set of six GIS raster layers was obtained from the global marine environmental dataset
185 Bio-ORACLE 2.0 (Assis et al., 2018) at 0.08° resolution. To encompass environmental
186 variation most likely related to offspring size, we selected the following variables: mean
187 temperature, chlorophyll-a and dissolved oxygen content, together with their ranges. In line
188 with Barneche et al. (2018), we used environmental data exclusively from the sea surface
189 layers because the preferred spawning depth was unknown for the majority of species in our
190 dataset. The mean values represented monthly averages from 2000 until 2014, while the
191 range values reflected the average of the absolute difference between the minimum and
192 maximum records per year throughout this time period. These values were then intersected
193 with species range polygons from the IUCN Red List of Threatened Species (IUCN, 2020)
194 and AquaMaps (Kaschner et al., 2019) to provide a mean value for each species, with
195 additional details available in Supporting Information Methods S1. Principal component
196 analysis (PCA) was used to reduce the dimensionality of the set of six environmental
197 variables per species because they were moderately to highly correlated with each other
198 (Dormann et al., 2013) (Supporting Information Table S1). All variables were mean centred
199 and expressed in units of standard deviation before PCA. The first three principal
200 components (PCs) captured ~ 98% of all variance in environmental data (Supporting
201 Information Table S2). In order to improve the interpretability of the results, a varimax
202 rotation (Kaiser, 1958) was applied to each component to reduce the number of variables
203 exhibiting high factor loadings. As the datasets of egg size and hatch size contained a
204 different combination of species, we ran separate PCAs on each set of environmental
205 variables, with qualitatively similar results in both A and A + B datasets (Supporting
206 Information Table S2), in a subset of species with both egg size and hatch size values
207 available and in subsets with fecundity values available (Supporting Information Table S3).

208 **2.3 Bayesian phylogenetic mixed models**

209 To test the relationship between offspring size (i.e., egg size or hatch size), parental care,
210 and the environment, we run Bayesian phylogenetic mixed models (BPMMs) in R package
211 'mulTree' (Guillerme & Healy, 2014), which runs Markov chain Monte Carlo (MCMC)
212 generalised linear mixed models (Hadfield, 2010) across a distribution of phylogenetic trees.
213 Offspring size and body size variables were log-transformed and latitude was square-root
214 transformed before the analysis. All continuous variables were mean centred and expressed
215 in units of standard deviation. We used three different sets of categorical variables relating to
216 reproduction: (1) place of egg development; (2) post-spawning care (3) seven reproductive
217 strategies. The variance inflation factor (VIF) of all non-interaction variables in all models
218 was less than five, demonstrating that multicollinearity was not a concern in our analyses
219 (Dormann et al., 2013). In order to account for non-independence of traits in species that
220 share common ancestry, a phylogenetic tree structure was included in the model as a
221 random effect. We used a distribution of 100 all-taxon assembled, time-calibrated
222 phylogenetic trees of ray-finned fishes (Rabosky et al., 2018). In advance of running the
223 BPMMs, we mapped the variation in offspring size and seven reproductive strategies on a
224 single tree extracted from this distribution in R package 'ggtree' (Yu et al., 2017). We also
225 visualised evolutionary change in offspring size using *fastAnc* function in R package
226 'phytools' (Revell, 2012).

227 Following the recommendations in Hadfield (Hadfield, 2010), we used inverse-Wishart priors
228 for the phylogenetic and residual variance ($V = 1$, $\nu = 0.002$) and diffuse normal priors for
229 fixed effects (mean 0, $V = 10^{10}$). For each of the 100 tree topologies in our sample, we ran
230 three MCMC chains for 240,000 iterations, discarded the first 40,000 iterations as burnin and
231 sampled every 100 iterations, which resulted in effective sample sizes of >1500 for all
232 parameters tested per phylogenetic tree. The model outputs were then summarised across
233 all trees following Karagicheva et al. (2018). Chain convergence was assessed using
234 Gelman-Rubin statistic (Gelman & Rubin, 1992), with potential-scale reduction values less
235 than 1.1 for all model outputs. The autocorrelation was determined using function *acf*, with
236 0.1 used as a target threshold.

237

238 **2.4 BayesTraits analysis of trait co-evolution**

239 We assessed the potential causal relationship between the presence of parental care and
240 offspring size using Pagel's Discrete algorithm (Pagel, 1994) implemented in BayesTraits
241 v3.0.1 (Pagel & Meade, 2017). The Discrete algorithm compares the marginal likelihood of a

242 dependent model where two binary traits co-evolve with each other to a model where these
243 traits evolve independently. The output from the BPMMs indicated that the presence of post-
244 spawning care was significantly correlated with size at hatching, with the strongest positive
245 effect in species that develop in association with parental body. As the method required the
246 use of binary discrete traits, we dichotomised the hatch size variable by the (1) median value
247 and (2) third quartile (Q3) values (i.e., by very large sizes at hatching vs the rest). We also
248 dichotomised the parental care variable in three different ways: (1) post-spawning care
249 presence/absence, $n = 1,187$; (2) post-spawning care in association with parental body (i.e.,
250 external and internal egg-bearing) presence/absence, $n = 1,187$; (3) post-spawning care
251 presence/absence in a subset of species with external egg development only (i.e., egg-
252 bearing species had been excluded), $n = 1,084$. The median value was 3 mm in both
253 datasets; the Q3 cut-point values were 4.7 mm and 4.29 mm in the full (1,2) and external (3)
254 datasets, respectively. We used the same distribution of phylogenetic trees (Rabosky et al.,
255 2018) as for BPMMs; all trees were scaled by a constant using the default setting of a mean
256 branch length of 0.1 as per the BayesTraits manual. Each BayesTraits model was run for 1.1
257 $\times 10^7$ iterations with an initial burn-in of 10^6 and was sampled at every 10^5 iterations which
258 resulted in a posterior distribution of 100 samples per tree. We forced Markov chains to
259 spend equal time on each tree using the *EqualTrees* command, and we ran two independent
260 chains per model to assess convergence. In all cases, we used a hyper-prior of an
261 exponential distribution (seeding from a uniform distribution on the interval 0–100) for a
262 reversible-jump MCMC procedure (Pagel & Meade, 2006). The marginal likelihood was then
263 estimated for each tree using a stepping stone sampler (Xie et al., 2011) where 50 stones
264 were distributed according to a beta distribution ($\alpha = 0.4$, $\beta = 1.0$) and each stone was run for
265 50,000 iterations. For each model, we compared the first chain's median likelihoods, across
266 the distribution of trees, using the log Bayes Factor. The inspection of all traces of parameter
267 estimates in Tracer v1.7.1 (Rambaut et al., 2018) confirmed adequate mixing and effective
268 sample sizes greater than 2000, with one exception. The dependent (co-evolutionary) model
269 for the subset of species with external egg development using Q3 as the cut-off point
270 exhibited substantial chain mixing problems due to the small sample size and high
271 phylogenetic signal in the data; we thus only use the median as a cut-off for this subsample.

272

273

274

275

276 **3. RESULTS**

277 **3.1 General trends in offspring size**

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

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

299 Males are the sole care providers in 76% of species with available information ($n = 403$)
300 while maternal care is present in 19% of care-giving species (Supporting Information Figure
301 S4). Biparental care (3%) and egg development in live invertebrates, e.g., in gills of crabs,
302 (2%) are the rarest types of care among marine fishes. The sex of caregiver is also closely
303 linked to the reproductive strategy. While nesters, external bearers and pouch brooders are
304 characterised predominantly by male care, all livebearing species exhibit maternal care.

305

306 **3.2 Drivers of variation in egg size**

307 A decrease in temperature together with an increase in dissolved oxygen content –
308 corresponding to the PC1 – is the strongest extrinsic predictor of an increase in egg size,

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

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

339

340 **3.3 Drivers of variation in hatch size**

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

344 size, larger-bodied species hatch at larger sizes compared to smaller-bodied species. While
345 species where eggs develop demersally or in association with parental body do not exhibit
346 larger eggs compared to pelagic spawners, they do yield markedly larger hatchlings (Figure
347 4d, Supporting Information Table S17). The presence of parental care after spawning is also
348 associated with significantly larger sizes at hatching, which highlights the contribution the
349 caring parent makes in addition to the initial maternal investment in eggs (Figure 4e,
350 Supporting Information Table S18). A further breakdown by reproductive strategy (Figure 4f,
351 Supporting Information Table S19) shows that all strategies with demersal eggs or egg-
352 bearing within/on the body exhibit increased size at hatching compared to pelagic spawners
353 – with the strongest positive association in external bearers, pouch brooders and
354 livebearers. Unexpectedly, demersal scatterers with no care after spawning exhibit a larger
355 positive shift from 0 compared to nesters that provide care for eggs. This is corroborated
356 with the results from the high-quality data (A, $n = 1,017$, Supporting Information Tables S20–
357 S22). The interaction between body size and the presence of parental care is positively
358 associated with hatch size, meaning that, for a given increase in parental body size, the
359 hatch size in species with care increases significantly more compared to non-caring species.
360 The relationship between parental body size and hatch size also varies depending on the
361 reproductive strategy, with external bearers and pouch brooders exhibiting a positive
362 interaction between body size and size at hatching. By contrast, we observe a negative
363 association in livebearing species which indicates that the hatch size of livebearers
364 increases significantly less with parental body size than that of species with no care
365 (Supporting Information Tables S23–S25). The output from models with fecundity as one of
366 the predictors ($n = 439$, Supporting Information Tables S26–S29) shows that this variable
367 does remove the significant association between hatch size and care after spawning – but
368 eggs developing demersally or in association with parental body still yield larger hatchlings
369 compared to pelagic eggs.

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

380 species with demersal or within/on body development than in pelagic spawners. The positive
381 relationship between hatch size and the presence of parental care also remains significant.

382

383 **3.4 Co-evolution of hatch size and parental care**

384 While we find a strong present-day positive association between post-spawning care and
385 size at hatching, there is no evidence that these two traits have co-evolved over
386 macroevolutionary time (log Bayes Factors [BF] -13.54 and -6.68 at median and third
387 quartile (Q3) cut-points, respectively; a log BF > 2 is interpreted as positive evidence for trait
388 co-evolution (Kass & Raftery, 1995)). We obtain the same result in a dataset that only
389 includes species with external egg development (log BF -5.54 at median cut-point). We do,
390 however, find support for the co-evolution of size at hatching and development in association
391 with the parental body, i.e., in external bearers, pouch brooders and livebearers, with log BF
392 3.35 at the median cut-point and 37.62 at Q3 (Figure 5; Supporting Information Tables S34–
393 S35). Overall, large hatch size is more likely to evolve from smaller hatch size in egg-bearing
394 species, rather than in species with external development (median $q_{24} = 8.85$, median $q_{13} =$
395 0.31 at Q3 cut-point), while transitions from external development to body development are
396 found only in species with large hatch size (median $q_{12} = 0.00$, $q_{34} = 0.30$ at Q3 cut-point).
397 The external development of large hatchlings is identified as the most likely ancestral state in
398 the analysis with Q3 as cut-point (median $p = 0.99$).

399

400 **4. DISCUSSION**

401 Our analyses of global drivers of marine teleost fish offspring size suggest that both
402 environmental and behavioural factors mediate the evolution of this key life-history trait. We
403 demonstrate that increases in both size at hatching and egg size are associated with lower
404 temperatures and higher oxygen content as well as lower fecundity and larger parental body
405 size. Furthermore, hatching size – but not egg size – is positively correlated with abundant
406 but variable food regime and reproductive strategies where eggs develop on the sea floor or
407 in association with parental body, with the strongest effect in advanced forms of parental
408 care, i.e., external and internal egg-bearing. While we find no evidence that size at hatching
409 co-evolves with post-spawning care in general, we show that external development of large
410 hatchlings acts as the first step towards the evolution of egg-bearing. This finding lends
411 support for the ‘offspring-first’ hypothesis, which posits that an increase in offspring size
412 drives the subsequent evolution of care behaviours (Nussbaum, 1987), above the ‘safe
413 harbour’ hypothesis (Shine, 1978; Sargent et al., 1987). Our analysis emphasises the

414 importance of incorporating phylogenetic history, environmental factors and different
415 developmental stages in the study of life-history trade-offs.

416

417 We find that size at hatching increases with the level of care provision – and that the trade-
418 off between offspring number and size can account for only some of this increase. By
419 contrast, egg size correlates primarily with environmental factors, suggesting that the
420 presence of care behaviours does not determine the initial maternal investment in young.
421 Our finding also reflects fundamental differences in life-history strategies associated with the
422 ‘fast-slow’ continuum (Stearns, 1992). Within this framework, pelagic spawners align closer
423 to ‘fast’ strategists with large numbers of small offspring and no parental care while non-
424 pelagic spawners cluster with ‘slow’ strategists that exhibit the opposite reproductive traits.
425 Hatching at large sizes is advantageous in demersal habitats because larger offspring are
426 better at exploiting limited resources, i.e., their mortality is size-dependent. This contrasts
427 with the production of many small offspring in the stochastic surface environments where
428 survival is more affected by chance (Duarte & Alcaraz, 1989; Winemiller & Rose, 1992,
429 1993).

430

431 Our results indicate that the increased hatchling size among demersal spawners remains
432 significant even after controlling for differences in fecundity and egg size, suggesting a
433 slowdown in the rate of egg development on the sea floor. Modelling approaches identify
434 slow egg development rate as one of the key conditions necessary for the evolution of
435 parental care, as it increases the time developing embryos are at risk from predators and
436 harsh environmental conditions (e.g., hypoxia in aquatic habitats) (Klug & Bonsall, 2010).
437 Most reports of a positive correlation between egg size and parental care arise from clades
438 with aquatic eggs (Sargent et al., 1987; Summers et al., 2006; Kasimatis & Riginos, 2016),
439 while animals with terrestrial development exhibit no such relationship (Gilbert & Manica,
440 2010; Stoddard et al., 2017), which suggests that oxygen availability represents a unique
441 constraint on the evolution of offspring size in water. Furthermore, brood defence and
442 provision of oxygen via fanning or mouthing – provided almost exclusively by males in this
443 group – are the most common types of care among fish species with demersal eggs (Green
444 & McCormick, 2005; Wootton & Smith, 2014). In co-evolutionary analyses that include such
445 external care behaviours, however, we find that care does not co-evolve with hatch size.
446 These results are consistent with a recent meta-analysis showing that male care is not
447 associated with higher offspring survival (Goldberg et al., 2020), and our analyses further
448 highlight other factors that might drive the evolution of external care, such as territoriality and

449 a polygynous mating system (Ah-King et al., 2004; Mank & Avise, 2006). Territoriality
450 promotes parent-offspring association as the two generations frequently encounter each
451 other (Lion & van Baalen, 2007); moreover, brood defence comes at little energetic cost to
452 the territorial male (Smith & Wootton, 1995; Goldberg et al., 2020). In addition, female
453 preference for more 'caring' males that, for example, fan their eggs more frequently (Östlund
454 & Ahnesjö, 1998) or provision broods from previous matings (Unger & Sargent, 1988) further
455 amplifies selection for external care among demersal spawners (Alonzo, 2012; Goldberg et
456 al., 2020).

457

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

477

478 Our results add to the large number of studies that report an inverse relationship between
479 offspring size and ambient temperature in aquatic species, or the Thorson-Rass rule
480 (Marshall, 1953; Marshall & Keough, 2007; Barneche et al., 2018). Importantly, we show that
481 both proxies for offspring size are sensitive to changes in temperature and oxygen levels,
482 which are highly correlated in surface waters. This implies that the ongoing trend of global
483 warming and the accompanying decline in oxygen levels in the world's oceans has the

484 potential to change the species composition of marine fish communities via effects on
485 reproductive output and dispersal over the next decades (Feary et al., 2014; Breitbart et al.,
486 2018). The strong link between offspring size and temperature has potential implications for
487 our finding that demersal habitats are associated with larger hatchlings compared to surface
488 waters. While we interpret this as evidence for size-dependent mortality, our result could
489 also reflect the impact of a temperature-depth gradient (Laptikhovsky, 2006) on the
490 developmental rate of demersal hatchlings. Future studies that incorporate the preferred
491 spawning depth for each species would help clarify whether demersal eggs in general are
492 exposed to a different set of environmental conditions compared to pelagic eggs. Our
493 analysis using a subset of high-quality data also indicates that, contrary to previous studies
494 (Robertson & Collin, 2015; Barneche et al., 2018), low food regimes are associated with
495 smaller, rather than larger, eggs – but we also note that in our dataset high chlorophyll
496 content is strongly correlated with large annual variation in this variable. If annual peaks in
497 food supply do not coincide with the reproductive season or are unpredictable, mothers
498 might invest relatively more in each offspring as part of a conservative ‘bet-hedging’ strategy
499 (Einum & Fleming, 2004).

500

501 **5. CONCLUSION**

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

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513

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713

714

715 **Figure Legends**

716

717 **FIGURE 1.** An overview of reproductive strategies in marine fishes; the place of egg
718 development is indicated above the grey line. 1 = 'Open Water', free-floating eggs; 2 =
719 'Structures', eggs develop in floating structures (left: goosefish egg rafts, Lophiidae family;
720 right: saury eggs with attaching filaments, Scomberesocidae family); 3 = 'Scatterers', eggs
721 develop in or under substrate/vegetation on the sea floor with no further care; 4 = 'Nesters',
722 eggs are cared for by the parent(s) after spawning (left: gunnels, Pholidae family, are clutch
723 tenders that care for eggs without modifying their nesting habitat; right: gobies, Gobiidae
724 family, are nest-builders that place eggs in specially constructed burrows); 5 = 'External
725 Bearers', eggs are brooded in close contact with parental body as exemplified by a
726 mouthbrooding male jawfish, Opistognathidae family; 6 = 'Pouch Brooders', eggs develop
727 within a pouch-like structure as exemplified by a brooding male seahorse, Syngnathidae
728 family; 7 = 'Livebearers', eggs develop within the reproductive tract of the mother as
729 exemplified by a gestating female rockfish, Sebastidae family. See Supporting Information
730 Methods S1 for further information.

731 **FIGURE 2.** Distribution of (a) egg size and (b) hatch size ($n = 1,187$ for each proxy) in
732 marine fishes across a single topology extracted from 100 phylogenetic trees provided in
733 Rabosky et al. (2018). The ancestral state reconstructions of offspring size using *fastAnc*
734 function in 'phytools' (Revell, 2012) are visualised on the tree structure. The outer circle
735 depicts seven reproductive strategies at branch tips (see Figure 1 and Supporting

736 Information Methods S1 for more information). For ease of interpretation, only the names of
737 families with records for 15 species or more have been displayed.

738 **FIGURE 3.** Geographic distribution of (a) mean egg size ($n = 1,187$), (b) mean hatch size (n
739 $= 1,187$), (c) proportion of species exhibiting post-spawning care ($n = 1,639$, species with at
740 least one proxy for offspring size), where 1 = all species exhibit care, 0 = no species exhibit
741 care, (d) species richness ($n = 1,639$), per 0.5° grid cell. Grid cells with fewer than three
742 species have been removed from the visualisations and therefore appear blank.

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

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

760

761 **Supporting Information Figure Legends**

762 **FIGURE S1.** Histograms of variation in (a) egg size and (b) size at hatching/leaving parental
763 body, in mm. Red and blue dashed lines indicate median and mean values, respectively.

764 **FIGURE S2.** Tukey box and whisker plots of variation in egg size ($n = 1,187$ species) with
765 respect to the (a) place of egg development, (b) presence of post-spawning parental care
766 and (c) seven reproductive strategies. The shaded area in (c) marks all reproductive
767 strategies with post-spawning care. The ends of the grey boxes correspond to the first and
768 third quartile of data distribution while the line in the middle represents the median value.

769 Whiskers indicate the minimum and maximum values excluding outliers, which are
770 calculated as the first and third quartile \pm 1.5 times the interquartile range.

771 **FIGURE S3.** Tukey box and whisker plots of variation in size at hatching/leaving parental
772 body ($n = 1,187$ species) with respect to the (a) place of egg development, (b) presence of
773 post-spawning parental care and (c) seven reproductive strategies. The shaded area in (c)
774 marks all reproductive strategies with post-spawning care. The ends of the grey boxes
775 correspond to the first and third quartile of data distribution while the line in the middle
776 represents the median value. Whiskers indicate the minimum and maximum values
777 excluding outliers, which are calculated as the first and third quartile \pm 1.5 times the
778 interquartile range.

779 **FIGURE S4.** Distribution by the sex of caregiver in species that exhibit reproductive
780 strategies characterised by post-spawning care ($n = 403$ species with available information).

781

782

783 **Supporting Information:**

784 1. Methods S1, Figures S1-S4, Tables S1-S35

785

786 **Supporting Data:**

787 Available from Dryad repository at <https://doi.org/10.5061/dryad.mw6m905x9>; see Data
788 accessibility statement

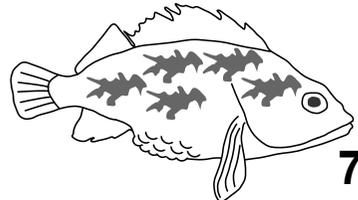
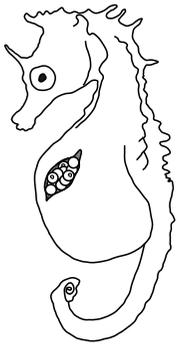
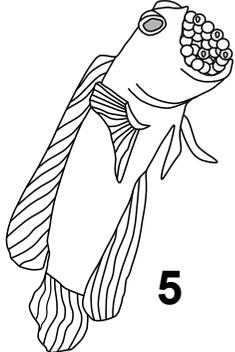
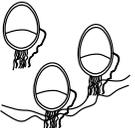
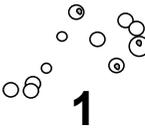
789 1. Key and Reference List for Supplementary Dataset

790 2. Supplementary Dataset

Fig. 1

Pelagic

Parental Body



Demersal

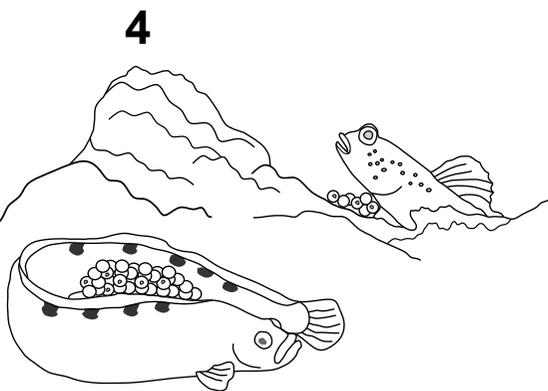
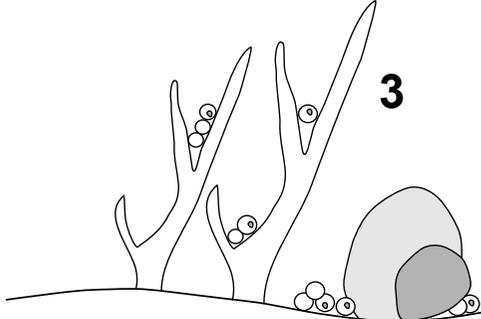


Fig. 2

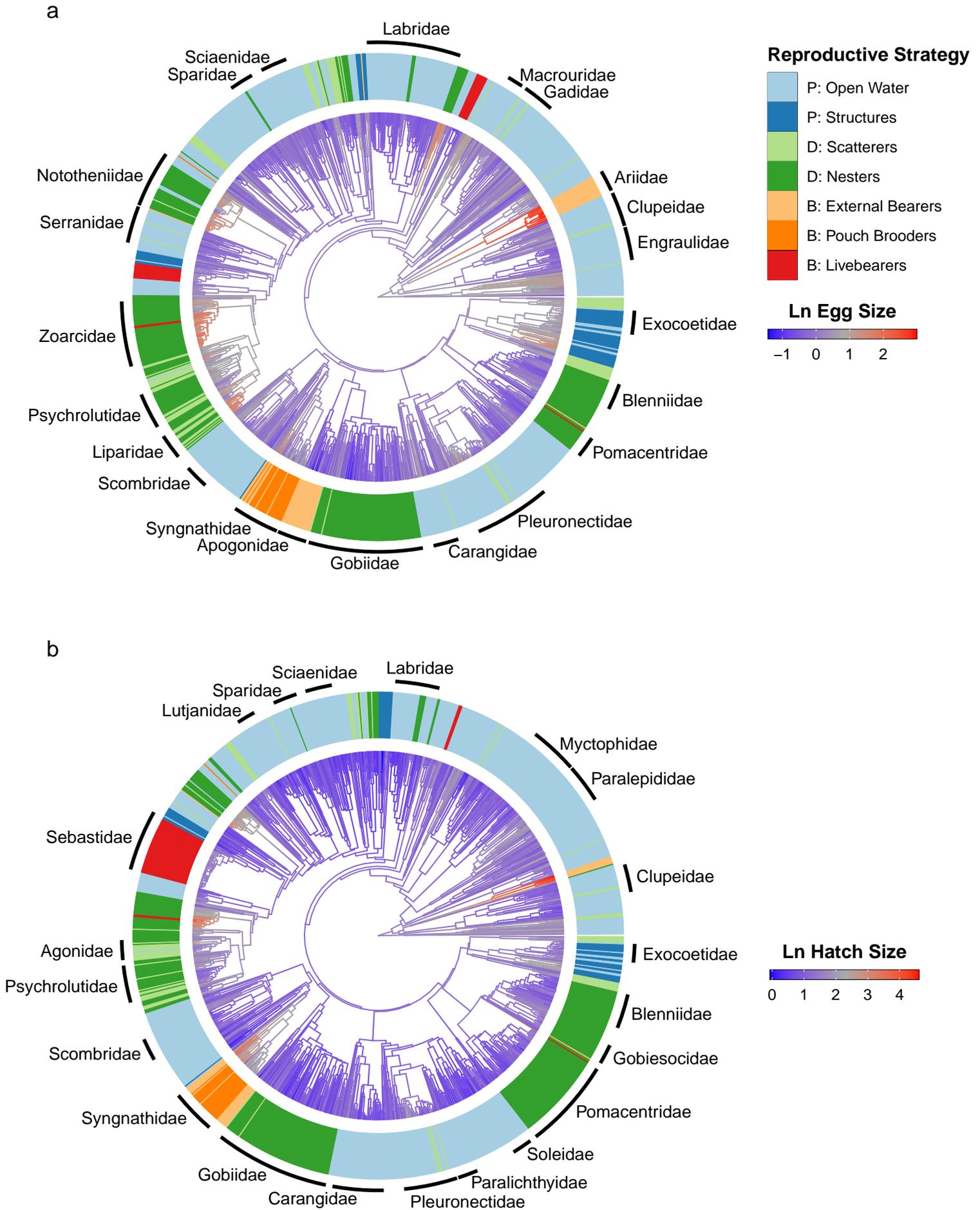


Fig. 3

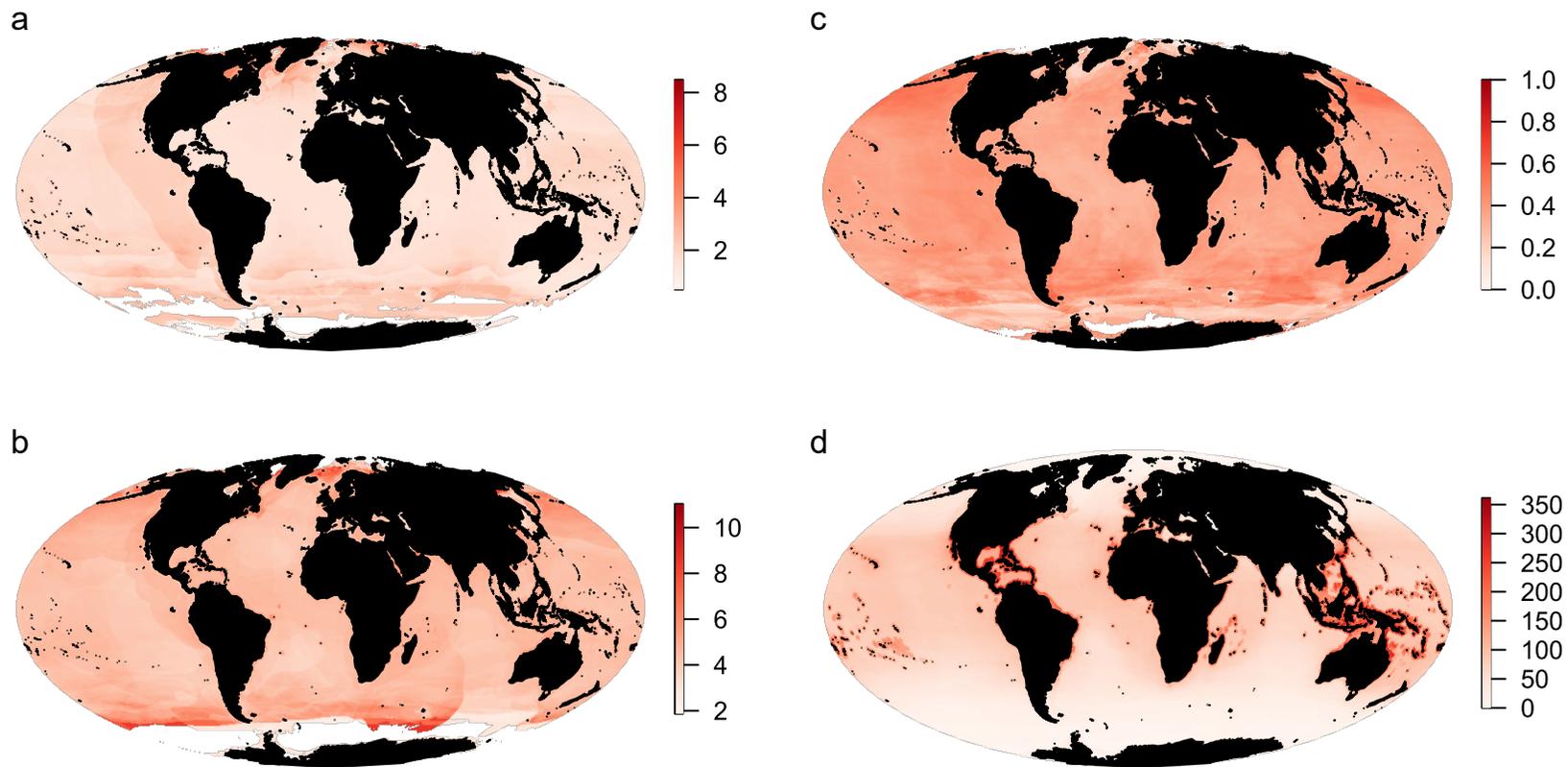


Fig. 4

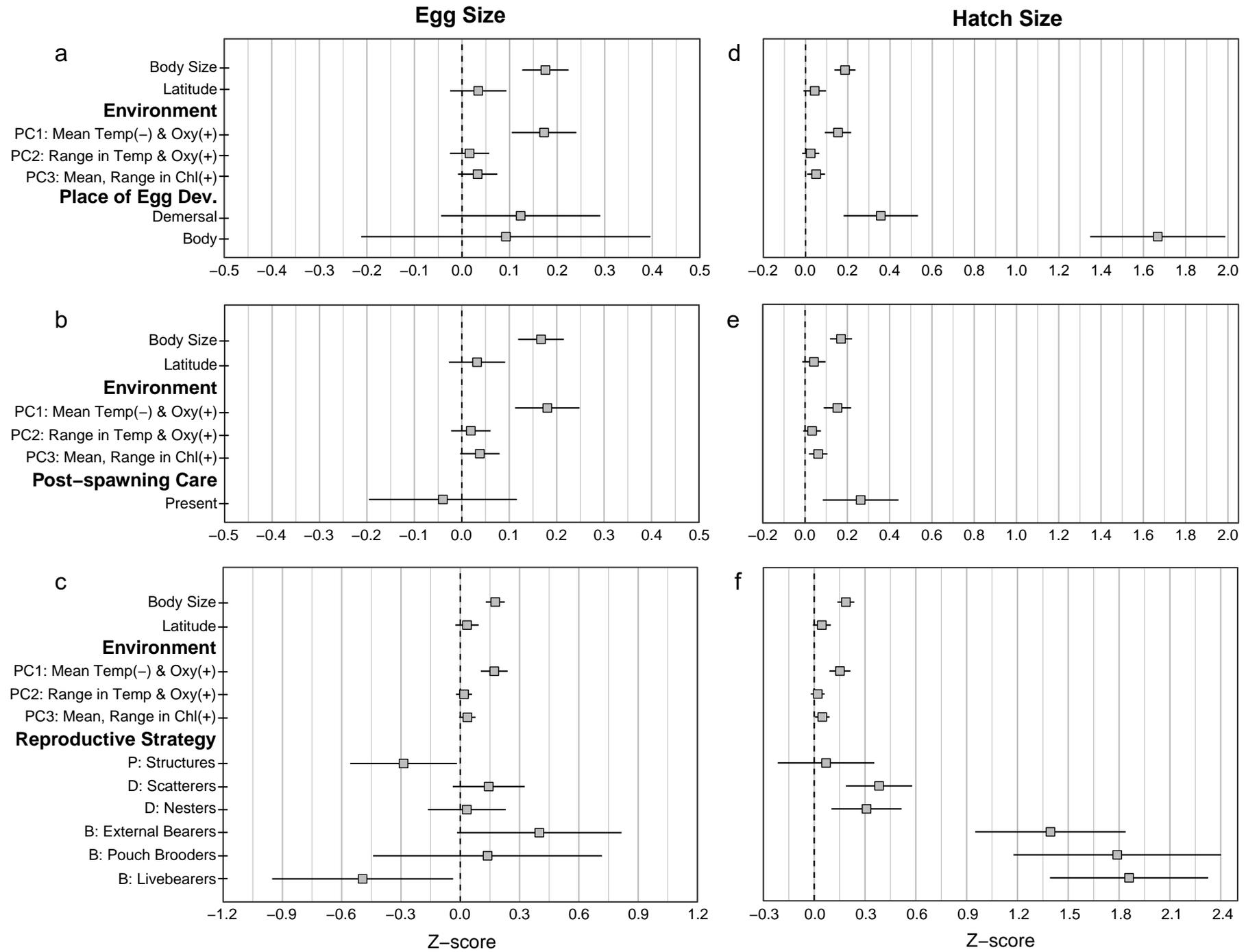


Fig. 5

