

1 **Selection for increased male size predicts variation in sexual size**
2 **dimorphism among fish species**

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13 **Key words:** Body size; Life history; Male-male competition; Fecundity Selection

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15 **Author Contributions**

16 CRH, AGH and DA designed the study and wrote the paper. CRH collated the data and performed
17 the statistical analyses.

18

19 **Data accessibility statement:** Raw data used in this study are available on Dryad:

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21 **ABSTRACT**

22 Variation in the degree of sexual size dimorphism (SSD) among taxa is generally considered to arise
23 from differences in the relative intensity of male-male competition and fecundity selection. One
24 might predict, therefore, that SSD will vary systematically with: 1) the intensity of sexual selection
25 for increased male size, and 2) the intensity of fecundity selection for increased female size. To test
26 these two fundamental hypotheses, we conducted a phylogenetic comparative analysis of SSD in
27 fish. Specifically, using records of body length at first sexual maturity from FishBase, we quantified
28 variation in the magnitude and direction of SSD in >600 diverse freshwater and marine fish species,
29 from sticklebacks to sharks. Although female-biased SSD was common, and thought to be driven
30 primarily by fecundity selection, variation in SSD was not dependent on either the allometric scaling
31 of reproductive-energy output or fecundity in female fish. Instead, systematic patterns based on
32 habitat and life history characteristics associated with varying degrees of male-male competition
33 and paternal care, strongly suggest that adaptive variation in SSD is driven by the intensity of sexual
34 selection for increased male size.

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41 INTRODUCTION

42 A difference in adult body size between males and females within a species, termed sexual size
43 dimorphism (SSD), is widespread in the animal kingdom. Life-history theory predicts that SSD will
44 arise from both natural and sexual selection, such that variation in reproductive success leads to
45 differences in the optimal body size of each sex. Male-biased SSD is commonly associated with a
46 high degree of sexual selection (e.g. male-male competition, intrasexual combat or territoriality),
47 whereas female-biased SSD is typically attributed to the positive correlation between maternal size
48 and fecundity (i.e. fecundity selection) [1-5]. Variation in the degree of SSD among species and taxa
49 is generally considered to arise from differences in the relative intensity of each of these selective
50 forces, but given such a vast array of reproductive strategies, even within closely related taxa, the
51 extent to which SSD is driven by sexual selection in males vs. fecundity selection in females
52 continues to fascinate ecologists and evolutionary biologists. Only by quantifying variation in both
53 the magnitude and direction of SSD, and identifying systematic patterns based on ecological and life
54 history characteristics, can we better understand its adaptive significance.

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56 Here, to improve our understanding of adaptive variation in SSD and make broad inferences about
57 its likely causation, we investigated the extent to which SSD is driven by selection for increased size
58 in males vs. in females (see Figure 1). Specifically, we aimed to establish whether:

- 59 i. SSD varies systematically with the intensity of sexual selection for increased male size (i.e.
60 the magnitude and direction of SSD is associated with the degree of intrasexual competition,
61 territoriality and/or paternal care).
- 62 ii. SSD varies systematically with the intensity of fecundity selection for increased female size
63 (i.e. the magnitude and direction of SSD is dependent on the allometric scaling of

64 reproductive-energy output and / or fecundity in females, and thus the extent to which
65 larger individuals reproduce disproportionately more than smaller individuals, and
66 theoretically have more to gain from maturing at a larger size).

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68 To test these fundamental hypotheses, we conducted a comprehensive, phylogenetically controlled
69 quantitative analysis of SSD in marine and freshwater fish species. Fish exhibit a remarkable array
70 of reproductive strategies, from extreme female-biased SSD in many angler fish, in which dwarf
71 males fuse to, and parasitize, the much larger females [6], to male-biased SSD in reef species
72 characterized by intense territoriality and sperm competition [e.g. 7, 8]. This makes fish excellent
73 model organisms for investigating the adaptive significance of SSD. Whereas previous comparative
74 studies have analysed patterns in SSD in a range of other taxa including birds [9, 10], copepods [11],
75 insects [12], mammals [13] and reptiles [14, 15], to our knowledge there have been no detailed
76 quantitative syntheses of SSD in fish, and there is a recognized need for more rigorous
77 phylogenetically controlled comparative analyses in this group [16, 17]. Some models have
78 previously been proposed to explain the evolution of SSD in fish [5], suggesting that, whereas large
79 female size is generally favoured because it increases fecundity, the intensity of selection for
80 increased male size is the most important predictor of SSD. However, almost thirty years since they
81 were proposed, these generalisations remain tentative, having only been tested qualitatively and at
82 relatively low taxonomic resolution. Here we provide a more robust test of these hypotheses,
83 considering 619 marine and freshwater species from 6 taxonomic classes, 44 orders and 162
84 families. We identify systematic patterns in SSD based on habitat and key reproductive life history
85 characteristics, many of which can be closely associated with varying degrees of male-male
86 competition and paternal care. In doing so, we find strong empirical support for the prediction that

87 SSD varies according to the intensity of sexual selection for increased male size, but no support for
88 the prediction that SSD varies with the allometric scaling of reproductive-energy output or fecundity
89 in females.

90

91 **MATERIALS AND METHODS**

92 ***Data Acquisition***

93 To quantitatively describe SSD in fish, we obtained data on length-at-maturity from FishBase [18].
94 FishBase contains almost 3000 records of body length at first sexual maturity for a wide range of
95 marine and freshwater fish species. We screened these records to include only those studies for
96 which mean length-at-maturity (L_m) was reported for both sexes separately and at the same
97 sampling location. If reported, we also recorded mean age at maturity (t_m). In each case, L_m and t_m
98 represent the point at which 50% of the population reached maturity. In addition to length data, we
99 also used FishBase to record important ecological attributes and reproductive life-history
100 characteristics that might explain variation in the degree of SSD between species. Specifically, we
101 categorized species by environment (freshwater vs. marine), habitat type (bathydemersal,
102 bathypelagic, benthopelagic, demersal, pelagic and reef), reproductive mode (dioecism, protandry,
103 protogyny), fertilization method (external vs. internal), reproductive guild (oviparous brooders,
104 oviparous guarders, oviparous non-guarders and viviparous), and level of parental care (none,
105 biparental, maternal and paternal). Definitions for each of these terms are provided in a glossary in
106 the Supporting Information.

107

108 For each species (within single studies and sampling locations) we calculated the degree of SSD using
109 the Sexual Dimorphism Index (SDI) of Lovich and Gibbons [19], where:

110

$$111 \text{ SDI} = (\text{size of larger sex} / \text{size of smaller sex}) - 1 \quad (1)$$

112

113 We followed the convention of assigning this metric a positive value when females were the larger
114 sex, and a negative value when males were larger [20]. Similarly, to provide a measure of the relative
115 difference in mean age at maturity between the sexes, we also calculated a sexual bimaturism index
116 (SBM) for each species (within single studies and sampling locations), where:

$$117 \text{ SBM} = (\text{age of later maturing sex} / \text{age of earlier maturing sex}) - 1 \quad (2)$$

118 We assigned this metric a positive value when females matured later, and a negative value when
119 males matured later. This allowed us to investigate whether the degree of SSD co-varied with the
120 relative difference in age at maturity (i.e. development time) between the sexes. Where we had
121 multiple records for the same species, we calculated the species-specific mean SDI and SBM prior
122 to any statistical analyses.

123 **Statistical Analyses**

124 Statistical analyses were conducted in R (version 3.5.2) [21]. Species have shared evolutionary
125 histories and are therefore not completely statistically independent. Thus, we began by determining
126 the relative degree of relatedness among species in our data set. Specifically, we used the package
127 'rotl' [22], which provides an interface to the Open Tree of Life [23], to retrieve and construct a

128 phylogenetic tree for our fish species. Branch lengths were computed following the Grafen method
129 [24] using the package 'ape' [25]. This phylogeny was used to create a variance-covariance matrix
130 among species, with a Pagel's Lambda Correlation Structure [26, 27], and was incorporated in all
131 our models to control for the phylogenetic correlation among observations. This phylogeny is
132 provided in our Supporting Information (Newick file format).

133 We began by deriving an overall phylogenetically-corrected mean SDI value for fish, calculated using
134 an intercept-only phylogenetic generalised least squares (PGLS) model in which SDI was the
135 independent variable (created using package 'nlme' [28] in combination with 'ape'). We then
136 determined whether the intercept (i.e. the phylogenetically-corrected mean SDI) differed
137 significantly from zero (two-sided *t*-test). Quantitative genetic theory predicts that the sex under
138 historically stronger directional selection will exhibit greater inter-specific variation in size, resulting
139 in covariation across taxa between the allometric slope of \log_{10} male versus \log_{10} female size and
140 the degree of SSD [29, 30]. Rensch's rule also suggests a similar correlation, but one in which males
141 are always the sex with greater inter-specific size variation [31]. Thus, we also quantified the
142 allometry of SSD by plotting a phylogenetic reduced-major-axis (RMA) regression of \log_{10} male
143 versus \log_{10} female size. Specifically, we used the function `phyl.RMA` in the package 'phytools' [32]
144 to determine whether the RMA regression slope (β) departed from isometry, i.e. differed
145 significantly from a slope value of 1 (two-sided *t*-test). Where *n* was ≥ 5 , mean SDI values, RMA
146 regressions and their significance were also examined separately by taxonomic classification (class,
147 order, family), environment, habitat type, and reproductive trait category.

148

149 Next, we compared several candidate models to best predict variation in SSD between species,
150 based on Akaike's information criterion corrected for small samples (AICc). Using SDI as the
151 dependent variable, we incorporated ecological attributes and reproductive life-history
152 characteristics as independent variables in a global PGLS model. These independent variables
153 included environment (freshwater vs. marine), habitat type (bathydemersal, bathypelagic,
154 benthopelagic, demersal, pelagic and reef), reproductive mode (dioecism, protandry, protogyny),
155 fertilization method (external vs. internal), reproductive guild (oviparous brooders, oviparous
156 guarders, oviparous non-guarders and viviparous), and level of parental care (none, biparental,
157 maternal and paternal care). We then compared all possible combinations of the global model terms
158 using the 'dredge' function in the 'MuMIn' package [33], including an intercept-only model, which
159 contained no independent variables and predicted that the best estimate of SDI was the intercept.
160 The best model was identified as that with the lowest AICc value. Where the difference between a
161 model's AICc and the lowest AICc (i.e. $\Delta AICc$) was <2 , a set of best fit models, rather than a single
162 best model, was assumed. Model averaging was then used to identify the best predictor variables
163 across the top candidate models and determine their relative importance (computed for each
164 variable as the sum of the Akaike weights from all models in which they appear) [34]. Specifically,
165 using package 'AICcmodavg' [35], we averaged over the entire set of candidate models (i.e. global
166 PGLS model and all possible simpler models) to calculate the 'full' model-averaged coefficients for
167 each of the best predictor variables and determine their significance (z-statistic, $p < 0.05$). Using the
168 'full' average assumes that each variable is included in every candidate model, but in some models
169 the corresponding coefficient (and its respective variance) is set to zero. This reduces the tendency
170 of biasing the estimated coefficients away from zero. Note that these AICc analyses were only
171 conducted on a subset of species for which we had data for all the independent variables ($n=364$),
172 i.e. species with any missing data were excluded.

173

174 In addition to AICc model selection, we also scored each species according to the categorical
175 variables in our analyses, many of which can be associated with varying degrees of selection for
176 increased male size (see Table 1). By scoring each of these traits and calculating the combined total,
177 we generated a selection-pressure index for increased male size; a comparative measure that
178 estimates the relative degree of selection for increased male size, predicted for each species. Total
179 scores varied from 0 to 8, ranging from dioecious pelagic species with internal fertilization and no
180 parental care or nest guarding (i.e. species with a relatively low likelihood of selection for increased
181 male size), to protogynous reef species with external fertilization and paternal care (i.e. species with
182 a relatively high likelihood of selection for increased male size). We then determined whether the
183 SDI varied significantly as a function of the selection-pressure index for increased male size (PGLS
184 regression).

185

186 To test the fecundity selection hypothesis, we investigated the extent to which SSD varied with the
187 allometric scaling of total reproductive-energy output and fecundity in females. Total reproductive-
188 energy output is a composite measure that incorporates not just estimates of fecundity, but also
189 egg size and egg energy content, and therefore is likely to provide a more robust estimate of how
190 reproductive investment scales with female body mass within a given species [36]. Theoretically,
191 selection for large female size, and by extension female-biased SSD, may be more prevalent in those
192 species with steeper allometric scaling of reproductive-energy output and/or fecundity, as females
193 may gain more from maturing at a larger size. To test these predictions, we acquired species-specific
194 reproductive-energy output and fecundity mass-scaling exponents from Barneche *et al.* [36], which
195 were available for 75 and 70 of the species in our data set, respectively. We then used a PGLS

196 regression to predict variation in i) female size, and ii) SDI as a function of both the reproductive-
197 energy output and fecundity mass-scaling exponents.

198

199 Whereas we use SDI as the dependent variable in our statistical analyses, to aid in the interpretation
200 of our findings, note that in our figures we express SDI as a percentage to indicate the degree of
201 female- or male-biased SSD (%). For example, an SDI value of 0.5 indicates that L_m (length at
202 maturity) in females is 50% larger than in males, whereas an SDI value of -0.5 indicates that L_m in
203 males is 50% larger than in females.

204

205 **RESULTS**

206 Our final screened data set consisted of 960 SDI values, representing 619 marine and freshwater
207 species from 6 taxonomic classes, 44 orders and 162 families. SSD varied considerably between
208 species, with species-specific SDI values ranging from 1.01 (i.e. female L_m 101% larger than male L_m)
209 to -1.34 (i.e. male L_m 134% larger than female L_m). SDI values were >0 in 68% of cases (female-
210 biased), <0 in 27% of cases (male-biased), and exactly zero in only 5% of cases (no difference in size
211 between the sexes). However, the overall phylogenetically-corrected mean SDI (0.076 ± 0.20 ; 95%
212 CI) did not differ significantly from zero ($t_{617} = -0.76$, $p = 0.45$, $\lambda = 0.67$). Thus, L_m was not consistently
213 larger in one sex than the other on average. Our data set included 34 families in which the number
214 of species was ≥ 5 . Fourteen of these families exhibited an overall mean SDI significantly greater than
215 zero, indicating female-biased SSD. Of these, the greatest difference in L_m was observed in the family
216 Gerreidae (mojarra), in which females were $\sim 28\%$ larger than males. Male-biased SSD was much
217 less common, with only two families having an overall mean SDI significantly less than zero

218 (Characidae and Scombridae). The remaining 18 families exhibited no significant difference in
219 length-at-maturity between the sexes, on average. A complete summary of these outcomes, where
220 data are divided by taxonomic classification, environment, habitat and reproductive characteristics,
221 is provided in Figure 2 and Table S1.

222

223 The best-supported model for explaining variation in SDI contained habitat type, reproductive mode
224 (dioecism, protandry, protogyny) and reproductive guild (oviparous brooders, oviparous guarders,
225 oviparous non-guarders and viviparous) as independent variables, which together accounted for
226 22% of the variation in SSD (AICc model selection). An alternative model that also included
227 fertilization method and parental care, but excluded reproductive guild, had a $\Delta AICc < 2$, and we
228 therefore calculated the combined parameter Akaike weights across both models to determine the
229 relative importance of each variable (see Table S2). Habitat type and reproductive mode were the
230 most important predictors, followed by reproductive guild, whereas fertilization and parental care
231 were relatively less important. Model averaging revealed significant effects of both habitat type and
232 reproductive mode on SDI, whereas none of the other independent variables had a significant effect.
233 A summary of these outcomes, including the full model-averaged coefficients, is presented in Table
234 S3.

235

236 A phylogenetic reduced-major-axis (RMA) regression of \log_{10} male L_m versus \log_{10} female L_m across
237 all species had a slope value (β) significantly less than 1, suggesting greater inter-specific variation
238 in female than male size (i.e. the inverse of Rensch's rule) [31]. However, RMA regressions for
239 individual taxa showed that most taxa exhibited isometry in SSD (Figure 2 and Table S1). Comparing
240 taxonomic classes, SSD in elasmobranchs did not depart from isometry, whereas females were the

241 more variable sex in Actinopterygii. However, male-female length isometry applied when all 34
242 families were examined separately, and only 3 of the 19 orders examined had β values significantly
243 <1 (i.e. greater variance in female size). At no level of organization tested was β significantly >1 (i.e.
244 greater variance in male size); thus, we found no evidence to support Rensch's rule [31]. Contrary
245 to the predictions of quantitative genetic theory [29, 30], there was no significant relationship
246 between family-specific phylogenetically-corrected mean SDI values and their respective β values
247 ($F_{1,34}=1.51$, $p=0.23$; Figure S1). We also collated data on time to maturity where this was reported
248 ($n=212$). In most cases ($\sim 69\%$) the smaller sex within a species reached maturity earlier. Those
249 species with the greatest relative difference in age at maturity between the sexes also exhibited the
250 strongest degree of SSD (PGLS regression; $t_{210}=13.60$, $p<0.001$, $\lambda=-0.05$; Figure S2).

251

252 **Importance of selection for increased male size**

253 We were able to significantly predict variation in SDI when species were scored based on the
254 selection-pressure index for increased male size (PGLS regression; $t_{362}=5.08$, $p<0.001$, $\lambda=0.24$; see
255 Figure 3a). The lowest scoring species generally exhibited female-biased SSD (L_m in females $\sim 18.5\%$
256 larger than in males), whereas the highest scoring species generally exhibited male-biased SSD (L_m
257 in males $\sim 20.0\%$ larger than in females). The sexes were much more similar in size in those species
258 with intermediate scores. As might be expected, SSD was female-biased in those species exhibiting
259 protandry (i.e. switching sex from male to female), whereas those species exhibiting protogyny (i.e.
260 switching sex from female to male) showed significant male-biased SSD. Even after removing those
261 species in which there was evidence of sex switching ($n=35$), we still found a significant relationship
262 between the selection-pressure index for increased male size and SDI (PGLS regression; $t_{327}=4.16$,
263 $p<0.001$, $\lambda=0.32$). Female L_m was $\sim 10.3\%$ larger male L_m in species with internal fertilization, whereas

264 in those species with external fertilization, males and females were similar in body size. Significant
265 male-biased SSD was evident in oviparous brooders (L_m in males $\sim 11\%$ larger than in females),
266 whereas species that did not guard their eggs exhibited female-biased SSD (L_m in females $\sim 8.9\%$
267 larger than in males). Finally, L_m in males was $\sim 11.5\%$ larger than in females in those species with
268 paternal care, whereas those species with no parental care exhibited female-biased SSD (L_m in
269 females $\sim 9.1\%$ larger than in males).

270

271 **SSD and the allometric scaling of female reproductive-energy output and fecundity**

272 To test the prediction that SSD varies systematically with the allometric scaling of reproductive-
273 energy output and/or fecundity in females, we used species-specific mass-scaling exponents
274 reported in Barneche *et al.* [36]. Reproductive-energy output mass-scaling exponents were available
275 for 75 of the species in our data set, with scaling exponents ranging from 0.77 to 1.87. Fecundity
276 mass-scaling exponents were available for 70 of the species in our data set, with scaling exponents
277 ranging from 0.67 to 1.76. We found no significant relationship between the intra-specific allometric
278 scaling exponent for reproductive-energy output and L_m in females (PGLS regression; $t_{73}=0.54$,
279 $p=0.59$, $\lambda=0.60$), nor with SDI (PGLS regression; $t_{73}=-0.12$, $p=0.90$, $\lambda=-0.02$; Figure 3b). Similarly, we
280 found no significant relationship between the intra-specific allometric scaling exponent for
281 fecundity and L_m in females (PGLS regression; $t_{68}=1.15$, $p=0.25$, $\lambda=0.70$), nor with SDI (PGLS
282 regression; $t_{68}=0.76$, $p=0.43$, $\lambda=-0.09$). Thus, variation in SSD was not dependent on the extent to
283 which larger females reproduce disproportionately more than smaller females.

284

285 **DISCUSSION**

286 Here we tested two fundamental hypotheses to better understand the adaptive significance of SSD:
287 that the magnitude and direction of SSD varies systematically with i) the intensity of sexual selection
288 for increased male size, and ii) with the intensity of fecundity selection for increased female size.
289 allometric scaling of reproductive-energy output and/or fecundity in females. We find compelling
290 empirical support for the former (i), but no support for the latter (ii).

291

292 Recent work has shown that, on average, both reproductive-energy output and fecundity scale
293 hyper-allometrically with body mass in female fish (i.e., larger females reproduce disproportionately
294 more than smaller females) [36]. Yet, although increased female size is commonly favoured because
295 it increases fecundity, selection pressures for increased male size appear to be the best predictor of
296 variation in the degree of SSD between fish species, supporting the predictions of Parker [5].
297 Examples of male-biased SSD in fish are generally observed where there is a high degree of
298 territoriality, sperm competition, or where there is evidence of paternal care [e.g. 37, 38-41]. Home
299 ranges have been documented in a wide range of coral reef fish, but this is rarely the case for pelagic
300 species, and consequently male-male competition, in the form of territoriality, is likely to be much
301 more intense in reef compared to pelagic habitats [42]. Differences in mating behaviour (e.g.
302 monogamy vs. polygamy, distinct pairing vs. communal spawning) will lead to variation in the
303 intensity of sperm competition, and at comparable levels of polygamy and communal spawning,
304 internal fertilization carries a lower risk of sperm competition than does external fertilization (since
305 the displacement of previous males' sperm and/or greater sperm mortality in internal fertilizers will
306 tend to decrease the intensity of sperm competition) [43]. Consequently, an increase in male body
307 size and aggression of external fertilizers may, among other factors, help to minimize multiple
308 paternity of female eggs [44, 45]. Similarly, the advantages of large male size are predicted to be

309 greater in those species with paternal care, or where male brooding and/or nest guarding is evident
310 [41, 46]. We generated a selection-pressure index for increased male size by scoring species based
311 on these traits. This index significantly predicted variation in SSD between fish species, not just in
312 direction but also in magnitude. At the extremes, L_m in females was ~18.5% larger than in males in
313 dioecious pelagic species with internal fertilization and no parental care, where territoriality and
314 sperm competition are predicted to be relatively low, and where high male mortality likely selects
315 for earlier reproduction, constraining male size, resulting in female-biased SSD. By contrast, L_m in
316 males was ~20.0% larger than in females in protogynous reef species with external fertilization and
317 paternal care, where male-male competition is predicted to be most intense. Assuming that most
318 fish exhibit isometric growth (i.e. they increase in their length with increasing weight in cubic form)
319 [18], these extremes would be equivalent to differences in body mass of 66.4% and 72.8%,
320 respectively.

321

322 We recognize that the traits used in our analyses only provide a proxy for the strength of selection
323 for increased male size, and do not capture the complexity of natural systems. For example, the
324 intensity of sperm competition varies enormously among fish species and is by no means entirely
325 dependent on fertilization method. Nevertheless, to make useful ecological generalizations from
326 the available data, categorizing species based on a few key life history characteristics provides a
327 more comprehensive hypothesis-driven approach to explaining the observed diversity in SSD. We
328 also acknowledge that in our analyses, scores for each of the different life-history traits were
329 allocated the same weighting, and some traits may be much more influential in driving SSD than
330 others. For example, in protogynous species, males will always be larger than the females they once
331 were. However, even after removing species that switch sex, there was still a significant relationship

332 between SSD and the selection-pressure index for increased male size. Although the underlying
333 scoring is subjective and not truly quantitative, in combination with AICc model selection, our
334 findings provide robust support for the prediction that adaptive variation in SSD among >600 diverse
335 fish species is primarily driven by the intensity of selection for increased male size.

336

337 Having established that the intensity of selection for increased male size is an important predictor
338 of SSD, we also examined to what extent selection for increased female size might contribute to the
339 observed patterns [e.g. 20, 47]. Specifically, one might predict that large female size, and by
340 extension female-biased SSD, will be more prevalent in those species with particularly steep
341 allometric scaling of female reproductive-energy output and/or fecundity, i.e. where larger
342 individuals reproduce disproportionately more than smaller individuals, and theoretically have
343 more to gain from maturing at a larger size. Yet, we found no such patterns in the species for which
344 we had suitable data. We postulate that this is because species with higher scaling exponents, and
345 hence disproportionately greater reproductive-energy output or fecundity with increasing body
346 size, may also have a disproportionate increase in the energetic costs of reproduction [36], and
347 these two components may counteract each other. These findings are particularly pertinent to the
348 recent debate on the extent to which constraints on growth *versus* the allometric scaling of costly
349 reproductive output may drive mature size and SSD, especially in fish [36, 48-51].

350

351 We acknowledge that there are several caveats associated with our test of the fecundity selection
352 hypothesis. Firstly, our analyses examining selection for increased size in males versus in females
353 differ markedly in their sample size, and this may increase the probability of a type 2 error when
354 examining the latter. Yet, were we to include only species for which we have both a selection-

355 pressure index score and a reproductive-energy output mass-scaling exponent, this would have
356 reduced the amount of available data by more than 88% (to n=42). We also note that similar tests
357 for other ectotherms, including broad scale analyses across lizards and snakes, find mixed support
358 for the fecundity selection hypothesis, but do find an association between SSD and proxies for the
359 degree of sexual selection in males [14, 15]. Whether relationships between SSD and the allometric
360 scaling of reproductive-energy output are evident in other taxa remains to be investigated.
361 Secondly, despite potentially variable selection for increased female size among species from
362 different habitats and with different reproductive traits, the high prevalence of female-biased SSD
363 and evidence for the inverse of Rensch's rule [31] (i.e. allometric slope values <1, indicating greater
364 variation in female size; see Figure 2) suggests that directional selection has generally favoured large
365 female size. These outcomes are consistent with findings for other taxa exhibiting female-biased
366 SSD, such as birds [52] and insects [12]. Directional selection for large female size is predicted to
367 result from the positive correlation between body size and fecundity [3, 53, 54]. Consequently,
368 although we cannot explain variation in the degree of SSD based on the allometric scaling of
369 reproductive-energy output or fecundity in females, fecundity selection is still likely to play an
370 important role in maintaining large female size and driving SSD. Indeed, only when the selection
371 pressures for increased male size intensify do we begin to observe deviations away from female-
372 biased SSD towards monomorphism and male-biased SSD (see Figure 3a). Ultimately, although
373 selection for increased male size predicts variation in SSD among fish species, we cannot dismiss the
374 effect of fecundity selection, and these drivers are by no means mutually exclusive.

375

376 SSD can arise due to differences in development time and/or growth rate between the sexes, and
377 the relative importance of each of these proximate mechanisms in generating SSD has been

378 debated, particularly in insects [17, 20, 55]. We found that the sex with the longer development
379 time also tended to mature at a larger size, and those species with the greatest relative difference
380 in age at maturity between the sexes also exhibited the strongest degree of SSD. Therefore, whilst
381 we cannot rule out that males and females may also differ in their growth rates, variation in
382 development time appears to be an important proximate correlate of SSD in fish (Figure S2). We
383 note that many fish exhibit indeterminate growth and, consequently, mean adult body size can be
384 much larger than size at maturation. As a result, sex-specific growth patterns beyond maturation
385 could lead to differences in SSD at maturity vs. SSD at asymptotic size, potentially confounding our
386 overall conclusions. Of the 619 species in our data set, we found paired male and female estimates
387 of asymptotic length for 240 species on FishBase [18], and therefore tested whether SSD derived
388 from asymptotic length (SSD L_{inf}) differed significantly from SSD derived from length at maturity (SSD
389 L_m). On average, we found no significant difference between SSD L_{inf} and SSD L_m , both when using a
390 phylogenetic paired t -test ($t_{237}=0.015$, $p=0.988$), and also when plotting a phylogenetically-
391 corrected RMA regression of SSD L_{inf} vs. SSD L_m , such that the slope of the regression did not differ
392 significantly from 1 ($t_{232}=1.00$, $p=0.32$). Furthermore, in agreement with our overall conclusions,
393 there was a significant positive relationship between SSD L_{inf} and the selection-pressure index from
394 increased male size (PGLS regression; $t_{167}=2.79$, $p=0.006$), but not with the allometric scaling of
395 reproductive-energy output (PGLS regression; $t_{33}=0.14$, $p=0.89$) or fecundity in females (PGLS
396 regression; $t_{32}=-0.24$, $p=0.81$ respectively). Thus, whereas many fish continue to grow beyond
397 maturation, we are confident in our use of length at maturity to identify systematic patterns in SSD.

398

399 **Conclusion**

400 Previous phylogenetic comparative analyses have investigated the extent to which SSD is driven by
401 selection for increased size in males vs. in females, including birds [9, 10], insects [12], mammals
402 [13] and reptiles [14, 15]. In the majority of cases, there were significant correlations between the
403 degree of SSD and various measures of sexual selection for large male size, whereas those that
404 incorporated estimates of fecundity selection (e.g. by quantifying the slope of the relationship
405 between clutch size and maternal size) found inconsistent support for this hypothesis. Yet, studies
406 of SSD in fish are under-represented in the literature [17], and to our knowledge, this is the first
407 rigorous, comparative analyses of SSD in this group. Whereas Parker [5] used a categorical measure
408 of SSD to test his predictions, our quantitative approach provides much greater statistical power,
409 whilst also accounting for the phylogenetic correlation among taxa. Adopting a trait-based
410 approach, combined with an increase in the availability of novel physiological data, such as intra-
411 specific reproductive-energy output mass-scaling exponents, allows for a more robust test of the
412 fundamental hypotheses proposed to explain adaptive variation in SSD. In this regard, we believe
413 our dataset and analyses provide a methodological template for future studies examining diversity
414 in SSD in other taxa.

415

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421

422 **REFERENCES**

- 423 1. Hedrick A.V., Temeles E.J. 1989 The evolution of sexual dimorphism in animals: hypotheses
424 and tests. *Trends in Ecology & Evolution* **4**(5), 136-138.
- 425 2. Slatkin M. 1984 Ecological causes of sexual dimorphism. *Evolution*, 622-630.
- 426 3. Darwin C. 1874 *The Descent of Man and Selection in Relation to Sex* (New York, AL Burt Co.
- 427 4. Lande R. 1980 Sexual dimorphism, sexual selection, and adaptation in polygenic characters.
428 *Evolution*, 292-305.
- 429 5. Parker G.A. 1992 The evolution of sexual size dimorphism in fish. *Journal of Fish Biology*
430 **41**(sB), 1-20.
- 431 6. Pietsch T.W. 1976 Dimorphism, parasitism and sex: reproductive strategies among deepsea
432 Ceratioid anglerfishes. *Copeia* **1976**(4), 781-793. (doi:10.2307/1443462).
- 433 7. Reese E.S. 1973 Duration of residence by coral reef fishes on " home" reefs. *Copeia* **1973**(1),
434 145-149.
- 435 8. Keenleyside M.H.A. 2012 *Diversity and adaptation in fish behaviour*, Springer Berlin
436 Heidelberg.
- 437 9. Lislevand T., Figuerola J., Székely T. 2009 Evolution of sexual size dimorphism in grouse and
438 allies (Aves: Phasianidae) in relation to mating competition, fecundity demands and resource
439 division. *J Evol Biol* **22**(9), 1895-1905. (doi:10.1111/j.1420-9101.2009.01802.x).
- 440 10. Serrano-Meneses M.A., Székely T. 2006 Sexual size dimorphism in seabirds: sexual
441 selection, fecundity selection and differential niche-utilisation. *Oikos* **113**(3), 385-394.
- 442 11. Hirst A.G., Kiørboe T. 2014 Macroevolutionary patterns of sexual size dimorphism in
443 copepods. *Proceedings of the Royal Society of London B: Biological Sciences* **281**(1791).
444 (doi:10.1098/rspb.2014.0739).

- 445 12. Blanckenhorn W.U., Meier R., Teder T. 2007 Rensch's rule in insects: patterns among and
446 within species. In *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism* (eds.
447 Fairbairn D.J., Blanckenhorn W.U., Székely T.). Oxford, Oxford University Press.
- 448 13. Lindenfors P., Gittleman J.L., Jones K.E. 2007 Sexual size dimorphism in mammals. *Sex, size
449 and gender roles: evolutionary studies of sexual size dimorphism*, 16-26.
- 450 14. Cox R.M., Butler M.A., John-Alder H.B. 2007 The evolution of sexual size dimorphism in
451 reptiles. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*, 38-49.
- 452 15. Shine R. 1994 Sexual size dimorphism in snakes revisited. *Copeia*, 326-346.
- 453 16. Blanckenhorn W.U. 2005 Behavioral causes and consequences of sexual size dimorphism.
454 *Ethology* **111**(11), 977-1016.
- 455 17. Fairbairn D.J., Blanckenhorn W.U., Székely T. 2007 *Sex, size and gender roles: evolutionary
456 studies of sexual size dimorphism*, Oxford University Press.
- 457 18. Froese R., Pauly D. 2019 FishBase. (World Wide Web electronic publication.
458 www.fishbase.org).
- 459 19. Lovich J.E., Gibbons J.W. 1992 A review of techniques for quantifying sexual size
460 dimorphism. *Growth Development and Aging* **56**(4), 269-281.
- 461 20. Blanckenhorn W.U., Dixon A.F., Fairbairn D.J., Foellmer M.W., Gibert P., Linde K.v.d., Meier
462 R., Nylin S., Pitnick S., Schoff C. 2007 Proximate causes of Rensch's rule: does sexual size
463 dimorphism in arthropods result from sex differences in development time? *The American
464 Naturalist* **169**(2), 245-257.
- 465 21. R Core Team. 2018 *R: A language and environment for statistical computing*. Vienna,
466 Austria, R Foundation for Statistical Computing.
- 467 22. Michonneau F., Brown J.W., Winter D.J. 2016 rotl: an R package to interact with the Open
468 Tree of Life data. *Methods in Ecology and Evolution* **7**(12), 1476-1481.

- 469 23. Hinchliff C.E., Smith S.A., Allman J.F., Burleigh J.G., Chaudhary R., Coghill L.M., Crandall K.A.,
470 Deng J., Drew B.T., Gazis R., et al. 2015 Synthesis of phylogeny and taxonomy into a
471 comprehensive tree of life. *PNAS* **112** 12764-12769.
- 472 24. Grafen A. 1989 The phylogenetic regression. *Philosophical Transactions of the Royal society*
473 *of London Series B Biological Sciences* **326**, 119-157.
- 474 25. Paradis E., Schliep K. 2018 ape 5.0: an environment for modern phylogenetics and
475 evolutionary analyses in R. *Bioinformatics* **35**, 526-528.
- 476 26. Freckleton R.P., Harvey P.H., Pagel M. 2002 Phylogenetic analysis and comparative data: a
477 test and review of evidence. *The American Naturalist* **160**(6), 712-726.
- 478 27. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**(6756),
479 877.
- 480 28. Pinheiro J., Bates D., DebRoy S., Sarkar D., Team R.C. 2019. *nlme: Linear and Nonlinear*
481 *Mixed Effects Models R package version 3.1-140*.
- 482 29. De Lisle S.P., Rowe L. 2013 Correlated evolution of allometry and sexual dimorphism across
483 higher taxa. *The American Naturalist* **182**(5), 630-639.
- 484 30. Zeng Z.B. 1988 Long-term correlated response, interpopulation covariation, and
485 interspecific allometry. *Evolution* **42**(2), 363-374.
- 486 31. Rensch B. 1960 *Evolution above the species level*. New York, NY, Columbia University Press.
- 487 32. Revell L.J. 2012 phytools: An R package for phylogenetic comparative biology (and other
488 things). *Methods in Ecology and Evolution* **3**, 217-233.
- 489 33. Barton K. 2017 MuMIn; multi-model inference. R package version 1.40.0. (
- 490 34. Burnham K.P., Anderson D.M. 2002 *Model selection and multimodel inference: A practical*
491 *information-theoretic approach*. 2nd ed. New York, Springer.

- 492 35. Mazerolle M.J. 2014 Model Selection and Multimodel Inference Based on (Q)AIC(c). R
493 package version 2.0-1.
- 494 36. Barneche D.R., Robertson D.R., White C.R., Marshall D.J. 2018 Fish reproductive-energy
495 output increases disproportionately with body size. *Science* **360**(6389), 642-645.
- 496 37. Erlandsson A., Ribbink A. 1997 Patterns of sexual size dimorphism in African cichlid fishes. *S*
497 *Afr J Sci* **93**, 498-508.
- 498 38. Schütz D., Taborsky M. 2000 Giant males or dwarf females: what determines the extreme
499 sexual size dimorphism in *Lamprologus callipterus*? *J Fish Biol* **57**(5), 1254-1265.
- 500 39. Kodric-Brown A. 1990 Mechanisms of sexual selection: insights from fishes. *Ann Zool Fenn*
501 **27**(2), 87-100.
- 502 40. Kolm N. 2002 Male size determines reproductive output in a paternal mouthbrooding fish.
503 *Anim Behav* **63**(4), 727-733. (doi:<https://doi.org/10.1006/anbe.2001.1959>).
- 504 41. Gagliardi-Seeley J.L., Itzkowitz M. 2006 Male size predicts the ability to defend offspring in
505 the biparental convict cichlid *Archocentrus nigrofasciatus*. *J Fish Biol* **69**(4), 1239-1244.
506 (doi:10.1111/j.1095-8649.2006.01174.x).
- 507 42. Hixon M.A. 2015 Territory area as a determinant of mating Systems. *ICB* **27**(2), 229-249.
508 (doi:10.1093/icb/27.2.229).
- 509 43. Stockley P., Gage M., Parker G., Møller A. 1997 Sperm competition in fishes: the evolution
510 of testis size and ejaculate characteristics. *The American Naturalist* **149**(5), 933-954.
- 511 44. Smith R.L. 2012 *Sperm competition and the evolution of animal mating systems*, Elsevier.
- 512 45. Constantz G.D. 1984 Sperm competition in poeciliid fishes. In *Sperm competition and the*
513 *evolution of animal mating systems* (ed. Smith R.L.), pp. 465-485, Elsevier.
- 514 46. Gross M.R., Sargent R.C. 1985 The evolution of male and female parental care in fishes. *Am*
515 *Zool* **25**(3), 807-822.

- 516 47. Clarke T. 1983 Sex ratios and sexual differences in size among mesopelagic fishes from the
517 central Pacific Ocean. *Marine Biology* **73**(2), 203-209.
- 518 48. Marshall D.J., White C.R. 2018 Have we outgrown the existing models of growth? *Trends*
519 *Ecol Evol*.
- 520 49. Marshall D.J., White C.R. 2019 Aquatic Life History Trajectories Are Shaped by Selection,
521 Not Oxygen Limitation. *Trends Ecol Evol*.
- 522 50. Pauly D. 2019 Female Fish Grow Bigger—Let's Deal with It. *Trends Ecol Evol*.
- 523 51. Kearney M. 2019 Reproductive Hyperallometry Does Not Challenge Mechanistic Growth
524 Models. *Trends Ecol Evol*.
- 525 52. Webb T.J., Freckleton R.P. 2007 Only half right: species with female-biased sexual size
526 dimorphism consistently break Rensch's rule. *PLoS One* **2**(9), e897.
- 527 53. Fairbairn D.J. 1997 Allometry for sexual size dimorphism: Pattern and process in the
528 coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659-
529 687. (doi:10.1146/annurev.ecolsys.28.1.659).
- 530 54. Abouheif E., Fairbairn D.J. 1997 A comparative analysis of allometry for sexual size
531 dimorphism: assessing Rensch's rule. *American Naturalist*, 540-562.
- 532 55. Teder T. 2014 Sexual size dimorphism requires a corresponding sex difference in
533 development time: a meta-analysis in insects. *Funct Ecol* **28**(2), 479-486.
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540 **FIGURE LEGENDS**

541

542 **Figure 1.** A summary of the key life-history characteristics that might select for increased body size
543 in females vs. in males. Female-biased sexual size dimorphism (SSD) is typically attributed to the
544 positive correlation between body size and fecundity (i.e. fecundity selection), and variation in the
545 degree of SSD may be dependent on the allometric scaling of reproductive-energy output (REO) or
546 fecundity in females (i.e. the extent to which larger females reproduce disproportionately more
547 than smaller individuals). Selection for increased male size may be associated with a high degree of
548 territoriality, sperm competition, and/or paternal care. Variation in the degree of SSD among species
549 and taxa is generally considered to arise from differences in the relative intensity of each of these
550 selective forces.

551

552 **Figure 2.** Multi-panel plot showing (i) the phylogenetically-corrected mean degree of sexual size
553 dimorphism (%), and (ii) the allometric slope values of phylogenetic reduced-major-axis (RMA)
554 regressions of \log_{10} male versus \log_{10} female length-at-maturity in fish. Data are divided by
555 taxonomic classification, environment, habitat and reproductive characteristics. Error bars denote
556 95% confidence intervals. Shaded data points indicate where the degree of SSD or allometric slope
557 value differs significantly from monomorphism or isometry, respectively (dashed grey lines). These
558 analyses were only performed when $n \geq 5$. Accompanying sample sizes and p-values are presented
559 in Table S1.

560

561 **Figure 3.** Variation in the degree of sexual size dimorphism (SSD) as a function of **A)** the selection-
562 pressure index for increased male size ($n=364$), and **B)** species-specific female reproductive-energy

563 output mass-scaling exponents reported in Barneche *et al.* [36]. Solid lines indicate the PGLS
564 regression through the data; 95% CIs are contained within the shaded area. In panel A, species were
565 scored according to categorical variables associated with varying degrees of selection for increased
566 male size (see Table 1). The combined total of these scores significantly predicts variation in the
567 degree of SSD, such that low-scoring species (i.e. species with a relatively low likelihood of selection
568 for increased male size) generally exhibit female-biased SSD, whereas high-scoring species (i.e.
569 species with a relatively high likelihood of selection for increased male size) generally exhibit male-
570 biased SSD. There is no significant relationship between the allometric scaling of female
571 reproductive-energy output and the degree of SSD. We postulate that this is because species with
572 higher scaling exponents, hence a disproportionately greater reproductive-energy output with
573 increasing body size, also have a disproportionate increase in the energetic costs of reproduction,
574 and these two components likely counteract each other. Similarly, we found no significant
575 relationship between the intra-specific allometric scaling of fecundity and SSD in females.

576 **Table 1.** Scores allocated to each species according to the categorical variables associated with
577 varying degrees of selection for increased male size. The total combined scores for each species,
578 termed the selection-pressure index, were then used to predict variation in the degree of sexual
579 size dimorphism (SSD) in fish, such that low-scoring species (i.e. species with a relatively low
580 likelihood of selection for increased male size) generally exhibited female-biased SSD, whereas high-
581 scoring species (i.e. species with a relatively high likelihood of selection for increased male size)
582 generally exhibited male-biased SSD (Figure 3a).

Trait	Score	
Habitat		
Bathypelagic	0	<i>(Low territoriality)</i>
Pelagic	0	<i>(Low territoriality)</i>
Bathydemersal	1	<i>(Moderate territoriality)</i>
Benthopelagic	1	<i>(Moderate territoriality)</i>
Demersal	1	<i>(Moderate territoriality)</i>
Reef	2	<i>(High territoriality)</i>
Fertilization Method		
Internal	0	<i>(Relatively low sperm competition)</i>
External	1	<i>(Relatively high sperm competition)</i>
Reproductive Guild		
Oviparous (non-guarder)	0	<i>(Low male size advantage)</i>
Viviparous	0	<i>(Low male size advantage)</i>
Oviparous (female-only brooder)	0	<i>(Low male size advantage)</i>
Oviparous (female-only guarder)	0	<i>(Low male size advantage)</i>
Oviparous (brooder)	1	<i>(Moderate male size advantage)</i>
Oviparous (guarder)	1	<i>(Moderate male size advantage)</i>
Oviparous (male-only brooder)	2	<i>(High male size advantage)</i>
Oviparous (male-only guarder)	2	<i>(High male size advantage)</i>
Parental Care		
None	0	<i>(Low male size advantage)</i>
Maternal	0	<i>(Low male size advantage)</i>
Biparental	1	<i>(Moderate male size advantage)</i>
Paternal	2	<i>(High male size advantage)</i>
Reproductive Mode		
Dioecism	0	<i>(Low selection intensity)</i>
Protandry (i.e. male → female)	0	<i>(Low selection intensity)</i>
Protogyny (i.e. female → male)	1	<i>(High selection intensity)</i>

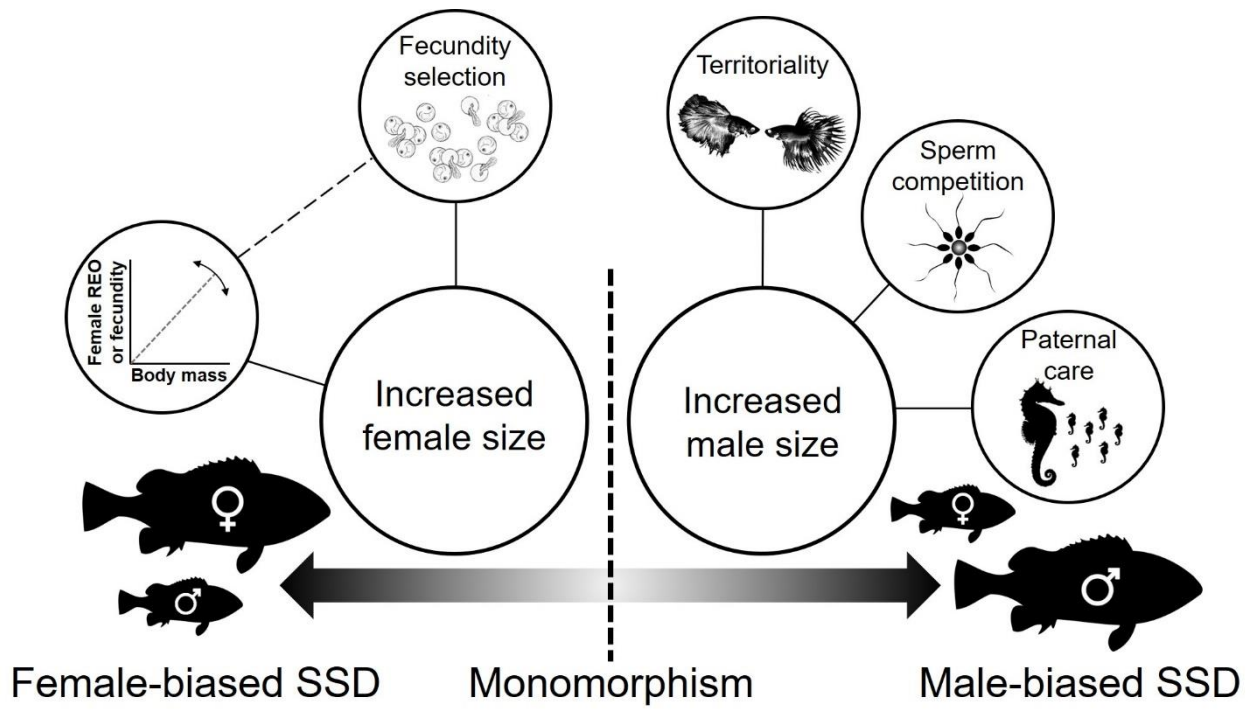


Figure 1

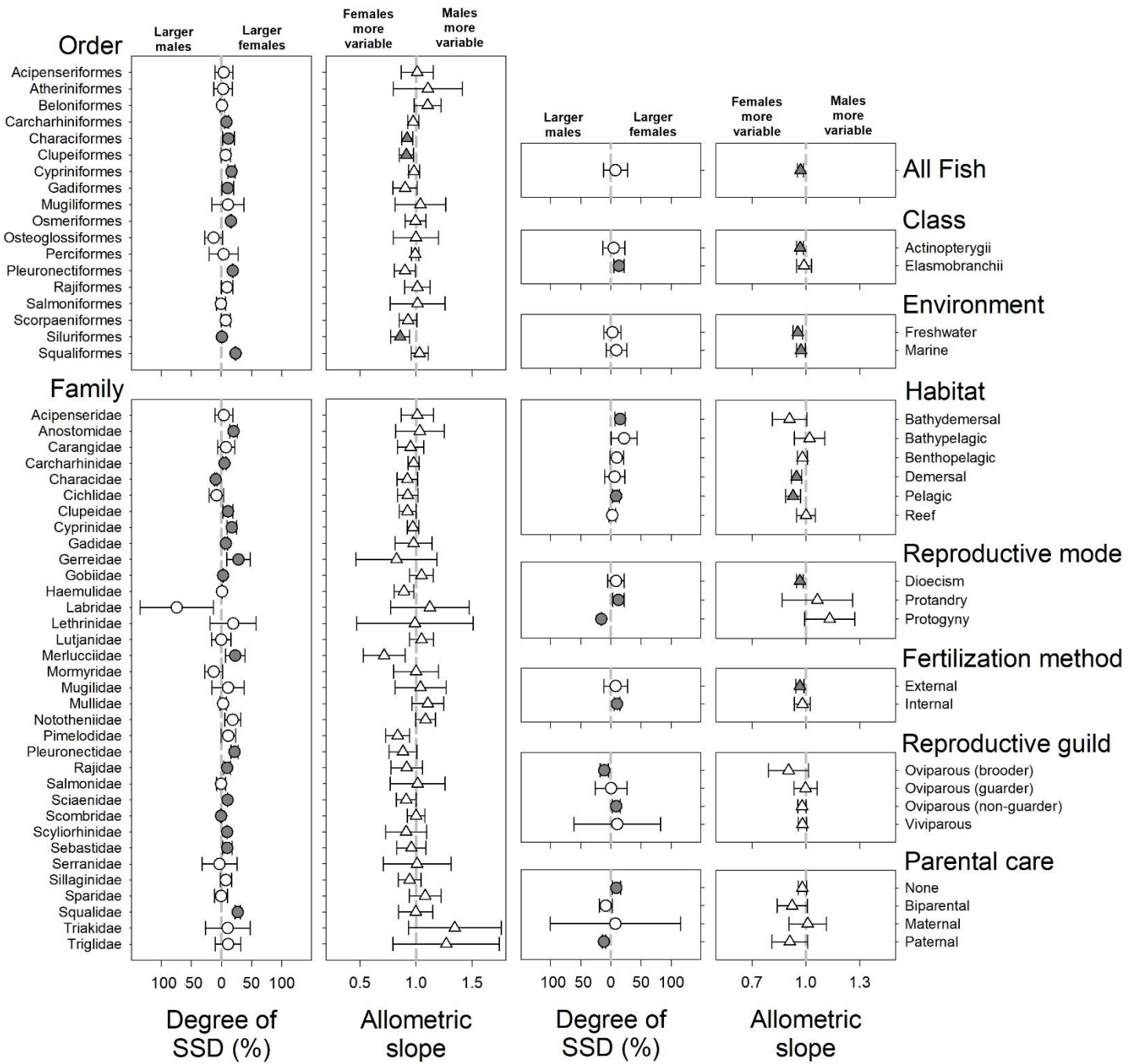


Figure 2

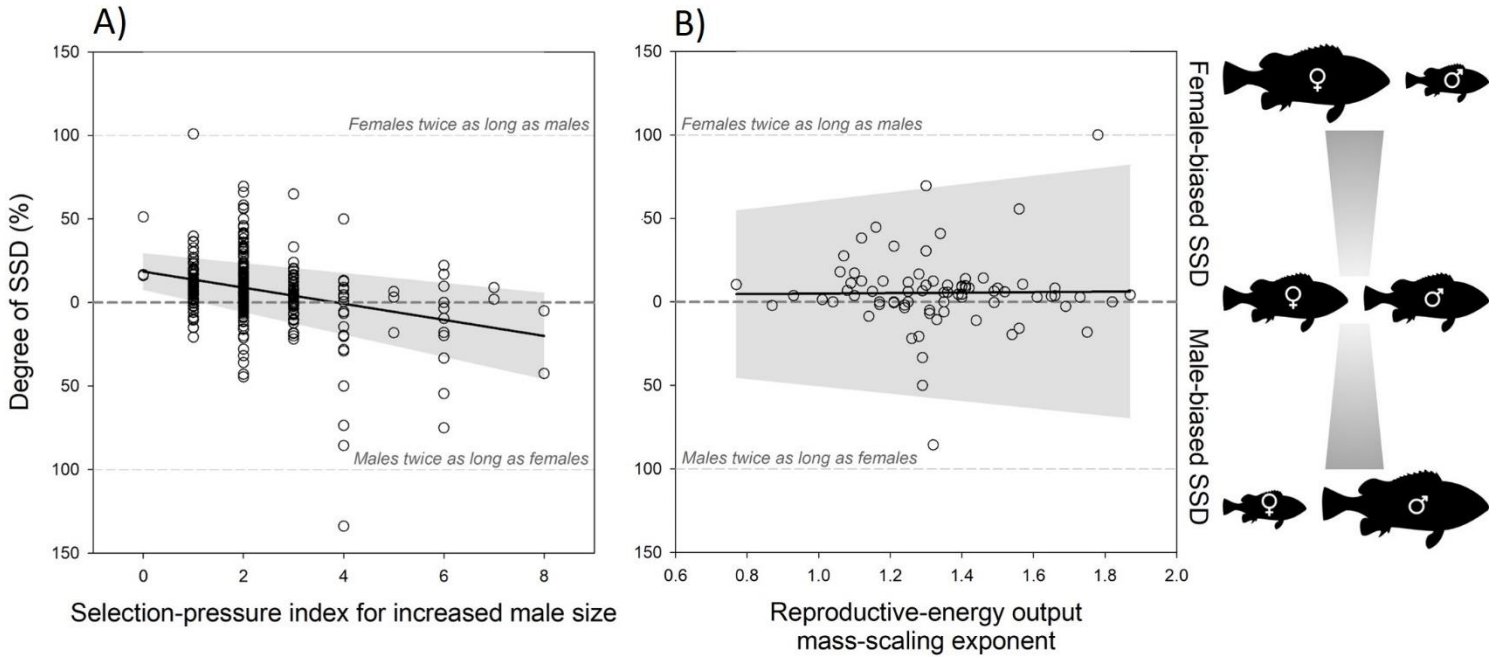


Figure 3