

# Age-specific survivorship and fecundity shape genetic diversity in marine fishes

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## Abstract

1

2 Genetic diversity varies among species due to a range of eco-evolutionary processes that  
3 are not fully understood. The neutral theory predicts that the amount of variation in the  
4 genome sequence between different individuals of the same species should increase with its  
5 effective population size ( $N_e$ ). In real populations, multiple factors that modulate the variance  
6 in reproductive success among individuals cause  $N_e$  to differ from the total number of individuals  
7 ( $N$ ). Among these, age-specific mortality and fecundity rates are known to have a direct impact  
8 on the  $\frac{N_e}{N}$  ratio. However, the extent to which vital rates account for differences in genetic  
9 diversity among species remains unknown. Here, we addressed this question by comparing  
10 genome-wide genetic diversity across 16 marine fish species with similar geographic distributions  
11 but contrasted lifespan and age-specific survivorship and fecundity curves. We sequenced the  
12 whole genome of 300 individuals to high coverage and assessed their genome-wide heterozygosity  
13 with a reference-free approach. Genetic diversity varied from 0.2 to 1.4% among species, and  
14 showed a negative correlation with adult lifespan, with a large negative effect ( $slope = -0.089$   
15 per additional year of lifespan) that was further increased when brooding species providing  
16 intense parental care were removed from the dataset ( $slope = -0.129$  per additional year of  
17 lifespan). Using published vital rates for each species, we showed that the  $\frac{N_e}{N}$  ratio resulting  
18 simply from life tables parameters can predict the observed differences in genetic diversity  
19 among species. Using simulations, we further found that the extent of reduction in  $\frac{N_e}{N}$  with  
20 increasing adult lifespan is particularly strong under Type III survivorship curves (high juvenile  
21 and low adult mortality) and increasing fecundity with age, a typical characteristic of marine  
22 fishes. Our study highlights the importance of vital rates as key determinants of species genetic  
23 diversity levels in nature.

24 **Key words:** genetic diversity, life tables, adult lifespan, variance in reproductive success,  
25 marine fishes

26

## Author Summary

27 Understanding how and why genetic diversity varies across species has important implica-  
28 tions for evolutionary and conservation biology. Although genomics has vastly improved our  
29 ability to document intraspecific DNA sequence variation at the genome level, the range and  
30 determinants of genetic diversity remain partially understood. At a broad taxonomic scale in  
31 eukaryotes, the main determinants of diversity are reproductive strategies distributed along a  
32 trade-off between the quantity and the size of offspring, which likely affect the long-term effective  
33 population size. Long-lived species also tend to show lower genetic diversity, a result which  
34 has however not been reported by comparative studies of genetic diversity at lower taxonomic  
35 scales. Here, we compared genetic diversity across 16 European marine fish species showing  
36 marked differences in longevity. Adult lifespan was the best predictor of genetic diversity, with  
37 genome-wide average heterozygosity ranging from 0.2% in the black anglerfish (*L. budegassa*)  
38 to 1.4% in the European pilchard (*S. pilchardus*). Using life tables summarizing age-specific  
39 mortality and fecundity rates for each species, we showed that the variance in lifetime reproduc-  
40 tive success resulting from age structure, iteroparity and overlapping generations can predict  
41 the range of observed differences in genetic diversity among marine fish species. We then used  
42 computer simulations to explore how combinations of vital rates characterizing different life  
43 histories affect the relationship between adult lifespan and genetic diversity. We found that  
44 marine fishes that display high juvenile but low adult mortality, and increasing fecundity with  
45 age, are typically expected to show reduced genetic diversity with increased adult lifespan.  
46 However, the impact of adult lifespan vanished using bird and mammal-like vital rates. Our  
47 study shows that variance in lifetime reproductive success can have a major impact on species  
48 genetic diversity and explains why this effect varies widely across taxonomic groups.

## 49 Introduction

50 Genetic diversity, the substrate for evolutionary change, is a key parameter for species adapt-  
51 ability and vulnerability in conservation and management strategies (Frankham, 1995; Lande,  
52 1995). Understanding the determinants of species' genetic diversity has been, however, a long-  
53 standing puzzle in evolutionary biology (Lewontin, 1974). Advances in DNA sequencing tech-  
54 nologies have allowed to describe the range of genetic diversity levels across eukaryote species  
55 and identify the main evolutionary processes governing that variation (Leffler et al., 2012;  
56 Romiguier et al., 2014). Yet, the extent and reasons for which life history traits, and in par-  
57 ticular reproductive strategies, influence genetic diversity remain to be clarified (Ellegren and  
58 Galtier, 2016).

59 The neutral theory provides a quantitative prediction for the amount of genetic variation  
60 at neutral sites (Kimura, 1983). Assuming equilibrium between the introduction of new vari-  
61 ants by mutations occurring at rate  $\mu$ , and their removal by genetic drift at a rate inversely  
62 proportional to the effective population size  $N_e$ , the amount of genetic diversity ( $\theta$ ) of a stable  
63 randomly mating population is equal to  $4N_e\mu$  (Kimura and Crow, 1964). This quantity should  
64 basically determine the mean genome-wide heterozygosity expected at neutral sites for any  
65 given individual in that population. However, since the neutral mutation-drift balance can be  
66 slow to achieve, contemporary genetic diversity often keeps the signature of past demographic  
67 fluctuations rather than being entirely determined by the current population size. Therefore,  
68 genetic diversity should be well predicted by estimates of  $N_e$  that integrate the long-term effect  
69 of drift over the coalescent time. Unfortunately, such estimates are very difficult to produce  
70 using demographic data only.

71 Demographic variations set aside, the most proximate determinant of  $N_e$  is the actual num-  
72 ber of individuals ( $N$ ), also called the census population size. Comparative genomic studies in  
73 mammals and birds have showed that current species abundance correlates with the long-term  
74 coalescence  $N_e$ , despite a potential deviation from long-term population stability in several of  
75 the species studied (Díez-Del-Molino et al., 2018; Leroy et al., 2020; Peart et al., 2020). Gen-  
76 eral laws in ecology, such as the negative relationship between species abundance and body size  
77 (White et al., 2007) have also been used to predict the long-term  $N_e$ . Higher genetic diver-  
78 sity in small body size species was found in butterflies and Darwin's finches (Mackintosh et al.,  
79 2019; Brüniche-Olsen et al., 2019), while in the latter genetic diversity also positively correlated  
80 with island size, another potential proxy for the long-term  $N_e$  (Brüniche-Olsen et al., 2019).  
81 Surprisingly, however, genetic diversity variation across Metazoans is much better explained by  
82 fecundity and propagule size than classical predictors of species abundance such as body size  
83 and geographic range (Romiguier et al., 2014). This result has been attributed to differences in  
84 extinction risk for species that have contrasted reproductive strategies. Under this hypothesis,  
85 species with low fecundity and large propagule size ( $K$ -strategists) would be more resilient to  
86 low population size episodes compared to species with high fecundity and small propagule size  
87 ( $r$ -strategists) which would go extinct if they reach such population sizes (Romiguier et al.,  
88 2014). By contrast, Mackintosh et al. (2019) found no effect of propagule size on genetic diver-  
89 sity within Papilionoidea, a family showing little variation in reproductive strategy. Therefore,  
90 the major effect of the  $r/K$  gradient on genetic diversity variation across Metazoa probably  
91 hides other determinants that act within smaller branches of the tree of life. In particular, how  
92 demography and evolutionary processes influence genetic variation in different taxa remains  
93 unclear.

94 Other factors than fluctuations in population size are known to reduce the value of  $N_e$  rela-  
95 tive to the census population size, impacting the  $\frac{N_e}{N}$  ratio to a different extent from one species  
96 to another. These factors include unbalanced sex-ratios, variance in lifetime reproductive suc-  
97 cess among individuals, age structure, kinship-correlated survival and some metapopulation



98 configuration (Wright, 1969; Falconer, 1989; Lande and Barrowclough, 1987). A potentially  
99 strong effect comes from variance in the number of offspring per parent ( $V_k$ ), which reduces  $N_e$   
100 compared to  $N$  following  $N_e = \frac{4N-4}{V_k+2}$  (Crow and Kimura, 1970). Variance in reproductive suc-  
101 cess can naturally emerge from particular age-specific demographic characteristics summarized  
102 in life tables that contain age- (or stage-) specific survival and fecundity rates (Ricklefs and  
103 Miller, 1999). The impact of life tables characteristics on expected  $\frac{N_e}{N}$  ratio has been the focus  
104 of a large body of theoretical and empirical works (Nunney, 1991, 1996; Waples, 2002, 2016b,a;  
105 Waples et al., 2018). Accounting for iteroparity and overlapping generations, a meta-analysis  
106 of vital rates in 63 species of plants and animals revealed that half of the variance in  $\frac{N_e}{N}$  among  
107 species can be explained by just two life history traits: adult lifespan and age at maturity  
108 (Waples et al., 2013). Interestingly, longevity was the second most important factor explaining  
109 differences in genetic diversity across Metazoans (Romiguier et al., 2014). However, there is still  
110 no attempt to evaluate the extent to which lifetime variance in reproductive success explains  
111 differences in genetic diversity between species with different life table components.

112 Marine fishes are good candidates to address this issue. They are expected to show a partic-  
113 ularly high variance in reproductive success as a result of high abundance, type III survivorship  
114 curves (i.e. high juvenile mortality and low adult mortality) and increasing fecundity with age.  
115 Consequently, it has been suggested that marine fish species show a marked discrepancy be-  
116 tween adult census size and effective population size, resulting in  $\frac{N_e}{N}$  ratios potentially smaller  
117 than  $10^{-3}$ . The disproportionate contribution of a few lucky winners to the offspring of the next  
118 generation is sometimes referred as the "big old fat fecund female fish" (BOFFFF) effect, a  
119 variant of the "sweepstakes reproductive success" hypothesis (Hedgecock, 1994; Hedrick, 2005;  
120 Hedgecock and Pudovkin, 2011) that is often put forward to explain low empirical estimates  
121 of effective population sizes from genetic data (Hauser and Carvalho, 2008). However, subse-  
122 quent theoretical work showed that low values of  $\frac{N_e}{N}$  below 0.01 can only be generated with  
123 extreme age-structure characteristics (Waples, 2016b). The real impact of lifetime variance  
124 in reproductive success on genetic diversity thus remains unclear, even in species like fish in  
125 which its impact is supposed to be strong. Contrasting results have been obtained by com-  
126 parative studies in marine fishes, including negative relationship between diversity and body  
127 size (Pinsky and Palumbi, 2014; Waples, 1991), fecundity (Martinez et al., 2018) and overfish-  
128 ing (Pinsky and Palumbi, 2014). However, these studies relied on few nuclear markers, that  
129 could provide inaccurate or biased estimates of genetic diversity (Väli et al., 2008). They also  
130 compared species sampled from different locations, thus, likely having different demographic  
131 histories, which could blur the relationship between species characteristics and genetic diversity  
132 (Ellegren and Galtier, 2016).

133 Here, we compared the genome-average heterozygosity to the life history traits and life  
134 table characteristics of 16 marine teleostean species sharing similar Atlantic and Mediterranean  
135 distributions. We estimated genetic diversity from unassembled whole-genome reads using  
136 **GenomeScope** (Vurture et al., 2017) and checked the validity of these estimates with those  
137 obtained using a high-standard reference-based variant calling approach. Using this data, we  
138 related species genetic diversity to eight simple quantitative and qualitative life history traits.  
139 Then, we built species life tables and determined if the lifetime variance in reproductive success  
140 induced by these tables could explain observed differences in genetic diversity using an analytical  
141 and a forward-in-time simulation approach. Finally, we generalized our findings by exploring  
142 the influence of age-specific survival and fecundity rates on the variance in reproductive success  
143 and ultimately genetic diversity via simulated lifetimes tables.

## 144 **Material and Methods**

### 145 **Sampling, DNA extraction and whole-genome sequencing**

146 We sampled 16 marine teleostean fish species presenting a wide diversity of life history strate-  
147 gies expected to affect genetic diversity (Table 1). All these species share broadly overlapping  
148 distributions across the North-eastern Atlantic and Mediterranean regions. Sampling was per-  
149 formed at the same four locations for all species: two in the Atlantic (the Bay of Biscay in  
150 South-western France or North-western Spain and the Algarve in Portugal), and two in the  
151 Western Mediterranean Sea (the Costa Calida region around Mar Menor in Spain and the Gulf  
152 of Lion in France see Fig 1A). Individual whole-genome sequencing libraries were prepared fol-  
153 lowing the Illumina TruSeq DNA PCR-Free Protocol and sequenced to an average depth of 20X  
154 on an Illumina NovaSeq 6000 platform by Genewiz Inc (USA). Raw reads were preprocessed  
155 with `fastp` v.0.20.0 (Chen et al., 2018) using default parameters (see Supplementary Material).

### 156 **Estimation of genetic diversity**

157 We used `GenomeScope` v.1.0 to estimate individual genome-wide heterozygosity (Vurture et al.,  
158 2017). Briefly, this method uses a  $k$ -mers based statistical approach to infer overall genome  
159 characteristics, including total haploid genome size, percentage of repeat content and genetic  
160 diversity from unassembled short-read sequencing data. We used `jellyfish` v.2.2.10 to com-  
161 pute the  $k$ -mer profile of each individual (Marçais and Kingsford, 2011). The genetic diversity  
162 of each species was determined as the median of the individual genome-wide heterozygosity val-  
163 ues. We chose the median instead of the mean diversity since it is less sensitive to the possible  
164 presence of individuals with non-representative genetic diversity values (e.g. inbred or hybrid  
165 individuals) in our samples.

166 In order to assess the reliability of `GenomeScope` and detect potential systematic bias, we  
167 compared our results with high-standard estimates of genetic diversity obtained after read  
168 alignment against available reference genomes (see details in Supplementary Material). To  
169 perform this test, we used the sea bass (*D. labrax*) and the European pilchard (*S. pilchardus*),  
170 two species that represent the lower and upper limits of the range of genetic diversity in our  
171 dataset (Table 1, Fig 1D).

### 172 **Life history traits database**

173 We collected seven simple quantitative variables describing various aspects of the biology and  
174 ecology of the 16 species: body size, trophic level, fecundity, propagule size, age at maturity,  
175 lifespan and adult lifespan (Table 1, Table S4 for detailed informations on bibliographic refer-  
176 ences). We used the most representative values for each species and each trait when reported  
177 traits varied among studies due to plasticity, selection or methodology. In addition, we collected  
178 two qualitative variables describing the presence/absence of hermaphroditism and brooding be-  
179 haviour, as revealed by males carrying the eggs in a brood pouch (*H. guttulatus* and *S. typhle*)  
180 or nest-guarding (*C. galerita*, *S. cinereus* and *S. cantharus*). Detailed information on data  
181 collection is available in Supplementary Material.

### 182 **Construction of life tables**

183 Life tables summarize survival rates and fecundities at each age during lifetime (Ricklefs and  
184 Miller, 1999). Thus, they provide detailed information on vital rates that influence the variance  
185 in lifetime reproductive success among individuals. This tool is well designed to describe popu-  
186 lation structure from the probability of survival to a specific age at which a specific number of

187 offspring are produced. Ideally, age-specific survival is estimated by direct demographic mea-  
188 sures, such as mark-recapture. Unfortunately, direct estimates of survival were not available  
189 for the 16 studied species. We thus followed Benvenuto et al. (2017) to construct species life  
190 tables. Age-specific mortality of species  $sp$ ,  $m_{sp,a}$ , is a function of species body length at age  
191  $a$ ,  $L_{sp,a}$ , species asymptotic Von Bertalanffy length  $L_{sp,inf}$ , and species Von Bertalanffy growth  
192 coefficient,  $K_{sp}$  :

$$m_{sp,a} = \left[ \left( \frac{L_{sp,a}}{L_{sp,inf}} \right) \right]^{-\frac{1}{5}} \times K_{sp} \quad (1)$$

193 Age-specific survival rates,  $s_{sp,a}$  were then estimated as:

$$s_{sp,a} = e^{-m_{sp,a}} \quad (2)$$

194 We collected age-specific length from empirical data and estimated  $L_{inf}$  and  $K$  values from  
195 age-length data as explained in the appendix, setting survival probability to zero at the maxi-  
196 mum age (Appendix 1). When differences in age-specific lengths between sexes were apparent  
197 in the literature, we estimated a different age-specific survival curve for each sex. The relation-  
198 ship between absolute fecundity and individual length is usually well fitted with the power-law  
199 function ( $F = \alpha L^\beta$ ), although some studies also used an exponential function ( $F = \alpha e^{\beta L}$ ) or  
200 a linear function ( $F = \alpha + L\beta$ ). We collected empirical estimates of  $\alpha$  and  $\beta$  and determined  
201 age-specific fecundity from the age-specific length and the fecundity-length function reported  
202 in the literature for each species. Fecundity was set to zero before the age at first maturity.

## 203 Effect of the variance in reproductive success on the $N_e/N$ ratio

204 To understand how differences in life tables drive differences in genetic diversity between species,  
205 we estimated the variance in lifetime reproductive success,  $V_k$  and the ensuing ratio  $\frac{N_e}{N}$  using the  
206 analytic framework developed in **AgeNe** (Waples et al., 2011). **AgeNe** infers  $V_k$  using informations  
207 from life tables only. Hence, the estimated variance in reproductive success estimated is only  
208 generated by inter-individual differences in fecundity and survival. **AgeNe** assumes constant  
209 population size, stable age structure, and no heritability of survival and fecundity. We used the  
210 life tables constructed as described above and set the number of new offspring to 1000 per year.  
211 This setting is an arbitrary value which has no influence on the estimation of either  $V_k$  nor  $\frac{N_e}{N}$   
212 by **AgeNe**. For all species, we set an initial sex ratio of 0.5 and equal contribution of individuals  
213 of the same age (i.e. no sweepstake reproductive success among same-age individuals). We ran  
214 **AgeNe** and estimated  $\frac{N_e}{N}$  for each species.

215 Four life tables components can generate differences in  $\frac{N_e}{N}$  between species: age at matu-  
216 rity, age-specific survival rates, age-fecundity relationships and sex-related differences in these  
217 components. To determine the role that each parameter plays in shaping levels of genetic diver-  
218 sity among species, we built 16 alternative life tables where the effect of each component was  
219 added one after the other, while the others were kept constant across species. Thus, in our null  
220 model, age at maturity was set at 1 year old for all species, fecundity and survival did not vary  
221 with age (constant survival chosen to have 0.01% of individuals remaining at maximum age,  
222 following Waples (2016b)), and there were no differences between sexes. Next, the effect of each  
223 component was tested by replacing these constant values with their biological values in species'  
224 life tables. For each of the 16 life tables thus constructed, we tested whether variation in  $\frac{N_e}{N}$   
225 explained the variation in observed genetic diversity after scaling these two variables by their  
226 maximum value. With this scaling, the correlation between  $\frac{N_e}{N}$  and genetic diversity should  
227 overlap with the  $y = x$  function in cases where a decrease in  $\frac{N_e}{N}$  predicts an equal decrease in  
228 genetic diversity, indicating a strong predictive power of the components induced in life tables.

## 229 Forward simulations

230 A complementary analysis of the contribution of life table properties on genetic diversity was  
231 performed using forward simulations in SLiM v.3.3.1 (Haller and Messer, 2017). Stochastic  
232 forward simulations allow a different formalization compared to the deterministic model im-  
233 plemented in AgeNe. Thus, they provide another approach to the problem and can lead to a  
234 more intuitive understanding of why vital rates affect  $N_e$  over the long-term, and ultimately  
235 genetic diversity. We simulated populations with overlapping generations, sex-specific lifespan,  
236 and age- and sex-specific fecundity and survival. We used life tables estimated as previously,  
237 and sex-specific lifespan estimates were collected in the literature as described above. Age and  
238 species-specific fecundity were determined as previously and scaled between 0 (age 0) and 100  
239 (maximum age) within each species. In the simulations, each individual first reproduces and  
240 then either survives to the next year or dies following a probability determined by its age and  
241 the corresponding life table. We kept population size constant and estimated the mean genetic  
242 diversity (i.e., the proportion of heterozygous sites along the locus) over the last 10000 years  
243 of the simulation after the mutation-drift equilibrium was reached and using 50 replicates (see  
244 Supplementary Material for further informations).

245 As previously, we evaluated the contribution of each component among 8 alternative life  
246 tables by comparing scaled observed and simulated genetic diversity.

## 247 Evaluating the impact of life tables beyond marine fish

248 To generalize our understanding of the influence of life tables on genetic diversity beyond the  
249 species analyzed in this study, we simulated a wide range of age-specific survival and fecundity  
250 curves and explored their effect on the relationship between adult lifespan and variance in  
251 reproductive success. To this end, we defined 16 theoretical species with age at first maturity  
252 and lifespan equal to that of our real species and then introduced variation in survival and  
253 fecundity curves. First, age-specific mortality was simulated following Pinder et al. (1978):

$$M(\text{Age}, \text{Age} + 1) = 1 - \exp\left(\frac{\text{Age}}{b}\right)^c - \left(\frac{\text{Age}+1}{b}\right)^c \quad (3)$$

254 where  $c$  defines the form of the survivorship curve, with  $c > 1$ ,  $c = 1$  and  $c < 1$  defining  
255 respectively a *Type I* (e.g. mammals), *Type II* (e.g. birds) and *Type III* (e.g. fish) survival  
256 curves. We took values of  $c$  from 0.01 to 30 (Fig 4A). Parameter  $b$  was equal to  $-\frac{\text{Lifespan}}{\log(0.01)^{1/c}}$  to  
257 scale survivorship curves in such a way that 1% of the initial population remains at maximum  
258 age.

259 Second, age-specific fecundity was simulated with two models: constant and exponential. In  
260 the first model, fecundity is constant for all ages since maturity. In the second model, fecundity  
261 increases or decreases exponentially with age following  $F_{\text{Age}} = \exp^{f \times \text{Age}}$ , as it is often observed  
262 in marine fishes (Curtis and Vincent, 2006). We first set  $f = 0.142$  as the median of the  $f$   
263 values for the 16 species. Secondly, we took values of  $f$  ranging from  $-1$  to  $1$  (Fig 4A). We  
264 scaled maximum fecundity to 1 for all simulations.

265 For each combination of  $c$  and  $f$ , and for each fecundity model, we simulated all species  
266 life tables given age at maturity and lifespan. Then, we ran AgeNe and estimated  $\frac{N_e}{N}$  for each  
267 simulated species and estimated the slope of the regression between adult lifespan and  $\frac{N_e}{N}$  across  
268 all 16 species. We explored the impact of alternative fecundity-age models on the relationship  
269 between adult lifespan and  $\frac{N_e}{N}$  (see details in Supplementary Material).

## 270 **Intraspecific variation in genetic diversity**

271 We addressed the potential effects of population structure, demography and historical contin-  
272 gencies on genetic diversity by examining the extent of spatial variation in genetic diversity  
273 between the four populations within each species. First, we evaluated the relative amount of  
274 intraspecific compared to interspecific variation in genetic diversity. Then, we applied a  $z$ -  
275 transformation of individual genetic diversity within each species to put spatial differences in  
276 within-species diversity on the same scale. In order to detect similar spatial patterns of genetic  
277 diversity among species, we finally performed a hierarchical clustering analysis of the matrix of  
278  $z$ -transformed genetic diversity values with `pheatmap` function available in `pheatmap v1.0.12`  
279 R package.

## 280 **Statistical analyses**

281 All statistical analyses were carried out using `R-3.6.1` (R Core Team, 2018). We fitted beta  
282 regression models between genetic diversity and any covariate with the R-package `betareg`  
283 `v.3.1-3` (Cribari-Neto and Zeileis, 2010). We tested statistical interactions between any quanti-  
284 tative and qualitative covariates using likelihood tests with the `lmtest v.0.9-37` package (Zeileis  
285 and Hothorn, 2002).



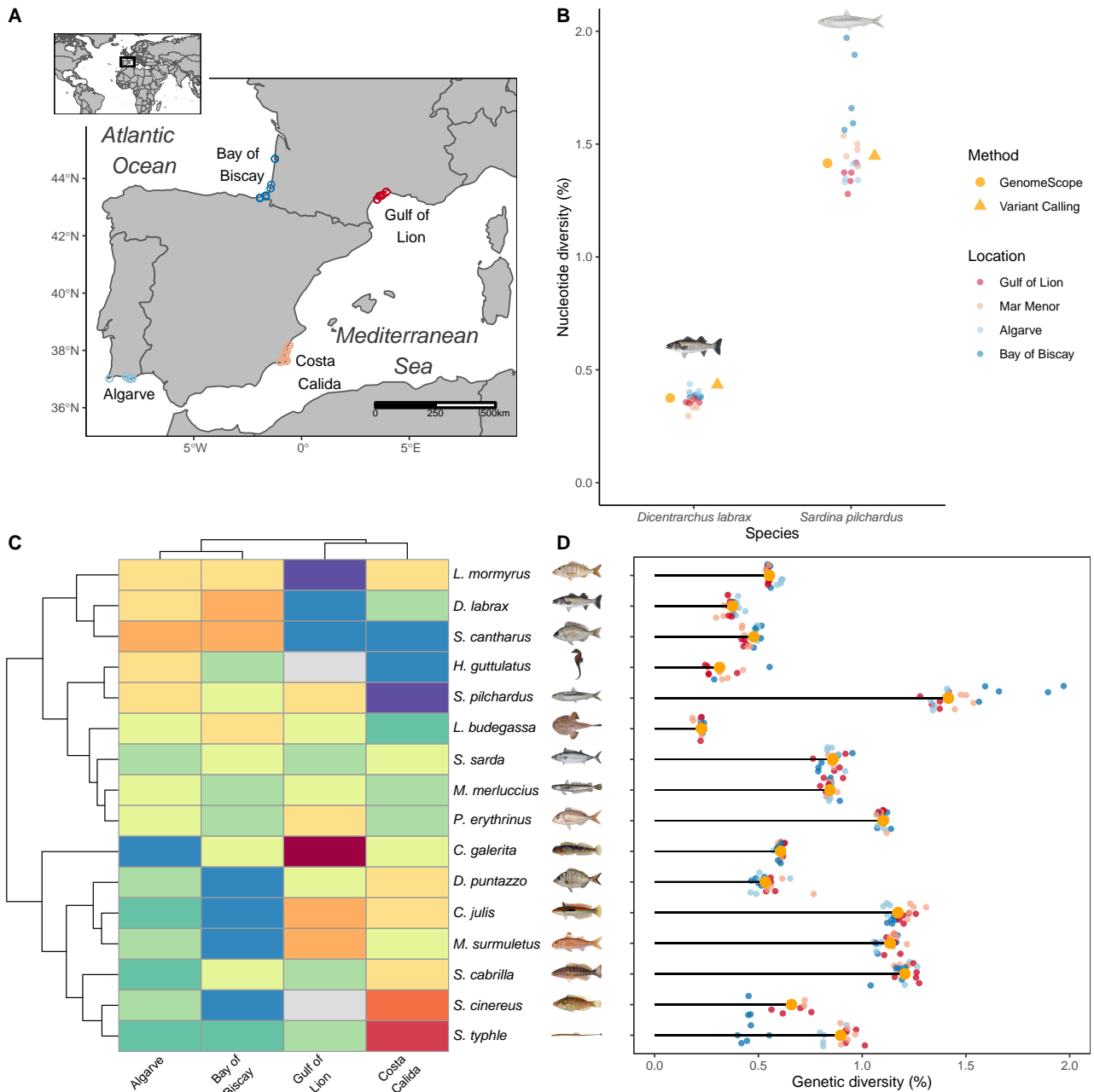


Figure 1: **Sampling and estimation of genetic diversity in 16 marine fish species** - In panels A, B and D, the geographical origin of samples is represented by colors. Atlantic: Bay of Biscay (dark blue), Faro region in Algarve (light blue). Mediterranean: Murcia region in Costa Calida (pink), Gulf of Lion (red). **(A)** Sampling map of all individuals included in this study. Each point represents the coordinates of a sample taken from one of four locations: two in the Atlantic Ocean and two in the Mediterranean Sea. **(B)** Genome-wide diversity in the European pilchard (*S. pilchardus*) and European sea bass (*D. labrax*) estimated after variant calling (orange triangle) or from GenomeScope (orange dot: median; smaller dots: individual estimates) **(C)** Heatmap clustering showing the variance in genetic diversity within species among locations. Each line represents one species, with the corresponding species name written on the right side; every column represents one location. Blue and red colors respectively indicate higher and lower genetic diversity within a location for a given species compared to the average species genetic diversity. **(D)** Individual and median genetic diversity within each species estimated with GenomeScope. Species illustrations were retrieved from Iglésias (2013) with permissions.

## 286 Results

### 287 Whole-genome resequencing data set

288 We resequenced 300 individual genomes from 16 marine teleostean species, with high read  
289 quality scores (mean Q30 rate = 92.4%) and moderate duplication rates (10.8%) (Fig S2).  
290 GC content was moderately variable among species and highly consistent among individuals  
291 of the same species, except for three individuals that showed a marked discrepancy with the  
292 overall GC content of their species (Fig S2). These three individuals were thus removed from  
293 downstream analyses to avoid potential issues due to contamination or poor sequencing quality.

### 294 Estimation of genetic diversity with GenomeScope

295 The **GenomeScope** model successfully converged for all of the 297 individual genomes retained  
296 (Fig S6E). The average depth of sequencing coverage per diploid genome exceeded 20X in  
297 most individuals. Estimated genome sizes were very consistent within species (Fig S6A-C).  
298 Estimated levels of genetic diversity were also homogeneous among individuals of the same  
299 species with some few exceptions (e.g. *S. cinereus* and *S. typhle*) and most of the variability  
300 in genetic diversity was observed between species (Fig 1D). Two individuals (one *D. pun-*  
301 *tazzo* and one *P. erythrinus*) showed a surprisingly high genetic diversity (more than twice  
302 the average level of their species), indicating possible issues in the estimation of genome-wide  
303 heterozygosity. Therefore we removed these individuals from subsequent analysis, although  
304 their estimated genome size and GC content matched their average species values (therefore  
305 excluding contamination as a cause of genetic diversity estimation failures).

306 Observed values of genetic diversity ranged from 0.225% for *L. budegassa* to 1.415% for  
307 *S. pilchardus*. We found no correlation between species genetic diversity and genome size  
308 ( $p$  - value = 0.983). The estimation of genetic diversity was robust to the choice for  $k$ -  
309 mer lengths ranging from 21 to 25, suggesting a low sensibility of **GenomeScope** regarding this  
310 parameter (Fig S4). The fraction of reads mapped against reference genomes ranged between  
311 96.72 and 98.50% for *D. labrax* and between 87.45 and 96.42 % for *S. pilchardus* (Table S2; Fig  
312 S3). We found similar species genetic diversity estimates between **GenomeScope** and the **GATK**  
313 reference-based variant calling approach for the two control species, representing the two limits  
314 of the range of genetic diversity in our dataset (Fig 1B).

### 315 Adult lifespan is the best predictor of genetic diversity

316 We evaluated the effect of several key life history traits that potentially affect species genetic  
317 diversity (Table S1).

318 Two widely used predictors of population size, body size and trophic level, were not sig-  
319 nificantly correlated to genetic diversity ( $p$ -value = 0.119 and 0.676 respectively, Fig S8A-B).  
320 Although we detected a significant negative relationship between the logarithm of fecundity  
321 and propagule size ( $p$ -value = 0.00131, slope =  $-0.4385 \pm 0.1076$ ) as in Romiguier et al. (2014),  
322 we found no significant correlation between either propagule size ( $p$ -value = 0.561), or the  
323 logarithm of fecundity ( $p$ -value = 0.785) and genetic diversity (Fig S8C-D).

324 By contrast, both lifespan ( $p$ -value = 0.011) and adult lifespan ( $p$ -value = 0.007) were  
325 significantly negatively correlated with genetic diversity (Table S1, Fig 2). The percentage of  
326 variance explained by each variable reached 43.8 and 42.9 %, respectively. Repeating the same  
327 statistical analyses with genetic diversity estimates either only from mediterranean or atlantic  
328 individuals led to the same results, revealing no effect of within-species population structure  
329 on the relationship between genetic diversity and life history traits (Fig 1C, Fig S9, Table S3).

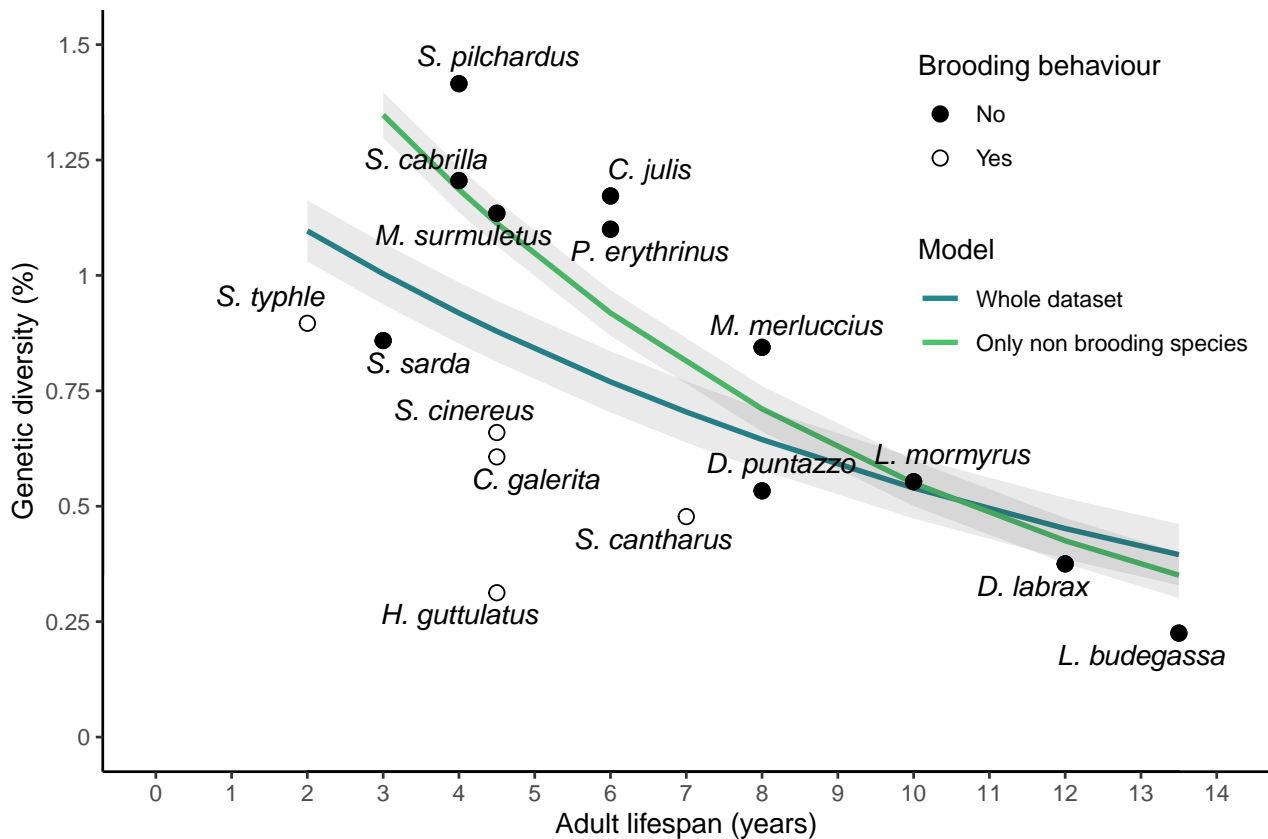


Figure 2: **Relationship between species median genetic diversity (%) and adult lifespan** - Each point represents the median of the individual genetic diversities for a given species. Adult lifespan is defined as the difference between lifespan and age at first maturity in years. Dot points and empty circles represent non-brooding species and brooding species, respectively. Blue and green lines represent the beta regression between adult lifespan and genetic diversity considering either the whole dataset (16 species), or the 11 non-brooding species only, respectively.



330 We found no significant interaction between hermaphroditism and any of the previous vari-  
331 ables on genetic diversity. By contrast, parental care showed a significant interaction with  
332 lifespan ( $p$ -value = 0.0011), adult lifespan ( $p$ -value = 0.0008) and body size ( $p$ -value = 0.0035)  
333 on genetic diversity. Brooding species (nest protection by males for *C. galerita*, *S. cinereus* and  
334 *S. cantharus* and male abdominal brood-pouch for *H. guttulatus* and *S. typhle*) had systemat-  
335 ically lower genetic diversity than non-brooding species with similar lifespan.

336 When considering only non-brooding species, we found steeper negative correlations and  
337 higher percentages of between-species variance in genetic diversity explained by lifespan ( $p$ -value =  
338  $1.017e^{-7}$ , pseudo- $R^2 = 0.851$ ) and adult lifespan ( $p$ -value =  $1.645e^{-7}$ , pseudo- $R^2 = 0.829$ , Fig  
339 2, Table S1). To test the relevance of considering this sub-dataset, we estimated the slope of the  
340 regression and the pseudo- $R^2$  for all combinations of 11 out of 16 species and compared the dis-  
341 tribution of these values to the estimated slope and pseudo- $R^2$  obtained for the 11 non-brooding  
342 species (Fig S13). The estimated slope for non-brooders lied outside of the 95% confidence in-  
343 terval of the distribution of estimated slopes ( $slope = -0.129$ , 95% CI =  $[-0.122, -0.049]$ ) and  
344 the same was found for pseudo- $R^2$  (pseudo- $R^2 = 0.829$ , 95% CI =  $[0.073, 0.727]$ ). Furthermore,  
345 considering non-brooding species only, there was still no significant correlation between genetic  
346 diversity and trophic level ( $p$ -value = 0.259), propagule size ( $p$ -value = 0.170), and fecundity  
347 ( $p$ -value = 0.390), but genetic diversity appeared significantly negatively correlated to body  
348 size ( $p$ -value =  $6.602e^{-5}$ , pseudo- $R^2 = 0.616$ ). We did not detect any significant correlation  
349 between any trait variable and genetic diversity within the sub-dataset of brooding species.  
350 However, this should be taken with caution given the very low number of brooding species  
351 ( $n = 5$ ) in our dataset.

352 Body size and lifespan were highly positively correlated traits in our dataset ( $p$ -value =  
353 0.0013,  $R^2 = 0.536$ , Fig S7). Thus, using empirical observations only, it was not possible to  
354 fully disentangle the impact of each of these traits among the possible determinants of genetic  
355 diversity in marine fishes. However, we found important differences in effect sizes for body size  
356 ( $slope = -0.014$ ), lifespan ( $-0.095$ ) and adult lifespan ( $-0.129$ ), which rule out body size as a  
357 major determinant of diversity in our dataset.

**Table 1 - Life history traits and observed genetic diversity of the 16 teleostean marine species.** - For each species, number of individuals used for the estimation of genetic diversity; observed median genetic diversity among all individuals ( $\pm$  standard deviation); body size (in centimeters); trophic level; age at first maturity (in years), lifespan (in years), adult lifespan (in years, defined as the difference between lifespan and age at maturity), parental care behaviour (- = no egg protection; NG = nest-guarders; MP = male brood-pouch) and hermaphroditism (- = no hermaphroditism; PG = protogynous; PA = protandrous, RUD = rudimentary). Detailed bibliographic references are provided in supplementary material.

Species	Vernacular name	N.	Genetic diversity (%)	Body size (cm)	Trophic level	Fecundity	Propagule Size (mm)	Maturity (years)	Lifespan (years)	Adult lifespan (years)	Parental care	Hermaphroditism
<i>Coryphoblennius galerita</i>	Montagu's blenny	16	0.607( $\pm$ 0.014)	7	2.28	NA	3.3	1.5	6	4.5	NG	P
<i>Coris julis</i>	Rainbow wrasse	20	1.172( $\pm$ 0.056)	27.2	3.24	169.81	0.63	1	7	6	-	P
<i>Dicentrarchus labrax</i>	European sea bass	20	0.375( $\pm$ 0.031)	102.15	3.47	12436.52	1.15	3	15	12	-	RUD
<i>Diplodus puntazzo</i>	Sharp-snout seabream	19	0.533( $\pm$ 0.074)	49.69	3.07	277.87	0.87	2	10	8	-	P
<i>Hippocampus guttulatus</i>	Long-snouted seahorse	12	0.313( $\pm$ 0.090)	19.8	3.5	1.21	12	0.5	5	4.5	MP	P
<i>Lophius budegassa</i>	Blackbellied angler	20	0.225( $\pm$ 0.015)	103	4.23	2304.03	1.88	7.5	21	13.5	-	P
<i>Lithognathus mormyrus</i>	Striped seabream	20	0.553( $\pm$ 0.027)	37.85	3.42	214.09	0.75	2	12	10	-	P
<i>Merluccius merluccius</i>	European hake	20	0.844( $\pm$ 0.025)	88.9	4.43	2294.54	1.07	3	11	8	-	P
<i>Mullus surmuletus</i>	Striped red mullet	19	1.135( $\pm$ 0.048)	30.18	3.46	2569.32	0.86	1.5	6	4.5	-	P
<i>Pagellus erythrinus</i>	Common pandora	19	1.100( $\pm$ 0.020)	36	3.46	2280.46	0.77	2	8	6	-	P
<i>Serranus cabrilla</i>	Comber	19	1.205( $\pm$ 0.055)	30.8	3.68	37.97	0.91	2	6	4	-	P
<i>Spondyliosoma cantharus</i>	Black seabream	19	0.478( $\pm$ 0.034)	35.7	3.27	425.62	2.1	3	10	7	NG	P
<i>Symphodus cinereus</i>	Grey wrasse	10	0.660( $\pm$ 0.125)	14.1	3.3	13.20	2.87	1.5	6	4.5	NG	P
<i>Sardina pilchardus</i>	European pilchard	20	1.415( $\pm$ 0.182)	20.35	2.94	22.89	1.64	1	5	4	-	P
<i>Syngnathus typhle</i>	Broadnosed pipefish	20	0.859( $\pm$ 0.047)	26.2	3.75	0.38	20	1	3	2	MP	P
<i>Sarda sarda</i>	Atlantic bonito	20	0.896( $\pm$ 0.208)	68.9	4.34	15647.73	1.3	1	4	3	-	P

## 359 Variance in reproductive success explains levels of observed genetic 360 diversity

361 To understand the mechanisms by which adult lifespan affects genetic diversity and test if  
362 it can alone explain our results, we built life tables for each of the 16 species by gradually  
363 incorporating age-specific fecundity and survival, age at first maturity, lifespan and sex-specific  
364 differences in these parameters.

365 Non-genetic estimates of  $\frac{N_e}{N}$  ratio obtained with **AgeNe** ranged from 0.104 in *L. budegassa*  
366 to 0.671 for *S. cinereus*. When considering the 16 species together, the  $\frac{N_e}{N}$  ratio was not  
367 significantly correlated with genetic diversity ( $p$ -value = 0.0935). However, four out of  
368 five brooding species had low genetic diversity despite high  $\frac{N_e}{N}$  ratios (Fig 3A). As previously  
369 observed, removing the 5 brooders increased the slope and the percentage of variance of genetic  
370 diversity explained by the  $\frac{N_e}{N}$  ratio above null expectations obtained by removing groups of  
371 5 species at random ( $slope = 1.849$ , 95% CI = [0.048, 1.582],  $pseudo-R^2 = 0.55$ , 95% CI =  
372 [0.004, 0.533], Fig S14). Thus, the  $\frac{N_e}{N}$  ratio predicted by life tables was positively correlated to  
373 genetic diversity when considering non-brooding species only (Fig 3A).

374 Our next step was to determine the impact of each component of life tables as well as their  
375 combinations on genetic diversity (Fig 3C-G). Starting from a null model (Fig 3C), in which  
376 species life tables differed only in lifespan, we found that the  $\frac{N_e}{N}$  ratio ranged from 0.558 to  
377 0.733, a variance much lower than that of observed genetic diversities. Then, adding separately  
378 age at maturity (Fig 3D) or age-specific survival (Fig 3E) did not better predict the range of  
379 observed genetic diversities. However, combining age at maturity and age-specific survival (Fig  
380 3F) or adding only age-specific fecundity (Fig 3G) enable us to explain the range of observed  
381 diversity values. Finally, combining these three parameters together (age at maturity, age-  
382 specific survival, and fecundity, model 8, Fig S10H) resulted in the best fit for both the slope  
383 and the intercept and for both non-brooding species and the whole data set. Adding sex-specific  
384 differences in life tables did not improve the fit, however (models 9 to 16, Fig S10I-P).

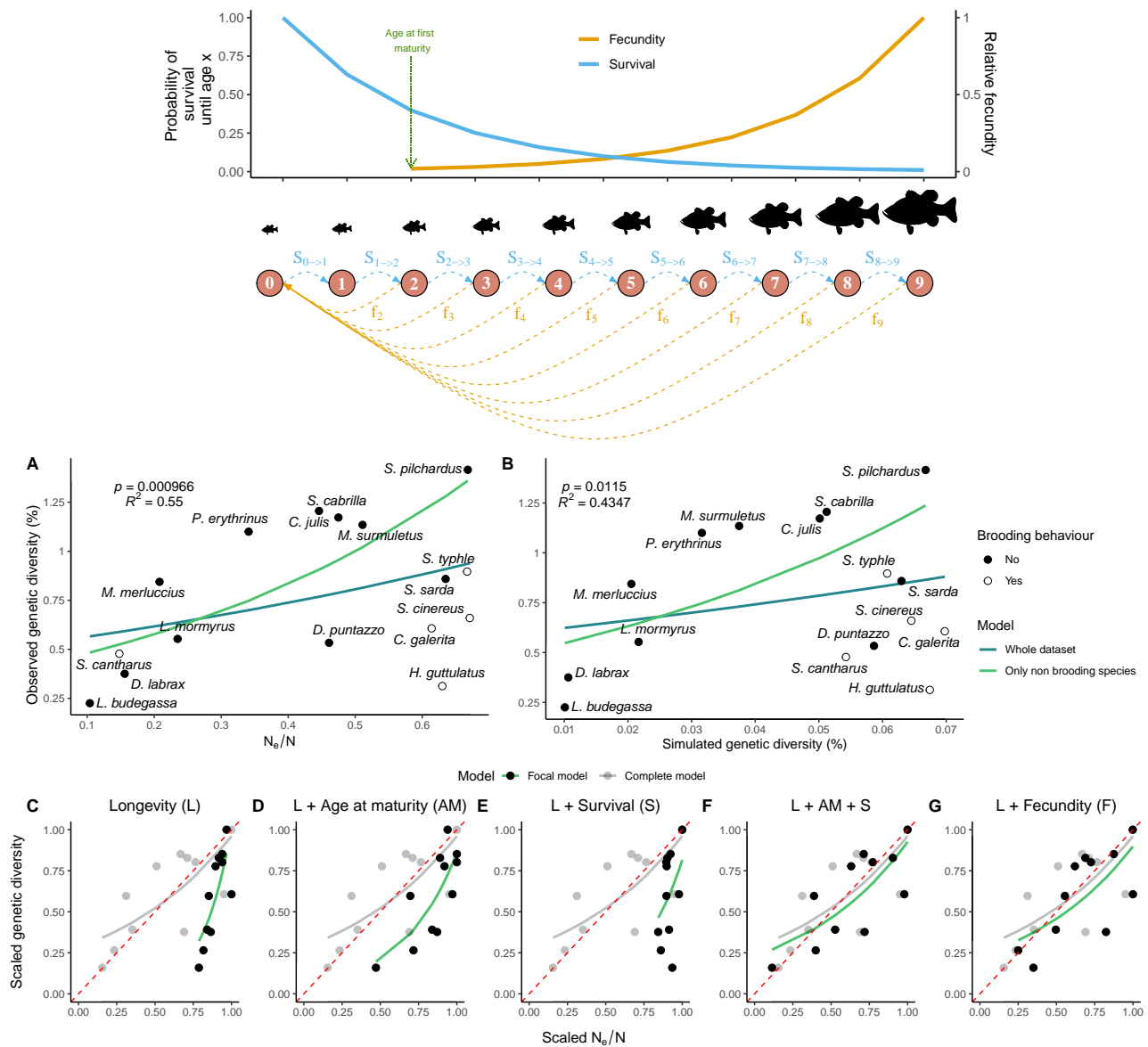
385 Our final step was to further explore the role of the variance in reproductive success on  
386 genetic diversity by simulating genetic diversity at mutation-drift equilibrium with the age-  
387 specific vital rates of the 16 species.

388 We simulated a population of 2000 individuals with age-specific survival and fecundity. As  
389 expected, including age-specific vital rates decreased the equilibrium level of genetic diversity  
390 compared to expectations under the classical Wright-Fisher model ( $\theta = 4N_e\mu = 0.08\%$ ). It was  
391 reduced to 0.070% in the species with the least effect of age-specific vital rates (*C. galerita*), and  
392 down to 0.010% in the species with the greatest effect (*L. budegassa*). Again, simulated genetic  
393 diversity was not correlated to genetic diversity considering all 16 species ( $p$ -value = 0.297,  
394 Fig 3B), but significantly positively correlated within the sub-sample of the 11 non-brooding  
395 species ( $p$ -value = 0.0115).

## 396 Life tables drive correlation between lifespan and the $N_e/N$ ratio

397 In order to determine the general effect of life table properties on the relation between adult  
398 lifespan and  $\frac{N_e}{N}$  beyond the case of marine fish, we modeled 16 life tables with age at maturity  
399 and lifespan similar to those observed in our species but with simulated age-specific survival  
400 and fecundity (Fig 4A).

401 Considering models including constant fecundity with age, we found a significant relation-  
402 ship between adult lifespan and  $\frac{N_e}{N}$  for species with type III survivorship curves ( $c < 1$ ) but not  
403 for species having an age-specific survivorship curve constant,  $c$ , superior to 2, including type  
404 I species (Fig 4B). The slope between adult lifespan and  $\frac{N_e}{N}$  was steepest for type III species,  
405 reaching -0.053 for  $c = 0.1$ . For  $c < 2$ , the percentage of variation in  $\frac{N_e}{N}$  explained by adult



**Figure 3: Variance in reproductive success induced by age-specific vital rates and adult lifespan correlate with observed genetic diversity** - On top, schematic illustration of age-specific fecundity ( $f_{age}$ , in orange) and survival ( $S_{age \rightarrow age+1}$ , blue) for a simulated species. (A) and (B) represents the relationship between observed genetic diversity on the  $y$ -axis and, respectively,  $\frac{N_e}{N}$  estimated by AgeNe, and simulated genetic diversity with forward-in-time simulations in SLiM v.3.31 (Haller and Messer, 2017), on  $x$ -axis. Life tables containing information on age-specific survival, fecundity and lifespan were used for the 16 species. Age at maturity was used only with AgeNe. Dot points represent non-brooding species and empty circles, brooding species. Blue and green lines represent the beta regression between adult lifespan and genetic diversity considering the whole dataset (16 species), and the 11 non-brooding species only, respectively. The  $p$ -value and the pseudo- $R^2$  are represented on the top left for each of the two top panels for the non-brooders model. Panels (C)-(G) represent the relationship between scaled genetic diversity and scaled  $\frac{N_e}{N}$  (i.e., divided by the maximum corresponding value) for the 11 non-brooding species. In each panel, the grey points represent scaled  $\frac{N_e}{N}$  estimated from life tables with age at maturity, age-specific fecundity and survival and sex-specific differences (as in panel A). Black points are scaled estimates of  $\frac{N_e}{N}$  from life tables with only: C) longevity (L), D) longevity (L) and age at maturity (AM), E) longevity (L) and age-specific survival (S), F) longevity (L), age at maturity (AM) and age-specific survival (S) and G) longevity (L) and age-specific fecundity (F). Beta regression models (grey and green lines) that closely overlap the red dotted line indicate that a decrease in  $\frac{N_e}{N}$  leads to a similar decrease in genetic diversity.

406 lifespan was higher than 60%. Interestingly, it reached a maximum for  $c = 1.03$  at 89% and  
407 abruptly dropped down around  $c = 2$  (Fig 4B).

408 Then, we added an exponential increase in fecundity with age, first taking  $f = 0.142$ , which  
409 is close to the empirical estimations for our 16 species (Fig 4B). The slope between adult  
410 lifespan and  $\frac{N_e}{N}$  became steeper for type I and type II species and reached -0.074 for extreme  
411 type III species ( $c = 0.01$ ). When we included this exponential increase of fecundity with age,  
412 the percentage of variation explained was superior for approximately all values of  $c$ , and the  
413 abrupt drop of the percentage of variation explained shifted toward higher  $c$  values, around  
414  $c = 3$ . Interestingly, we found significant positive relationships associated with low slope values  
415 when  $c$  became superior to 10 (type I species).

416 Then, we compared values of slope and  $R^2$  for all  $c$  values and for  $f$  ranging from -1 to 1  
417 (Fig 4C-D). The steepest slope between adult lifespan and  $\frac{N_e}{N}$  that we obtained reached -0.076  
418 for extreme type III species ( $c$  around 0.1), and exponential constant,  $f$ , between 0.18 and  
419 0.31. For type III and type II species ( $c < 1$ ), both the slope and the percentage of variation  
420 explained first increased with increasing exponential constant and then decreased. Significant  
421 negative relationships were found for  $c < 1$  for any values of  $f$ , except some extreme values near  
422 -1, whereas no significant relationship was found for  $c > 1$  when  $f$  is negative except for values  
423 of  $c$  near 1 and values of  $f$  near 0. The steepest slope and the highest percentage of variation  
424 explained were obtained for type III species with intermediate values of  $f$  ( $0.1 < f < 0.5$ )  
425 and for type II species ( $1 < c < 5$ ) for positive values of  $f$ . For type I species, as  $c$  values  
426 increased, higher values of  $f$  are needed to obtain a significant negative relationship between  
427 adult lifespan and the  $\frac{N_e}{N}$  ratio. Above  $c > 20$ , no significant negative relationship was found  
428 for any values of  $f$ . Again, we found significant positive relationships and low slopes for  $c > 15$   
429 and intermediate positive values of  $f$ .

430 We found similar results considering a power-law relationship between age and fecundity,  
431 with slightly flatter slopes between  $\frac{N_e}{N}$  and adult lifespan, and no significant correlations for  
432 extreme positive values of  $f$  and extreme low values of  $c$ . In contrast, we found limited or no  
433 impact of  $f$  on the relationship between  $\frac{N_e}{N}$  and adult lifespan, respectively, for the linear and  
434 the polynomial age-fecundity model.

## 435 Discussion

436 In this study, we used whole-genome high-coverage sequencing data to estimate the genetic  
437 diversity of 16 marine teleost fish with similar geographic distribution ranges. We found that  
438 adult lifespan was the best predictor of genetic diversity, species with long reproductive lifespans  
439 generally having lower genetic diversities (Fig 2). Longevity was already identified as one of  
440 the most important determinants of genetic diversity across Metazoans and plants, in which  
441 it also correlates with the efficacy of purifying selection (Romiguier et al., 2014; Chen et al.,  
442 2017). A positive correlation between longevity and the ratio of nonsynonymous to synonymous  
443 substitutions ( $dN/dS$ ) was also found in teleost fishes (Rolland et al., 2020), thus suggesting  
444 lower  $N_e$  in long-lived species. However, the mechanisms by which lifespan impacts genetic  
445 diversity remain poorly understood and may differ among taxonomic groups. Here we showed  
446 that age-specific fecundity and survival (i.e. vital rates), summarized in life tables, naturally  
447 predict the empirical correlation between adult lifespan and genetic diversity in marine fishes.

## 448 Impact of life tables on genetic diversity

449 On a broad taxonomic scale including plants and animals, Waples et al. (2013) showed that  
450 almost half of the variance in  $\frac{N_e}{N}$  estimated from life tables can be explained with only two life  
451 history traits: age at maturity and adult lifespan. Therefore, the effect of adult lifespan on



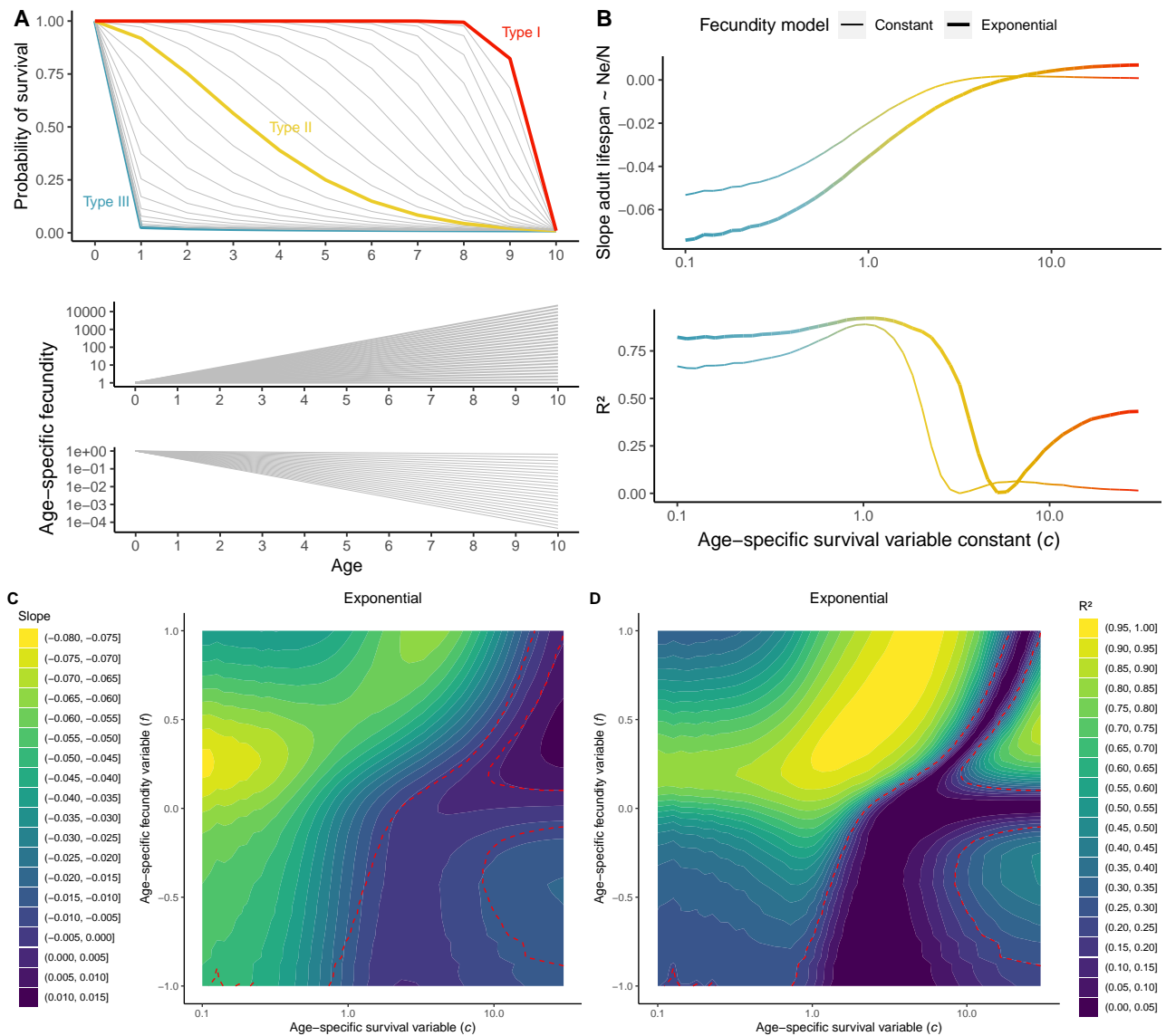


Figure 4: **Slope of the linear model between adult lifespan and  $\frac{N_e}{N}$  ratio estimated with AgeNe for different combinations of age-specific survival and fecundity** - A) On top, gradient of survivorship curves simulated, ranging from type III (blue,  $c < 1$ ), high juvenile mortality and low adult mortality; to type II (orange,  $c$  around 1), constant mortality and type I (red), low juvenile mortality high adult mortality. At the bottom, simulated fecundity either increases or decreases exponentially with age as  $F_{Age} = exp^{f \times Age}$ , with  $f$  ranging from -1 to 1. 16 simulated life tables were constructed with the same values of age at maturity and lifespan as the 16 studied species, and all possible survivorship curve and fecundity-age relationship shown in Panel A. B) Slope and  $R^2$  of the regression between adult lifespan and  $\frac{N_e}{N}$  ratio for the 16 simulated species as a function of  $c$ , for constant fecundity with age (thin line) and exponential increase of fecundity with age with  $f = 0.142$  (thick line). C) Slope and D)  $R^2$  of the regression between adult lifespan and  $\frac{N_e}{N}$  ratio for the 16 simulated species for a gradient of values of  $c$  and  $f$ . In C), warmer colors indicate steeper slopes; in D) higher  $R^2$ .

452 genetic diversity should reflect variations in age-specific fecundity and survival across species.  
453 If the species vital rates used to derive  $\frac{N_e}{N}$  ratios are relatively stable over time, the reduction in  
454  $N_e$  due to lifetime variance in reproductive success should not only apply to contemporary time  
455 scales but more generally throughout the coalescent time. Thus, a direct impact of life tables  
456 on genetic diversity can be expected for iteroparous species with overlapping generations.

457 Using both an analytical (with AgeNe) and a simulation-based (with SLiM) approach, we  
458 showed that age-specific survival and fecundity rates alone can explain a significant fraction of  
459 the variance in genetic diversity among species (Fig 3A-B). This may appear surprising at first  
460 sight, considering that we did not account for among species variation in population census  
461 sizes, which vary by several orders of magnitude in marine fishes (Hauser and Carvalho, 2008).  
462 Our results thus support that intrinsic vital rates are crucial demographic components of the  
463 neutral model to understand differences in levels of genetic diversity in marine fishes. But how  
464 generalizable is this finding to other taxa?

465 Age-specific survivorship curves are one of the main biological components of life tables.  
466 Three main types of survivorship curves are classically distinguished: type I curves are charac-  
467 terized by low juvenile and adult mortality combined with an abrupt decrease of survival when  
468 approaching the maximum age (e.g. mammals); in type II curves, survival is relatively constant  
469 during lifetime (e.g. birds) while type III curves are characterized by high juvenile mortality  
470 followed by low adult mortality (e.g. fishes and marine invertebrates). Type III survivorship  
471 curves favor the disproportionate contribution of a few lucky winners that survive to old age,  
472 compared to type I survivorship curves, where individuals have more equal contributions to  
473 reproduction, generating a lower variance in reproductive success. Thus, in type III species,  
474 higher lifetime variance in reproductive success is expected as the lifespan of a species increases.  
475 By simulating extreme type III survivorship curves ( $c = 0.1$ ) for our 16 species while keeping  
476 their true adult lifespans, we found that  $\frac{N_e}{N}$  can decrease by at most 0.05 per year of lifespan  
477 (Fig 4B, extreme left). This can theoretically induce up to 60% difference in genetic diversity  
478 between the species with the shortest and the longest lifespans of our dataset. In contrast, we  
479 found no correlation between adult lifespan and  $\frac{N_e}{N}$  when simulating type I survivorship curves  
480 with the true lifespan values of the 16 species studied here (Fig 4B,  $c > 2$ ), meaning that  
481 lifespan and variance in reproductive success may have limited influence in other taxonomic  
482 groups, such as birds or mammals.

483 Another important component of life tables is age-specific fecundity. In marine fishes,  
484 fecundity is positively correlated to female ovary size, and the relationship between fecundity  
485 and age is usually well approximated with an exponential ( $F = aexp^{Ab}$ ) or power-law ( $F = aA^b$ )  
486 function. By adding an exponential increase in fecundity with age to our simulations, we found  
487 that  $\frac{N_e}{N}$  decreases even more strongly with increasing adult lifespan ( $\frac{N_e}{N}$  decreases by up to  
488 0.07 per extra year of reproductive life). Using both type III survivorship and exponentially  
489 increasing fecundity with age, we could thus predict up to 84% of the variance in genetic  
490 diversity between species with the shortest and longest lifespans.

491 We found that  $\frac{N_e}{N}$  predicted from fecundity alone or age at maturity combined with age-  
492 specific survival, explained as much variation in genetic diversity as life tables with both of  
493 these components (Fig 3). This is because both of these two scenarios create sharp differences  
494 in fitness between young and old age classes. By contrast, variation in age at maturity alone (all  
495 other parameters being held constant across species) introduces some variation in  $\frac{N_e}{N}$  because  
496 the onset of reproduction varies from 1 to 7 years old depending on the species, but this effect  
497 is buffered by the long subsequent period during which adults will reproduce equally. Similarly,  
498 the effect of survival alone is insufficient because individuals of all species start reproducing  
499 early enough (1 year old).

500 Although these predicted relationships were pretty close to our empirical findings, genome-  
501 wide heterozygosity decreased by about 0.09 per additional year of lifespan in our real dataset

(Fig 2), which seems to be a stronger effect compared to theoretical predictions based on vital rates alone. It is thus likely that other correlates of adult lifespan and unaccounted factors also contribute to observed differences in genetic diversity among species.

## Correlated effects

When relating measures of diversity with the estimates of  $\frac{N_e}{N}$  derived from life tables, we did not take into account differences in census size ( $N$ ) between species. Population census sizes can be huge and are notoriously difficult to estimate in marine fishes. For that reason, abundance data remain largely unavailable for the 16 species of this study. We nevertheless expect long-lived species to have lower abundance compared to short-lived species because in marine fishes  $N$  is generally negatively correlated to body size (White et al., 2007), which is itself positively correlated to adult lifespan in our dataset (Fig S7). Hence, while we have demonstrated here that variation in vital rates has a direct effect on long-term genetic diversity, the slope between adult lifespan and genetic diversity may be inflated by uncontrolled variation in  $N$ . Recent genome-wide comparative studies found negative correlations between  $\frac{N_e}{N}$  and  $N$  in Pinnipeds (Peart et al., 2020) as well as between genetic diversity and body size in butterflies and birds (Mackintosh et al., 2019; Brüniche-Olsen et al., 2019). Here, a highly significant negative correlation was found between genetic diversity and body size and the strength of that correlation was comparable to that found in a meta-analysis of microsatellite diversity using catch data and body size as proxies for fish abundance (Mccusker and Bentzen, 2010). We note, however, that body size was not as good a predictor of genetic diversity as lifespan and adult lifespan for the 11 non-brooding species and it was even not significant in the whole dataset of the 16 species (Table S1).

Another potentially confounding effect is the impact of r/K strategies which are the main determinant of genetic diversity across Metazoans (Romiguier et al., 2014). In our dataset, fecundity and propagule size (proxies for the r/K gradient) showed only little variance compared to their range of variation across Metazoans, and none of them were correlated to adult lifespan. However, we found that the 5 brooding species of our dataset, which are typical K-strategists, displayed lower genetic diversities with respect to their adult lifespan (Fig 2). Most interestingly, when these species were removed from the analysis, the effect of adult lifespan on genetic diversity was amplified, indicating a potentially confounding effect of parental care in marine fishes. Alternatively, low levels of genetic diversity in brooding species can also be explained by underestimated lifetime variance in reproductive success by **AgeNe** due to unaccounted variance in reproductive success within age-class. This may be particularly important in males as the age-fecundity relationship is empirically estimated for females only. This effect could be high for species with strong sexual selection and mate choice (Hastings, 1988; Naud et al., 2009). Moreover, most of these species inhabit lagoons and coastal habitats, corresponding to smaller ecological niches compared to species with no parental care, thus potentially resulting in lower long-term abundances. The discrepancy introduced by brooders in the relationship that we observed here between adult lifespan and genetic diversity may thus involve a variety of effects that remain to be elucidated.

Temporal fluctuations of effective population size may also have impacted observed levels of genetic diversity (Nei et al., 1975). All studied species possibly went through a bottleneck during the Last Glacial Maximum (Jenkins et al., 2018), which may have simultaneously decreased their genetic diversities. As the time of return to mutation-drift equilibrium is positively correlated to generation time, which is itself directly linked to adult lifespan, we may expect long-lived species to have recovered less genetic variation than short-lived species following their latest bottleneck. Moreover, long-lived species may not have recovered their pre-bottleneck population sizes as rapidly as short-lived species. If true, the negative relationship between adult



550 lifespan and genetic diversity may be inflated compared to the sole effect of life tables.

551 Variation in mutation rates between species could not be accounted for due to a lack of  
552 estimates. However, if species-specific mutation rates were correlated with adult lifespan, we  
553 would expect mutation rate variation to have a direct effect on genetic diversity. Mutation  
554 rate could be linked with species life history traits through three possible mechanisms. First,  
555 the drift-barrier hypothesis predicts a negative correlation between species effective population  
556 size and the per-generation mutation rate (Sung et al., 2012). However, this hypothesis can  
557 not explain our results since species with the highest effective population sizes have the highest  
558 genetic diversity. Second, species with larger genome size tend to have more germline cell  
559 divisions, hence possibly higher mutation rates. But we did not find any correlation between  
560 genome size and genetic diversity or any other qualitative and quantitative life history traits.  
561 Third, species with longer generation time, which is positively correlated to lifespan and age  
562 at maturity, may have higher per-generation mutation rate as older individuals accumulate  
563 more germinal mutations throughout their lives. Again, under this assumption, we would  
564 expect species with longer lifespan to have higher mutation rate and genetic diversity, which  
565 goes against our observations. In summary, variation in mutation rates among species due  
566 to differences in lifespan is unlikely to explain the negative lifespan-diversity relationship we  
567 observed. If anything, variation in mutation rates should theoretically oppose this relationship.

568 Using one of the few direct estimates of the per-generation mutation rate in fish, Feng  
569 et al. (2017) explained the surprisingly low nucleotide diversity found in the Atlantic herring  
570 *Clupea harengus* ( $\pi = 0.3\%$ ) by a very low mutation rate of  $2 \times 10^9$  estimated from pedigree  
571 analysis. Although the herring is one of the most abundant and fecund pelagic species in  
572 the North Atlantic Ocean, its genetic diversity appears approximately 80% lower than that  
573 of the European pilchard *S. pilchardus*, another member of the *Clupeidae* family that shows  
574 the highest diversity in our study. Even if *C. harengus* has a larger body size (approximately  
575 30 cm, compared to 20 cm for *S. pilchardus*, Froese et al. (2000)), it has above all a much  
576 longer lifespan (between 12 and 25 years) and a later age at maturity (between 2 and 6.5 years)  
577 (Jennings and Beverton, 1991). Considering even the lowest estimate of adult lifespan reported  
578 for the herring (10 years), the corresponding genetic diversity predicted by our model linking  
579 adult lifespan to genetic diversity would be around 0.5 %, which is pretty close to the empirical  
580 estimate.

581 Finally, we did not take into account the erosion of neutral diversity through linked se-  
582 lection. Addressing that issue would need to generate local estimates of nucleotide diversity  
583 and population recombination rate along the genome of each species using resequencing data  
584 aligned to a reference assembly, which was out of the scope of this study. The predicted effect  
585 of linked selection could be, however, to remove more diversity in species with large compared  
586 to small  $N_e$ . It is therefore likely that linked selection would rather attenuate the negative  
587 relationship between adult lifespan and genetic diversity compared to neutral predictions.

## 588 Conclusion

589 Here we used a simple approach to generate reference-free genome-wide estimates of diversity  
590 with  $k$ -mer analyses. Tested on two species with genetic diversities ranging from 0.22 to 1.42%  
591 the  $k$ -mer approach performed close to the level of a high-standard reference-based method in  
592 capturing fine-scale variation in diversity between evolutionary lineages and even populations  
593 of the same species. This opens the possibility to address the determinants of genetic diversity  
594 in other groups of taxa at limited costs without relying on existing genomics resources. Across  
595 Metazoans, the level of genetic diversity showed no significant relationship with the species'  
596 conservation status (Romiguier et al., 2014). Studies performed at lower phylogenetical scales  
597 such as in Darwin's finches and Pinnipeds, however, found reduced contemporary genetic di-

598 versity in threatened compared to non-threatened species (Brüniche-Olsen et al., 2019; Peart  
599 et al., 2020). Our results complement and extend this literature by showing the importance of  
600 taking into account life tables in comparisons of genetic diversity between species.

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## 613 **Author contributions**

614 P.B., T.B. and P.-A.G. wrote the manuscript. P.B. and P.-A.G. performed fieldwork. P.B.  
615 performed molecular experiments, and all bioinformatics and evolutionary genomics analyses  
616 with inputs from T.B. and P.-A.G. P.-A.G. conceived the project and managed financial support  
617 and genome sequencing.

## 618 **Data archiving**

619 Data and scripts used in this study are freely available in the GitHub repository [https://](https://github.com/pierrebarry/life_tables_genetic_diversity_marine_fishes)  
620 [github.com/pierrebarry/life\\_tables\\_genetic\\_diversity\\_marine\\_fishes](https://github.com/pierrebarry/life_tables_genetic_diversity_marine_fishes). All sampling  
621 metadata are accessible under GEOME at the CoGeDiv Project Homepage: [https://geome-db.](https://geome-db.org/workbench/project-overview?projectId=357)  
622 [org/workbench/project-overview?projectId=357](https://geome-db.org/workbench/project-overview?projectId=357). Sequence reads have been deposited in  
623 the GenBank Sequence Read Archive under the accession code BioProject PRJNAXXXX.

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