

1 **Title: Determinants of lifetime reproductive success in a wild clownfish**
2 **population: strong habitat and weak genetic effects**

3
4 **Authors:** Océane C. Salles^{1,2}, Glenn R. Almany^{1,2†}, Michael L. Berumen³, Geoffrey P. Jones⁴,
5 Pablo Saenz-Agudelo⁵, Maya Srinivasan⁴, Simon R. Thorrold⁶, Benoit Pujol^{1,2*}, and Serge Planes^{1,2*}

6 **Affiliations:**

7 ¹ *PSL Université Paris: EPHE-UPVD-CNRS, USR 3278 CRIOBE, Université de Perpignan, 52*
8 *Avenue Paul Alduy, 66860 Perpignan Cedex, France.*

9 ² *Laboratoire d'Excellence 'CORAIL', 58 avenue Paul Alduy, F-66360 Perpignan, France.*

10 ³ *Red Sea Research Center, Division of Biological and Environmental Sciences and Engineering,*
11 *King Abdullah University of Science and Technology, Thuwal, 23955, Saudi Arabia.*

12 ⁴ *ARC Centre of Excellence for Coral Reef Studies, and College of Science and Engineering, James*
13 *Cook University, Townsville, Queensland 4811, Australia.*

14 ⁵ *Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, 5090000 Valdivia,*
15 *Chile.*

16 ⁶ *Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, United*
17 *States of America.*

18 [†]*Deceased 24 March 2015.*

19 **Both authors share senior authorship of this article*

20 **Correspondence:** Océane Salles and Benoit Pujol; Emails: oceane.salles@gmail.com and
21 benoit.pujol@univ-perp.fr

22 **Running title:** Habitat drives clownfish local success

23 **Abstract**

24 Lifetime reproductive success (LRS), the number of offspring an individual contributes to the next
25 generation, is of fundamental importance in ecology and evolutionary biology. LRS may be
26 influenced by environmental, maternal and additive genetic factors, and the relative contributions of
27 each are critical in determining whether species can adapt to rapid environmental change. However,
28 studies quantifying LRS across multiple generations in wild populations are extremely rare, and to
29 date, non-existent for marine species. Here we use pedigrees of up to 5 generations resolved from a
30 10-year data-set for a wild orange clownfish population from Kimbe Island (PNG) to assess the
31 contribution of every breeder to the local population. We quantified the additive genetic, maternal
32 and environmental contributions to variation in LRS for the self-recruiting portion of the population
33 using a genetic linear mixed model approach. We found that the habitat of the breeder, including the
34 anemone species and geographic location, made the greatest contribution to LRS, explaining ~97%
35 of the variation. There were low to negligible contributions of genetic (1.3%) and maternal factors
36 (1.9%) equating with low heritability and evolvability. Our findings imply our population will be
37 extremely susceptible to short-term, small-scale changes in habitat structure and may have limited
38 capacity to adapt to these changes.

39

40 **Keywords:** multi-generational pedigree, additive genetic variation, maternal effects,
41 environmental effects, adaptation, selection, heritability, evolvability.

42 INTRODUCTION

43 Darwinian fitness or lifetime reproductive success (LRS) – the number of successful offspring an
44 individual contributes to the next generation – is a critical variable underpinning ecological and
45 evolutionary responses to the environment (Clutton-Brock 1988; Roff 2002; Clutton-Brock &
46 Sheldon 2010; Hendry *et al.* 2018). LRS may be influenced by several factors including phenotypic
47 responses to different environmental parameters, parental effects, and additive genetic variance
48 (Kruuk *et al.* 2000; McCleery *et al.* 2004; McFarlane *et al.* 2014). Apportioning these contributions
49 is critical to understanding the potential for short-term ecological effects and longer-term
50 evolvability in response to rapid environmental change. If LRS is exclusively a phenotypic response
51 to the conditions experienced by individuals, populations will be severely impacted by rapid
52 environmental change and there is no prospect of adaptive microevolution. Maternal responses to
53 change environmental conditions may reduce the effect of those changes on the next generation
54 through acclimation (Bernardo 1996; Mousseau & Fox 1998; Danchin *et al.* 2011; Donelson *et al.*
55 2017). However, it is the additive genetic variation in LRS that determines the rate of adaptation of
56 a population to the environmental demand (Fisher 1930; Frank 1997; Lessard 1997; Crow 2002).
57 To date, few studies have distinguished the relative importance of environmental and genetic
58 contributions to LRS over multiple generations in wild populations, where genetic contributions to
59 fitness may be complex (Kruuk & Hadfield 2007). This situation is changing as long-term,
60 individual-based ecological studies in which multi-generational pedigrees have been established
61 provide the necessary longitudinal information to quantify the different components of LRS
62 (Pemberton 2008; Clutton-Brock & Sheldon 2010; Wolak *et al.* 2018; Cava *et al.* 2019). Such
63 studies are imperative as we seek to understand the ability of species to withstand or adapt to
64 accelerating climate change (Charmantier *et al.* 2008; Munday *et al.* 2017).

65

66 Intergenerational responses to selection are a product of the interplay between genetic and
67 environmental mechanisms that ultimately shape the genetic variation in fitness-related traits.

68 Environmentally driven mechanisms (*e.g.*, phenotypic plasticity, genetic assimilation) can facilitate
69 (Price *et al.* 2003; Ghalambor *et al.* 2007, Ledón-Rettig *et al.* 2014; Hoffmann & Merilä 1999;
70 Danchin *et al.* 2019) or constrain the microevolutionary response to selection (Kruuk *et al.* 2003;
71 Pujol *et al.* 2018). However, in the absence of genetic variation for LRS, these mechanisms will
72 likely have little effect on a negligible rate of adaptive evolution. In quantifying additive genetic
73 variation, it is important to distinguish between *heritability* and *evolvability* (Wheelwright *et al.*
74 2014; Cava *et al.* 2019). Narrow sense heritability, the additive genetic variance standardized by the
75 total phenotypic variance, is widely used as a measurement of the population evolutionary potential
76 to respond to selection (Falconer & Mackay 1996; Mousseau & Roff 1987; McCleery *et al.* 2004).
77 It is directly affected both by the additive genetic variation and magnitude of direct environmental
78 effects. Low heritability values can either reflect low additive genetic variance or large
79 environmental, or residual effects (Price & Schluter 1991; Houle 1992; Hansen *et al.* 2011).
80 Evolvability is the mean-standardized additive genetic variance (Houle 1992; Hansen *et al.* 2011).
81 This is the expected proportional change per generation in population mean fitness given a unit
82 strength of selection (Hendry *et al.* 2018). Evolvability is not affected by environmental or maternal
83 effects, which makes it a more appropriate metric in the comparison of evolutionary potential
84 between traits, populations and species. Heritability reveals whether the additive genetic variance
85 for LRS represents a non-trivial proportion of the total variance of LRS in the actual environmental
86 context of a given wild population. Together, evolvability and heritability inform us about how
87 much environmental change a wild population can withstand on the basis of its evolutionary
88 potential.

89

90 The few ($n = 15$) long-term, individual-based studies that have quantified additive genetic variation,
91 heritability and evolvability of LRS in wild populations have all focused on terrestrial species
92 (Postma 2014; Hendry *et al.* 2018; Table S1). These have largely confirmed that LRS have low
93 additive genetic variation and evolvability (~ 0.08), which nevertheless reflects some evolutionary

94 potential (Burt 1995; Hendry *et al.* 2018). Until recently, quantifying LRS in marine organisms with
95 a pelagic larval stage has been considered impossible because of the difficulties in following the
96 fate of offspring from one generation to the next. However, there is increasing evidence of some
97 degree of natal philopatry or self-recruitment in local marine populations (Jones *et al.* 1999;
98 Swearer *et al.* 1999; Swearer *et al.* 2002; Jones *et al.* 2009). The application of genetic parentage
99 analysis is making it possible to assign a significant proportion of successful offspring to their
100 parents (Planes *et al.* 2009; Jones 2015; Le Port *et al.* 2017; Mobley *et al.* 2019) and construct
101 multigenerational pedigrees (Salles *et al.* 2016a; Aykanat *et al.* 2014; Reed *et al.* 2019), at least for
102 the offspring that return to their natal population.

103

104 For coral reef fishes, quantifying the environmental and genetic components of LRS and assessing
105 evolvability in wild populations is of great contemporary importance. Between 30 to 50% of the
106 world's coral reefs have been lost and those remaining are considered highly vulnerable (Jackson
107 2010; De'ath *et al.* 2012; van Hooijdonk *et al.* 2016). The rapid loss of suitable habitat is widely
108 acknowledged to be contributing to a decline in reef fish populations and biodiversity (Jones *et al.*
109 2004; Wilson *et al.* 2006; Paddock *et al.* 2009; Pratchett *et al.* 2018). Laboratory studies have
110 shown that near future environmental conditions predicted under climate change can have a
111 dramatic effect on reef fish reproductive success, and despite some levels of phenotypic plasticity
112 and transgenerational acclimation, the potential for adaptation is uncertain (Donelson *et al.* 2017;
113 Munday *et al.* 2013; Munday *et al.* 2017). To date, environmental, maternal and additive genetic
114 contributions to LRS in wild coral reef fish populations have not been assessed. However, recent
115 work establishing high levels of natal philopatry in some coral reef fishes (Jones *et al.* 2005,
116 D'Aloia *et al.* 2015; Salles *et al.* 2015; Almany *et al.* 2017) and the success of parentage analysis in
117 detecting family relationships across multiple generations (Salles *et al.* 2016a,b) opens the way for
118 quantifying LRS for the first time.

119

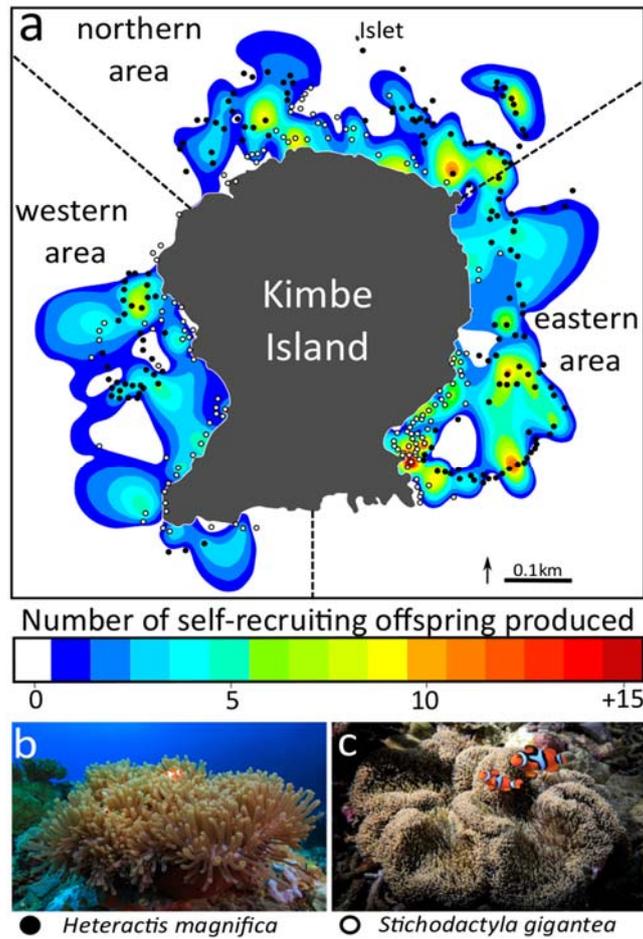
120 Here, we focus on the entire population of the orange clownfish *Amphiprion percula* at Kimbe
121 Island, Papua New Guinea where each year ~half the juveniles successfully recruiting are progeny
122 of local breeding pairs (Salles *et al.* 2016a, Almany *et al.* 2017). We use multi-generational
123 pedigrees of up to 5 generations obtained from biennial DNA sampling over 10 years (Salles *et al.*
124 2016a,b) and apply a quantitative genetic linear mixed model approach (Kruuk & Hill 2008) to
125 quantify the additive genetic, maternal and environmental components of variation in LRS for the
126 self-recruiting portion of the population. Habitat effects were quantified by examining LRS for
127 individuals resident in two different anemone species and from different both geographic locations
128 around the island (Salles *et al.* 2016a). By integrating habitat data with the pedigree information in a
129 quantitative genetic generalized linear mixed model, we were able to assess the relative contribution
130 of additive genetic, maternal and habitat effects to local LRS. We also calculated the evolvability
131 and heritability of LRS to evaluate its evolutionary potential to respond to selection at the local
132 population scale.

133

134 **METHODS**

135 **Study population and data collection**

136 A natural population of orange clownfish (*A. percula*) living in the reef surrounding Kimbe Island
137 (Fig. 1a; 5°12'22.56" S, 150°22'35.58" E), West New Britain Province of Papua New Guinea, was
138 surveyed every second year from 2003 to 2013. Here, *A. percula* lives in a mutualistic association
139 with one of two host sea anemone species, *Heteractis magnifica* (Fig. 1b) and *Stichodactyla*
140 *gigantea* (Fig. 1c). We geographically located and tagged a total of 310 anemones (176 *H.*
141 *magnifica* and 134 *S. gigantea*) that were occupied by *A. percula* on the entire reef surrounding the
142 island.



143

144 **Figure 1. Variation of the total number of offspring orange clownfish produced on each anemone around Kimbe**145 **Island between 2003 and 2013. (a)** The studied region was divided in three areas (northern, eastern and western areas).

146 Colors correspond to the variation of the total number of juveniles locally self-recruited that were produced on each

147 anemone (varying from 0 to 27) over a 10-year period. The expected value is interpolated from those around it (using

148 default algorithms implemented in *Origin* software). Dots correspond respectively to the location of the two host149 anemones species: (b) *Heteractis magnifica* (black dots) and (c) *Stichodactyla gigantea* (white dots). Photos by Tane

150 Sinclair-Taylor.

151 These two anemone species are remarkably different in terms of the micro-habitat they provide,

152 including a wide range of shapes, sizes, depth distributions and surrounding substrata (Dunn 1981;

153 Chausson *et al.* 2018). Although we did not directly measure these variables (other than depth), the154 combination of host the anemone species (*H. magnifica* or *S. gigantea*) with one of the three

155 geographical areas covering the entire reef around the island (northern, western or eastern areas,

156 Figure 1a) where it is located describes a ‘habitat’ variable for each fish that encompasses a suite of

157 biotic and abiotic environmental conditions. These geographical areas correspond to the different

158 coasts of the island that reflect possible environmental effects of the geographic location (Salles *et*
159 *al.* 2016b). In total, the combination of the two host anemone species with the three geographical
160 areas allowed us to describe six different habitats.

161

162 Clownfish within one anemone live in group of typically three to five individuals in the Kimbe
163 Island population (Salles *et al.* 2015). The size-based dominance hierarchy in *Amphiprion* allows us
164 to determine the reproductive status of each individual (Fricke 1979). The female is the largest, the
165 male is the second largest, and the non-breeders rank progressively lower in the hierarchy as they
166 decrease in size. If the single female adult of a group dies, then the male changes sex to female, and
167 the largest non-breeder from the anemone becomes sexually mature as male. Reproduction occurs
168 year round, with females laying several hundred eggs in a clutch near the pedal disk of the host
169 anemone each lunar month. The eggs hatch after ~7 days of paternal care into larvae that spend ~10
170 days in the pelagic environment (Berumen *et al.* 2010) before settling on an anemone that may or
171 may not be in the population (Planes *et al.* 2009).

172

173 Fish were captured by divers by using hand nets. Individuals were measured *in situ* using calipers,
174 fin-clipped (size > 35mm) or collected whole (size < 35mm) for genetic analysis and then released
175 back on the same anemone. Small pieces of fin tissue were preserved in 95% ethanol in 2-mL vials.
176 The biggest fish in each anemone was identified as the female, the second largest individual was
177 assumed to be the male, and all other individuals were classified as non-breeders. We extracted
178 DNA from all samples at 22 polymorphic microsatellite loci (Bonin *et al.* 2015). Then, we
179 identified the individuals sampled multiple times over the years by using the Excel macro GenAlex
180 v6.5 (Peakall & Smouse 2012) to compare multilocus genotypes from 2003, 2005, 2007, 2009,
181 2011 and 2013. Individuals were in average sampled 2.88 ± 0.04 times (mean \pm SE) over the six
182 surveys (1% of individuals persisted over the 10-yr period, Salles *et al.* 2016a). The 2-yr sampling
183 scheme precluded calculating a precise measurement of the age of individuals (Salles *et al.* 2016b),

184 in particular for fish sampled in 2003 during the first sampling period, which age was unknown.
185 The total duration of this long term survey did not allow us to obtain many replicated measurements
186 within individuals before and after sex change ($n = 41$ individuals). Estimating sex dependent
187 additive genetic variance is precluded in this case because some effects cannot be disentangled as
188 the clownfish only changes sex in one direction (from male to female). This change is always
189 associated with a change of sexual partner and with an increase in female body size, which we
190 expect to generate a confounding effect between a female condition and its genetic quality. We
191 therefore did not consider sex in our model as a result of data and analytical limitations.

192

193 **Pedigree used for quantitative genetic analysis**

194 Pedigree reconstruction was conducted by assigning juvenile fish to parental pairs on the basis of
195 their multilocus genotypes (Salles *et al.* 2016a). We used the software FaMoz (Gerber *et al.* 2003).
196 This approach is based on the calculation of LOD scores (Log of the odd-ratio comparison) for any
197 potential parentage relationship. It determined critical thresholds to accept or reject assignments by
198 simulating true and false parent-offspring pairs. Further details on parentage analyses and pedigree
199 reconstruction are given in Salles *et al.* (2016a). Assignments to single parents were rejected. We
200 kept assignments of parental pairs. In the context of overlapping generations, we used the year of
201 first sampling and the anemone of each parental couple as information to avoid possible false
202 assignments. As a result, sibship links could not be confused with parental links. Because the sex
203 changes through the life of the clownfish, the same individual can be related to its offspring with
204 either a paternal or maternal link. Based on the size of the two parents and the year of first capture,
205 we can identify the mother and the father. The original population pedigree includes 2927 clownfish
206 over five generations including 121 families, 987 paternal, 987 maternal, 1809 full-sib, 412
207 maternal half-sibs, 248 paternal half-sib, 135 maternal grandmothers, 135 maternal grandfathers,
208 278 paternal grandmothers, 278 paternal grandfathers and 218 cousins (Salles *et al.* 2016a). For this
209 study, we excluded from the original pedigree the 1192 individuals that were removed from the

210 habitat at the juvenile stage (size < 35mm, 10 to 458 days old). The final pedigree used for this
211 study includes 1735 individuals from five generations (Fig. S1). We used the R package ‘pedantics’
212 (Morrissey & Wilson 2010) to assess the power of the resolved pedigree to detect significant
213 quantitative genetic parameters (Fig. S1).

214

215 **Individual contribution to self-recruitment**

216 The contribution of an individual to self-recruitment corresponds to the total number of offspring
217 produced during its lifetime and recruiting into Kimbe Island (*e.g.*, the local breeder population). To
218 deal with the fact that some fish were still alive at the end of sampling and that some fish might
219 have already reproduced before the first sampling year, we used biennial measurements of the
220 reproductive success (using field-data from 2003, 2005, 2007, 2009, 2011 and 2013) to compare
221 LRS between individuals. The LRS corresponds here to the total number of descendants produced
222 on a biennial basis that successfully recruited into Kimbe Island population, which provided us with
223 repeated measures over the period of the survey from 2003 to 2013. In the Supplementary
224 information we present results from an alternative approach based on the De-lifing method (DL).
225 The calculation of DL takes into account the temporal variation of the population growth and
226 estimates the contribution of every clownfish to biennial changes in population size through both
227 reproduction and survival (Coulson *et al.* 2016). Statistical problems potentially leading to precision
228 issues and invalid conclusions have been associated with the use of DL (Dupont *et al.* 2017) but DL
229 has only been used in two of the 15 studies where the genetic variation of fitness was quantified in
230 wild populations (Table S1), which limits our ability to discuss its properties.

231

232 **Quantitative genetic generalized linear mixed model approach**

233 Similarities between relatives living in contrasted micro-habitats allowed us to evaluate
234 simultaneously the genetic and habitat components of LRS. Repeated ‘records’ on individuals made
235 it possible to estimate permanent environmental effects, which allowed us to account for intra-

236 individual and unmeasured environmental trait variation across time. Permanent environmental
 237 effects also account for a part of non-additive genetic effects (Wilson *et al.* 2010). The LRS
 238 variance was partitioned into six random effects: Additive genetic (V_A), Maternal (V_M), Natal
 239 Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environment (V_{PE}) and Residual (V_R) variances
 240 by using the ‘animal model’ quantitative genetic approach (Kruuk 2004). This Linear Mixed Model
 241 (LMM) approach uses pedigree information to extract the additive genetic component. This
 242 approach is more powerful than traditional analyses (*e.g.*, parent–offspring regressions) because it
 243 takes into account every relationship link in a pedigree. Maternal variance was modeled using the
 244 mother’s identity as a random effect, allowing maternal effects to include both genetic and
 245 environmental maternal effects. Permanent environmental effects were modeled by including the
 246 identity of individuals as a random effect. The LRS variance is the sum of six variance components:

$$247 \quad V_{LRS} = V_A + V_M + V_{NH} + V_{RH} + V_{PE} + V_R \quad (1)$$

248 Quantitative genetic models were computed as univariate GLMMs using the ‘MCMCglmm’
 249 package (Hadfield 2010) in R version 3.5.1 (R.Core.Team 2018), with LRS as a Poisson response
 250 variable. Using this Bayesian framework facilitated parameter estimation for non-Gaussian traits.
 251 We used parameter expanded priors for all analyses ($V=1$, $nu=0.02$), which are often referred to as
 252 ‘non informative’ priors although such denomination can be debated, as we wanted posterior
 253 estimates to be determined from the data and not from the priors (Morrissey *et al.* 2014). We ran
 254 model MCMC chains over 1,000,000 iterations with initial burning of 10,000 iterations and a
 255 thinning of 1,000 iterations. Historically, the Deviance Information Criterion (DIC) was often used
 256 to compare models and assess the significance of the random variance components in this type of
 257 approach. However, it is becoming less commonly used since it was recognized as an inappropriate
 258 tool for model comparisons of the same type than quantitative genetic GLMM analyses (Gelman *et*
 259 *al.* 2014; Spiegelhalter *et al.* 2014). Effects of variance components were considered statistically
 260 supported if their posterior distributions did not overlap zero (Wilson *et al.* 2010).

261

262 Variance Components

263 Variance components were estimated as the mode of the posterior distributions established on the
264 MCMC sample and we reported the lower and the upper limits of the 95% credible interval. For the
265 six variance components, we calculated their relative contribution to the sum of all variance
266 components, thereby expressing their effects as percentages of the total phenotypic variance (V_{LRS}).
267 As a result, we obtained standard narrow sense heritability estimates for LRS (h^2) by applying the
268 basic formula ($h^2 = V_A / V_P$, see Falconer & McKay 1996), and similarly maternal effects by
269 estimating the proportion of total phenotypic variance explained by the maternal variance ($m^2 = V_M /$
270 V_P). Evolvability (I_A) of LRS, equal to the additive genetic variance divided by the squared mean of
271 the LRS (Wagner & Altenberg 1996), was estimated to evaluate the capacity for adaptive
272 evolutionary change of the number of offspring that self-recruit in the population. The analyses
273 conducted in the ‘MCMCglmm’ framework assumed a Poisson distribution and therefore provided
274 parameter estimates for evolutionary inference or future comparisons on a statistically convenient
275 latent scale for non-Gaussian traits. We therefore endeavored to back-transform all the estimates of
276 the latent scale variables included in the model (see equation 1) onto the observed data scale to
277 improve our inferences. We used the ‘QGlmm’ package (de Villemereuil *et al.* 2016) to back-
278 transform the estimates, specifically the function ‘QGparams’ to estimate additive components such
279 as V_A and h^2 , and ‘QGicc’ to estimate broader sense components such as V_M and m^2 , V_{NH} , V_{RH} , V_{PE}
280 and V_R . Although parameter estimates transformed back on the data-scale are expected to be upward
281 biased, their ratio is reliable, and hence the estimators derived from their relative proportions such
282 as h^2 . It is necessary to point out two specific aspects of the back transformation on the observed
283 data scale. First, V_R is estimated on the basis of the additive over-dispersion term in the nonlinear
284 model and its value cannot be interpreted similarly to the usual residual variance term estimated by
285 classical quantitative genetics generalized linear mixed models. Second, the sum of the variance
286 components estimated on the data scale are not additive and therefore not expected to sum up to the
287 value of the phenotypic variance calculated directly on the raw data. For the sake of clarity and

288 comparison, we present the results on the latent scale and the observed data scale. We calculated the
289 95% credibility intervals from the posterior distributions of observed parameters for all the variance
290 components and other estimates expressed on their basis by using the ‘HDInterval’ package
291 (Meredith & Kruschke 2016).

292

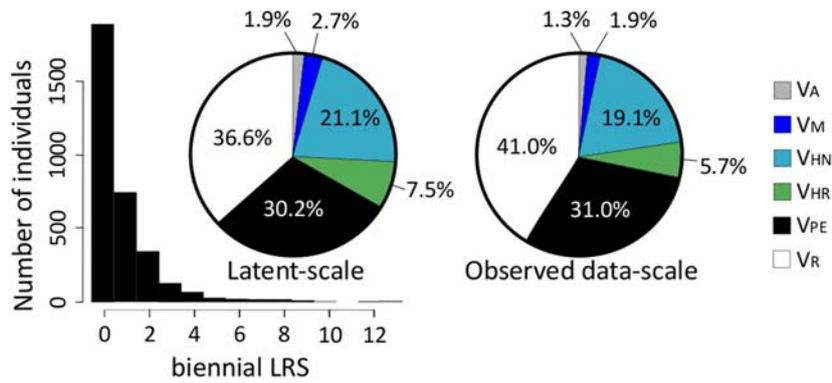
293 **RESULTS**

294 **Habitats dominantly shape the Lifetime Reproductive Success in the clownfish population**

295 Biennial estimates of the Lifetime Reproductive Success (LRS) ranged from 0 to 13, with a
296 phenotypic variance $V_{LRS}=1.31$ and an average value of 0.54 ± 0.05 (mean \pm SE) offspring per
297 individual for a two-year period. Because clownfish live in strong association with their anemone,
298 we were able to identify and geo-locate the precise position and habitat where breeders contributed
299 more to the local replenishment of the population (Fig. 1a). For example, breeders that produced
300 more self-recruiting offspring lived in Kimbe Island’s eastern area and mostly in *S. gigantea*
301 anemones. Our analysis also revealed fish that did not contribute at all to the local replenishment of
302 the population over the 10-year monitoring period. These fish were located in 48 *H. magnifica* and
303 30 *S. gigantea* of the 310 anemones monitored in both deep and shallow waters (Fig. 1a). We found
304 that that 25% of the pairs of local breeders did not contribute at all to the renewal of the population
305 over a period of 10 years.

306

307 Quantitative genetic linear mixed models on the latent and the observed data scale gave very close
308 results. Our results on the scale of observed data showed that Natal Habitat and Resident Habitat
309 explained respectively 19.1% and 5.7% of the variance in LRS, furthermore, residual and
310 permanent environment explained respectively 41.0% and 31.0%, whereas additive genetic effects
311 and maternal effects were very weak and explained 1.3% and 1.9% respectively (Fig. 2a, variances
312 on observed data-scale). Similar results were obtained for DL (see Supplementary Information for
313 more details).



314

315 **Figure 2. Sources of variation in the biennial estimate of the Lifetime Reproductive Success (LRS) of the Kimbe**
 316 **Island orange clownfish.** Distribution of the biennial estimate of the LRS (histograms). Variance components on both
 317 latent-scale and observed data-scale (pie charts) for the biennial estimate of the LRS explained by Additive genetic
 318 (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environmental (V_{PE}) and Residual (V_R)
 319 variances. These proportions were calculated from the values of the posterior modes of a quantitative genetics
 320 generalized linear mixed model analysis (for details see Table 1).

321

322 Low evolvability and low heritability for LRS

323 The modes of the posterior distributions estimating additive genetic variance, expressed on
 324 observed data-scale, were extremely small for the two measures of self-recruitment (Table 1).

325

326 Table 1. Sources of variation in Lifetime Reproductive Success (LRS) for the Kimbe Island orange clownfish.

327 Here we reported variance component estimates quantified by using the animal model approach: Additive genetic (V_A),
 328 Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environmental (V_{PE}) and Residual (V_R)
 329 Variances. We also report size effects as proportions of explained phenotypic variance: narrow-sense heritability (h^2),
 330 maternal effects (m^2) and the mean standardized additive genetic variance: evolvability (I_A) for biennial LRS. Measures
 331 are expressed on a latent-scale (direct *MCMCglmm* R results) and the observed data-scale (*QGglmm* R back-
 332 transformation). 95% credible intervals (CI) are reported for each estimate.

	LRS	LRS
	Latent scale	Observed data-scale
V_A	0.046	0.030
(CI)	(1.381×10^{-3} to 0.146)	(4.94×10^{-4} to 0.060)

V_M	0.067	0.046
(CI)	(2.000×10^{-3} to 0.211)	(8.822×10^{-3} to 0.287)
V_{NH}	0.516	0.450
(CI)	(0.015 to 1.529)	(0.126 to 1.524)
V_{RH}	0.184	0.135
(CI)	(0.264 to 0.473)	(0.038 to 0.457)
V_{PE}	0.737	0.726
(CI)	(0.496 to 0.952)	(0.203 to 2.460)
V_R	0.894	0.963
(CI)	(0.717 to 1.105)	(0.270 to 3.264)
V_{LRS}	2.44	2.35
(CI)	(1.71 to 3.65)	(0.65 to 8.05)
h^2	0.019	0.013
(CI)	(6.827×10^{-4} to 0.057)	(4.951×10^{-5} to 1.227×10^{-2})
m^2	0.027	0.019
(CI)	(9.157×10^{-4} to 0.083)	(2.966×10^{-5} to 2.044×10^{-2})
I_A	0.154	0.103
(CI)	(4.643×10^{-4} to 0.492)	(1.661×10^{-3} to 0.511)

333

334 We found $V_A=0.030$ (CI_{95%} 4.94×10^{-4} to 0.060). This could be linked to the statistical power of our
335 pedigree (Fig. S1). Our model nevertheless placed fairly restricted bands on the 95% credible
336 intervals (Table 1). Credible intervals did not overlap the zero but were close. The extent to which
337 these very low values of genetic estimates are not null must therefore be considered with caution.
338 LRS evolvability estimated on the observed data-scale, which evaluated the micro-evolutionary
339 change of the number of self-recruiting offspring that can be reached by the population, was equal
340 to 0.103 (CI_{95%} 1.661×10^{-3} to 0.511). In other words, 0.104 additional juveniles were added to the
341 average number of juveniles originating and recruiting in the population per generation. The
342 heritability estimate expressed on the observed data-scale was $h^2=0.013$ (CI_{95%} 4.951×10^{-5} to
343 1.227×10^{-2}) for LRS (Table 1). We can therefore estimate the maximum response (R) to selection

344 (*S*), in the presence of strong selection pressures acting on the Kimbe Island orange clownfish
345 population by using the Breeder's equation $R=h^2 \times S$ (Falconer & Mackay 1996; Lush 2008). The
346 low to negligible value of the LRS heritability means that the maximum genetic change of the
347 population average LRS would never exceed ~ 0.020 offspring per generation. Similar results were
348 obtained for DL (see Supplementary Information for more details).

349

350 **Low maternal effects for LRS**

351 We found that maternal variance for the LRS was extremely small, to the extent that it might be
352 considered as null (Table 1): $V_M=0.019$ ($CI_{95\%} 2.966 \times 10^{-5}$ to 2.044×10^{-2}). While our analysis
353 detected maternal variance, it made very little contribution to the total variance in LRS ($m^2=1.9\%$,
354 expressed on observed data-scale, Fig. 2). The habitat occupied by the mother (Natal Habitat) had a
355 stronger effect on LRS than the mother herself. The relative contribution of individuals to the
356 population replenishment was indeed influenced by the Natal Habitat to an extent of 19.1% for
357 LRS. Similar results were obtained for DL (see Supplementary Information for more details).

358

359 **DISCUSSION**

360 *Strong habitat and weak genetic effects on LRS*

361 Our study revealed that LRS in the Kimbe Island orange clownfish population quantified over five
362 generations was largely explained by host anemone species and geographical location ($\sim 97\%$), with
363 only weak maternal (1.9%) and additive genetic effects (1.3%). The strong effects of habitat can be
364 attributed to the intrinsic biological characteristics of the anemone species (*e.g.*, size, shape and
365 toxicity) and their effects of on life-history traits of their resident clownfish (Salles *et al.* 2016b;
366 Chausson *et al.* 2018). In addition, the higher toxicity of *S. gigantea* (Nedosyko *et al.* 2014) might
367 provide better protection against predators of eggs attached near the pedal disk of the host anemone,
368 but this hypothesis remains to be tested. The geographical location of the different host-anemones
369 also appears to be important, with more successful individuals in shallow water, close to the land on

370 *S. gigantea* and in deeper lagoons for *H. magnifica*, which might promote greater local retention of
371 larvae. To date, the mechanisms responsible for geographical differences in LRS around Kimbe
372 Island remain unknown (Berumen *et al.* 2010). The weak genetic effects on LRS that shows a very
373 low to negligible rate of adaptation raise concern about the ability of this reef fish population to
374 exhibit longer-term adaptive evolution in response to rapid climate change.

375

376 *Susceptibility to habitat change*

377 Habitat is clearly the main driver of the variation in LRS and individuals that happen to settle on
378 particular anemones and particular places do well. The dependence of LRS on habitat quality
379 suggests this species will be extremely susceptible to habitat degradation over ecological time
380 scales. Direct and indirect human impacts on clownfish populations and their anemone habitats are
381 already affecting the habitat quality for numerous clownfish species (Jones *et al.* 2008; Saenz-
382 Agudelo *et al.* 2011; Bonin *et al.* 2016). *S. gigantea* anemones located in shallow waters are likely
383 to be disproportionately more impacted by increasing water temperatures and irradiance (Bak *et al.*
384 2005; Hobbs *et al.* 2013). If these locations are differentially impacted, this will affect the
385 individual contribution to the local replenishment of the population and compromise population
386 persistence.

387

388 *Low to negligible evolutionary potential*

389 Our findings provide the first empirical support for a wild marine population to Fisher's
390 fundamental theorem of selection that additive genetic variance in fitness is depleted under
391 selection and tends towards zero in a population reaching evolutionary equilibrium (Fisher 1930;
392 Gustafsson 1986; Falconer 1989). Although normal and expected, low heritability and evolvability
393 in LRS is concerning given the increasing rate of environmental change. The low to negligible
394 scope for adaptive evolution (estimated by evolvability) and the low to negligible genetic potential
395 for responding to selection (estimated by heritability) may not be a problem for gradual

396 environmental change. At this rate, it would take around at least 10 generations for the population
397 average LRS to increase by one juvenile, which highlights the stability of the demographic rate of
398 self-recruitment in this population. Our results therefore support the hypothesis that the population
399 is at evolutionary equilibrium (no genetic changes) in a context of environmental stability over the
400 timescale of the survey.

401

402 *Connectivity as a plausible cause*

403 Our finding that the Kimbe Island clownfish population harbored low to negligible additive genetic
404 variation for LRS over a ten-year period was at first surprising because immigration accounts for on
405 average 44% of the juvenile recruitment (Salles *et al.* 2015; 2016a). The average dispersal distance
406 in Kimbe Bay is between 10 and 20km, providing substantial connectivity among adjacent reefs and
407 potential dispersal of up to 100km (Almany *et al.* 2017; Pinsky *et al.* 2017). The associated gene
408 flow would be expected to bring new genetic variants and thereby increase genetic variation for
409 LRS (Keller *et al.* 2001; Lavergne & Molofsky 2007; Facon *et al.* 2008). Under such scenario,
410 selection for self-recruitment, and thereby against migrants, would have to be strong to keep the
411 population at evolutionary equilibrium. An alternative scenario is that homogenization by gene flow
412 results in most immigrants sharing a similar genetic background. As a result, low genetic variation
413 would be maintained because no new genetic variants were brought in the population by gene flow
414 (Pujol *et al.* 2010). Low genetic variation for LRS implies that evolution by selection at the local
415 scale is extremely limited in its current state. However, this does not imply a dead end for the
416 adaptive evolution of this population because several mechanisms can provide adaptive
417 evolutionary potential over the long term (Pujol *et al.* 2018).

418

419 *Slight but probably negligible maternal genetic effect*

420 Additional adaptive evolutionary potential can in theory be provided to a population by maternal
421 effects (Räsänen & Kruuk 2007). In the Kimbe Island orange clownfish, we found that maternal

422 effects explained up to 2.7% of the LRS variance, which is quite small, even if it was more than
423 additive genetic effects. Our findings thereby revealed that maternal effects increased slightly the
424 low to negligible rate of LRS change by adaptive evolution. One should note that this increase was
425 nearly negligible. It is likely that this low value represents the genetic component of the maternal
426 effect because the identity of each mother was taken into account. The habitat of birth, on the other
427 hand, which is also the maternal habitat, might encompass some direct effect of the maternal
428 environment (Germain & Gilbert 2014). The environmental component can represent a non-
429 negligible part of parental effects (Chirgwin *et al.* 2017). In fact, there is growing awareness that
430 maternal environmental effects can contribute to adaptation in natural populations, especially when
431 maternal and offspring environments are positively correlated (Burgess & Marshall 2014; Shama
432 2015; Dey *et al.* 2016). It might even buy some time for adaptive evolution through slow genetic
433 change to occur (Levis & Pfenning 2016).

434

435 *Towards a wider sample of contemporary rates of adaptive evolution in the wild*

436 In our study, LRS estimates the individual fish contribution to the local population replenishment.
437 This excludes the dispersal fitness because the amount of offspring produced and which dispersed
438 to live somewhere else is unknown on wild population pedigrees (Kruuk *et al.* 2000; Merilä &
439 Sheldon 2000, McCleery *et al.* 2004). Its genetic variation evaluates the rate of adaptive evolution.
440 While there are no comparable data from marine systems, 15 studies conducted on terrestrial
441 vertebrates have also estimated the additive genetic variation and the heritability of LRS (Table S1).
442 It is noteworthy that the number of estimates of maternal effects on LRS variation are extremely
443 rare (Kruuk *et al.* 2000, Foerster *et al.* 2007; Schroeder *et al.* 2012; McFarlane *et al.* 2014). A
444 majority of these studies similarly found low to negligible contributions of additive genetic effects,
445 while the situation is less clear for maternal effects, partly because studies remain scarce. The
446 existence of additive and maternal genetic variation for fitness, even when very low, implies that
447 the population was not totally at equilibrium because there was a small genetic change in the wild

448 population over the course of the long term survey. It also implies very limited genetic adaptive
449 potential.

450

451 **CONCLUSION**

452 The major outcome of this study is that the heterogeneity of the habitat of the Kimbe Island orange
453 clownfish had a profound influence on the individual contribution to the local population
454 replenishment over five generations. This finding implies that habitat ecology is crucial for this
455 clownfish population. In terms of future persistence, expected changes in habitat quality and
456 configuration over relatively short time scales might affect the ability of fish to self-recruit. This
457 ability harbored low to negligible additive genetic and maternal genetic variation. As a
458 consequence, this population potential for rapid evolutionary change of LRS by selection, and
459 therefore its rate of adaptive evolution, can be considered negligible in the current state of the
460 population. This finding, which is in line with other studies on the topic, stresses the importance of
461 environmental mechanisms (*e.g.*, plasticity) that have the potential to enable rapid adaptive
462 responses (Donelson *et al.* 2017; Munday *et al.* 2017). Our findings suggest a further evaluation of
463 maternal environmental effects is needed to better evaluate their role in the resilience of wild
464 populations (Shama 2015; Chirgwin *et al.* 2017). From the perspective of management, our results
465 caution against hoping for local adaptive responses and lend support to focusing conservation
466 efforts on maintaining habitat quality.

467

468 **ACKNOWLEDGMENTS**

469 This research was supported by Laboratoire d'Excellence CORAIL, Expenditure Review
470 Committee, Coral Reef Initiatives for the Pacific, the Global Environment Facility Coral Reef
471 Targeted Research Connectivity Working Group, National Science Foundation, the Australian
472 Research Council Centre of Excellence Coral Reef Studies, The Nature Conservancy, Total
473 Foundation, James Cook University, King Abdullah University of Science and Technology, and

474 Woods Hole Oceanographic Institution. Research visas were approved by the Papua New Guinea
475 (PNG) government and research protocols were endorsed by the Board of Mahonia Na Dari
476 Research and Conservation Centre, Kimbe, PNG.

477 We thank the large number of volunteers who assisted in the field and collected tissue samples.
478 Mahonia and FeBrina provided essential logistic support. We are grateful to the traditional owners
479 of the reefs near Kimbe Island for allowing us access to their reefs. We also thank Pierre de
480 Villemereuil, Jarrod Hadfield, Michael Morrissey, Caroline Thomson and Isabel Winney for useful
481 discussions, comments, and help with the method.

482 **AUTHORSHIP**

483 GPJ, SLRT, and SP designed the research program; OCS, BP, GRA, and MLB contributed new
484 reagents/analytic tools; OCS and BP analyzed data; OCS, BP et SP wrote the manuscript and all
485 authors contributed substantially to revise the paper.

486 **DATA ACCESSIBILITY STATEMENT**

487 All data from this study are available on the CRIOBE data portal (<http://www.criobe.pf>)

488 **REFERENCES**

- 489 Almany, G.R., Planes, S., Thorrold, S.R., Berumen, M.L., Bode, M. *et al.* (2017). Larval fish
490 dispersal in a coral-reef seascape. *Nat. Ecol. Evol.*, 1, 0148.
- 491 Aykanat, T., Johnston, S.E., Cotter, D., Cross, T.F., Poole, R. *et al.* (2014). Molecular pedigree
492 reconstruction and estimation of evolutionary parameters in a wild Atlantic salmon river
493 system with incomplete sampling: a power analysis. *BMC Evol. Biol.*, 14, 68.
- 494 Bak, R.P., Nieuwland, G. & Meesters, E.H. (2005). Coral reef crisis in deep and shallow reefs: 30
495 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs*, 24, 475-479.
- 496 Bernardo J. (1996). Maternal effects in animal ecology. *Amer. Zool.* 36:83-105.
- 497 Berumen, M.L, Walsh, H.L., Raventos, N., Jones, G.P., Starczak, V. *et al.* (2010). Otolith
498 geochemistry does not reflect dispersal history of clownfish larvae. *Coral Reefs*, 29, 883-891.

- 499 Bonin, M.C., Harrison, H.B., Williamson, D.H., Frisch, A.J., Saenz Agudelo, P. *et al.* (2016) The
500 role of marine reserves in the replenishment of a locally-impacted population of anemonefish
501 on the Great Barrier Reef. *Mol. Ecol.* 25:487-499.
- 502 Bonin, M.C., Saenz-Agudelo, P., Harrison, H.B., Nanninga, G.B., van der Meer, M.H. *et al.* (2015).
503 Characterisation and cross-amplification of microsatellite markers in four species of
504 anemonefish (*Pomacentridae, Amphiprion spp.*). *Mar. Biodivers.*, 46, 135-150.
- 505 Burgess, S.C. & Marshall, D.J. (2014). Adaptive parental effects: the importance of estimating
506 environmental predictability and offspring fitness appropriately. *Oikos*, 123, 769-776.
- 507 Burt, A. (1995). The evolution of fitness. *Evolution*, 49, 1-8.
- 508 Cava, J.A., Perlut, N.G & Travis, S.E. (2019). Heritability and evolvability of morphological traits
509 of Savannah sparrows (*Passerculus sandwichensis*) breeding in agricultural grasslands. *PLoS*
510 *ONE* 14(1): e0220472.
- 511 Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. & Sheldon, B.C. (2008).
512 Adaptive phenotypic plasticity un response to climate change in a wild bird population.
513 *Science*, 320:800-803.
- 514 Chausson J, Srinivasan M & Jones GP (2018). Host anemone size as a determinant of social group
515 size and structure in the orange clownfish (*Amphiprion percula*). *Peer J* 6:e5841.
- 516 Chirgwin, E., Marshall, D.J., Sgrò, C.M. & Monro, K. (2017). The other 96%: Can neglected
517 sources of fitness variation offer new insights into adaptation to global change? *Evol. Appl.*,
518 10, 267-275.
- 519 Clutton-Brock, T.H. (1988). Reproductive success. In *Reproductive Success* (Clutton-Brock, T.H.
520 ed.), 472-486, University of Chicago Press.
- 521 Clutton-Brock, T. & Sheldon B.C. (2010). Individuals and populations: the role of long-term,
522 individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.*,
523 25, 562-573.

- 524 Coulson, T., Benton, T.G., Lundberg, P., Dall, S.R.X., Kendall, B.E. & Gaillard, J.M. (2006).
525 Estimating individual contributions to population growth: evolutionary fitness in ecological
526 time. *Proc. R. Soc. Lond. B. Biol. Sci.*, 273, 547-555.
- 527 Crow, J.F. (2002). Perspective: here's to Fisher, additive genetic variance, and the fundamental
528 theorem of natural selection. *Evolution*, 56, 1313-1316.
- 529 D'Aloia CC, Bogdanowicz, S.M., Francis, R.K., Majoris, J.E., Harrison, R.G. & P.M. Buston
530 (2015) Patterns, causes, and consequences of marine larval dispersal. *Proc. Natl. Acad. Sci.*
531 *USA*, 112(45):13940–13945.
- 532 Danchin, E., Charmantier, A., Champagne, F.A., Mesoudi, A., Pujol, B. & Blanchet, S. (2011).
533 Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nat.*
534 *Rev. Genet.*, 12, 475-486.
- 535 Danchin, E., Pocheville, A., Rey, O., Pujol, B. & Blanchet, S. (2019). Epigenetically facilitated
536 mutational assimilation: epigenetics as a hub within the Inclusive Evolutionary Synthesis.
537 *Biol. rev.*, 94, 259-282.
- 538 De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. (2012). The 27-year decline of coral
539 cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci. USA*, 109, 17995-17999.
- 540 de Villemereuil, P., Schielzeth, H., Nakagawa, S. & Morrissey, M. (2016). General methods for
541 evolutionary quantitative genetic inference from generalized mixed models. *Genetics*, 204,
542 1281-1294.
- 543 Dey, S., Proulx, S.R. & Teotonio, H. (2016). Adaptation to temporally fluctuating environments by
544 the evolution of maternal effects. *PLoS Biol*, 14, e1002388.
- 545 Donelson, J.M., Salinas, S., Munday, P.L. & Shama, L.N.S. (2017). Transgenerational plasticity
546 and climate change experiments: Where do we go from here? *Global Change Biol.* 24:13-34.
- 547 Dunn, D.F. (1981). The clownfish sea-anemones - *Stichodactylidae* (coelenterata, actiniaria) and
548 other sea-anemones symbiotic with pomacentrid fishes. *T. Am. Philo. Soc.*, 71, 3-113.

- 549 Dupont, P., Cohas, A., Allainé, D. & Pradel, R. (2017). Testing determinants of the annual
550 individual fitness: An overall mean mixture model for de-lifing data. *Methods Ecol. Evol.*,
551 doi: 10.1111/2041-210X.12908.
- 552 Facon, B., Pointier, J.-P., Jarne, P. Sarda, V. & David, P. (2008). High genetic variance in life-
553 history strategies within invasive populations by way of multiple introductions. *Curr. Biol.*,
554 18, 363-367.
- 555 Falconer, D.S. (1989). *Introduction to Quantitative Genetics*. Longman, New York.
- 556 Falconer, D.S. & Mackay, T.F.C. (1996). *Introduction to Quantitative Genetics*. Longman, New
557 York.
- 558 Fisher, R.A. (1930). *The genetical theory of natural selection*. Clarendon Press, Oxford, U.K.
- 559 Foerster, K., Coulson, T., Sheldon, B.C., Pemberton, J.M., Clutton-Brock, T.H. & Kruuk, L.E.B.
560 (2007). Sexually antagonistic genetic variation for fitness in red deer. *Nature*, 447, 1107-
561 U1109.
- 562 Frank, S.A. (1997). The Price equation, Fisher's fundamental theorem, kin selection, and causal
563 analysis. *Evolution*, 51, 1712-1729.
- 564 Fricke, H.W.Z. (1979), Mating system, resource defense and sex change in the anemonefish
565 *Amphiprion akallopisos*. *Tierpsychol.*, 50, 313-326.
- 566 Gelman, A., Hwang, J. & Vehtari, A. (2014) Understanding predictive information criteria for
567 Bayesian models. *Statistics and Computing*, 24, 997-1016.
- 568 Gerber, S., Chabrier, P., Kremer, A. (2003). FaMoz: A software for parentage analysis using
569 dominant, codominant and uniparentally inherited markers. *Mol. Ecol. Res.*, 3(3), 479-481.
- 570 Germain, R.M. & Gilbert, B. (2014). Hidden responses to environmental variation: maternal effects
571 reveal species niche dimensions. *Ecol. Lett.*, 17, 662-669.
- 572 Ghalambor , C.K., MacKay J.K., Carroll, S.P., *et al.* (2007). Adaptive versus non-adaptive
573 phenotypic plasticity and the potential for contemporary adaptation in new environments.
574 *Funct. Ecol.*, 21, 394-407.

- 575 Gustafsson, L. (1986). Lifetime reproductive success and heritability: Empirical support for Fisher's
576 fundamental theorem. *Am. Nat.*, 128: 761-764.
- 577 Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: The
578 MCMCglmm R Package. *J. Stat. Softw.*, 33, 1-22.
- 579 Hansen, T.F., Pélabon, C. & Houle, D. (2011) Heritability is not evolvability. *Evol. Biol.*, 38(3),
580 258.
- 581 Hendry, A.P., Schoen, D.J., Wolak, M.E. & Reid, J. (2018). The contemporary evolution of fitness.
582 *Ann. Rev. Ecol. Evol. Syst.*, 49, 457-476.
- 583 Hobbs, J.P.A., Frisch, A.J., Ford, B.M., Thums, M., Saenz-Agudelo, P., Furby, K.A. *et al.* (2013).
584 Taxonomic, spatial and temporal patterns of bleaching in anemones inhabited by
585 anemonefishes *Plos One*, 8, e70966.
- 586 Hoffmann, A.A. & J. Merilä (1999). Heritable variation and evolution under favourable and
587 unfavourable conditions. *Trends Ecol. Evol.*, 14(3), 96-101.
- 588 Houle, D. (1992). Comparing evolvability and variability of quantitative traits. *Genetics*, 130, 195-
589 204.
- 590 Jackson, J.B.C. (2010). The future of the oceans past. *Philos. Trans. R. Soc. Lon. B. Biol. Sci.*, 365,
591 3765-3778.
- 592 Jones, A. M., Gardner, S. & Sinclair, W. (2008). Losing “Nemo”: bleaching and collection appear
593 to reduce inshore populations of anemonefishes. *J. Fish Biol.* 73, 753–761.
- 594 Jones, G.P. (2015) Mission impossible: unlocking the secrets of dispersal in coral reef fishes. In:
595 “Ecology of Fishes on Coral Reefs: The Functioning of an Ecosystem in a Changing World”
596 (Mora C., ed). Pp 16-27. Cambridge University Press.
- 597 Jones, G.P., Milicich, M.J., Emslie, M.J., Lunow, C. (1999) Self-recruitment in a coral reef fish
598 population. *Nature* 402, 802-804.

- 599 Jones, G.P., Almany, G.R., Russ, G.R., Sale, P.F., Steneck, R.S. *et al.* (2009) Larval retention and
600 connectivity among populations of corals and reef fishes: history, advances and challenges.
601 *Coral Reefs* 28, 307-325.
- 602 Jones, G.P., McCormick, M.I., Srinivasan & M., Eagle, J.V. (2004) Coral decline threatens fish
603 biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA*, 101, 8251-8253.
- 604 Jones, G.P., Planes, S., Thorrold, S.R., (2005) Coral reef fish larvae settle close to home. *Curr. Biol.*
605 15, 1314-1318.
- 606 Keller, L.F., Jeffery, K.J., Arcese, P., Beaumont, M.A., Hochachka, W.M., Smith, J.N. *et al.* (2001).
607 Immigration and the ephemerality of a natural population bottleneck: evidence from
608 molecular markers. *Proc. R. Soc. Lond. B. Biol. Sci.*, 268, 1387-1394.
- 609 Kruuk, L.E.B., Clutton-Brock, T.H., Slate, J., Pemberton, J.M., Brotherstone, S. & Guinness, F.E.
610 (2000). Heritability of fitness in a wild mammal population. *Proc. Natl. Acad. Sci. USA*, 97,
611 698-703.
- 612 Kruuk, L.E.B., Merilä, J. & Sheldon, B.C. (2003). When environmental variation short-circuits
613 natural selection. *Trends Ecol. Evol.*, 18, 207-209.
- 614 Kruuk, L.E.B. (2004). Estimating genetic parameters in natural populations using the 'animal
615 model'. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 359, 873-890.
- 616 Kruuk, L.E.B. & Hadfield, J.D. (2007). How to separate genetic and environmental causes of
617 similarity between relatives. *J. Evol. Biol.*, 20, 1890-1903.
- 618 Kruuk, L.E.B. & Hill, W.G. (2008). Introduction. Evolutionary dynamics of wild populations: the
619 use of long-term pedigree data. *Proc. R. Soc. Lond. B. Biol. Sci.*, 275, 593-596.
- 620 Lavergne, S. & Molofsky, J. (2007). Increased genetic variation and evolutionary potential drive the
621 success of an invasive grass. *Proc. Natl. Acad. Sci. USA*, 104, 3883-3888.
- 622 Ledón-Rettig, C.C., Pfennig, D.W., Chunco, A.J. *et al.* (2014). Cryptic genetic variation in natural
623 populations: a predictive framework. *Integr. Comp. Biol.*, 54, 783-793.

- 624 Le Port, A., Montgomery, J.C., Smith, A.N.H., Croucher, A.E., McLeod, I.M., Lavery, S.D.(2017).
625 Temperate marine protected area provides recruitment subsidies to local fisheries. *Proc. R.*
626 *Soc. B.* 284: 20171300.
- 627 Lessard, S. (1997). Fisher's fundamental theorem of natural selection revisited. *Theor. Popul. Biol.*,
628 52, 119-136.
- 629 Levis, N.A. & Pfenning, D.W. (2016). Evaluating 'Plasticity-First' Evolution in Nature: Key
630 Criteria and Empirical Approaches. *Trends Ecol. Evol.*, 31, 563-574.
- 631 Lush, J.L. (2008). *Animal Breeding Plans*. Orchard Press, 444 pp.
- 632 McCleery, R.H., Pettifor, R.A., Armbruster, P., Meyer, K., Sheldon, B.C. & Perrins, C.M. (2004).
633 Components of variance underlying fitness in a natural population of the great tit *Parus*
634 *major*. *Amer. Nat.*, 164, 62-72.
- 635 McFarlane, S.E., Gorrell, J.C., Coltman, D.W., Humphries, M.M., Boutin, S. & McAdam, A.G.
636 (2014). Very low levels of direct additive genetic variance in fitness and fitness components
637 in a red squirrel population. *Ecol. and Evol.*, 4, 1729-1738.
- 638 Meredith, M. & Kruschke, J. (2016) HDInterval: highest (posterior) density intervals. R package
639 version 0.1.3. <https://CRAN.R-project.org/package=HDInterval>.
- 640 Merilä, J. & Sheldon, B.C. (2000) Lifetime reproductive success and heritability in nature. *Amer.*
641 *Nat.*, 155, 301-310.
- 642 Mobley, K.B., Granroth-Wilding, H., Ellmen, M., Vähä, J-P., Aykanat, T. *et al.* (2019). Home
643 ground advantage: Local Atlantic salmon have higher reproductive fitness than dispersers in
644 the wild. *Science Adv.* 5 : eaav1112.
- 645 Morrissey, M.B., de Villemereuil, P., Doligez, B. & Gimenez, O. (2014). Bayesian approaches to
646 the quantitative genetic analysis of natural populations. In: *Quantitative genetics in the wild*,
647 228-253.

- 648 Morrissey, M.B. & Wilson, A.J. (2010). Pedantics: an r package for pedigree-based genetic
649 simulation and pedigree manipulation, characterization and viewing. *Mol. Ecol. R.*, 10, 711-
650 719.
- 651 Mousseau, T.A. & Roff, D.A. (1987). Natural selection and the heritability of fitness components.
652 *Heredity*, 59: 181-197.
- 653 Mousseau, T.A. & Fox, C.W. (1998). The adaptative significance of maternal effects. *Trends Ecol.*
654 *Evol.*, 13, 403-407.
- 655 Munday, P.L., Donelson, J.M. & Domingos, J.A. (2017). Potential for adaptation to climate change
656 in a coral reef fish. *Glob. Change Biol.*, 23, 307-317.
- 657 Munday, P.L., Warner, R.R., Monro, K., Pandolfi, J.M. & Marshall, D.J. (2013) Predicting
658 evolutionary responses to climate change in the sea. *Ecol. Lett.*, 16, 1488–1500.
- 659 Nedosyko, A.M., Young, J.E., Edwards, J.W. & da Silva, K.B. (2014) Searching for a toxic key to
660 unlock the mystery of anemonefish and anemone symbiosis. *Plos One* 9, 970–976.
- 661 Paddack, M.J., Reynolds, J.D., Aguilar, C., Appeldoorn, R.S., Beets, J., Burkett, E.W. *et al.* (2009)
662 Recent region-wide declines in Caribbean reef fish abundance. *Curr. Biol.* 19, 590-595.
- 663 Peakall, R. & P.E. Smouse (2012). GenAlex 6.5: Genetic analysis in Excel. Population genetic
664 software for teaching and research-an update. *Bioinformatics*, 28(19), 2537-2539.
- 665 Pemberton, J.M. (2008). Wild pedigrees: the way forward. *Proc. Roy. Soc. B.* 175, 613-621.
- 666 Pinsky, M.L., Saenz-Agudelo, P., Salles, O., Almany, G.R., Bode, M. *et al.* (2017). Marine
667 dispersal scales are congruent over evolutionary and ecological time. *Curr. Biol.*, 27, 149-154.
- 668 Planes, S., Thorrold, S.R. & Jones, G.P. (2009) Larval dispersal connects fish populations in a
669 network of marine protected areas. *Proc. Nat. Acad. Sci. USA*, 106, 5693–5697.
- 670 Postma, E. (2014). Four decades of estimating heritabilities in wild vertebrate populations:
671 Improved methods, more data, better estimates? in *Quantitative Genetics in the Wild*.
672 Charmantier, A., Garant, D., Kruuk, L.E.B. (2014) Oxford, Oxford University Press.

- 673 Pratchett, M.S., Thompson, C.A., Hoey, A.S., Cowman, P.F. & Wilson, S.K. (2018) Effects of coral
674 bleaching and coral loss on the structure and function of reef fish assemblages. p 265-293. In:
675 Coral Bleaching, Ecological Studies 233, van Oppen, M.J.H., Lough, J.M. (eds.), Springer
676 International Publishing AG, part of Springer Nature. doi.org/10.1007/978-3-319-75393-5_11
- 677 Price, T.D., Qvarnström, A. & Irwin, D.E. (2003). The role of phenotypic plasticity in driving
678 genetic evolution. *Proc. Biol. Sci.*, 270(1523), 1433-1440.
- 679 Price, T., & Schluter, D. (1991). On the low heritability of life-history traits. *Evolution* 45, 853–
680 861.
- 681 Pujol, B., Blanchet, S., Charmantier, A. *et al.* (2018). The missing response to selection in the wild.
682 *Trends Ecol. Evol.*, 33, 337-346.
- 683 Pujol, B., Obbard, D.J. & Pannell, J.R. (2010). Symptoms of population range expansion: lessons
684 from phenotypic and genetic differentiation in hexaploid *Mercurialis annua*. *Plant Ecol. Div.*,
685 3, 103-108.
- 686 Räsänen, K. & Kruuk, L.E.B. (2007). Maternal effects and evolution at ecological time-scales.
687 *Funct. Ecol.*, 21, 408-421.
- 688 R.Core.Team (2018). R: A language and environment for statistical computing. R Foundation for
689 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org/)
690 [project.org/](http://www.R-project.org/).
- 691 Reed, T.E., Prodöhl, P., Bradley, C., Gilbey, J., McGinnity, P., Primmer, C.R. & Bacon, P.J.
692 (2019). Heritability estimation via molecular pedigree reconstruction in a wild fish population
693 reveals substantial evolutionary potential for sea age at maturity, but not size within age
694 classes. *Can. J. fish. Aquat. Sci.*, 76, 790-805.
- 695 Roff, D.A. (2002). Life history evolution. 1st ed. Sinauer Associates, Inc., Sunderland, Mass.
- 696 Saenz-Agudelo, P., Jones, G.P., Thorrold, S.R. & Planes, S. (2011). Detrimental effects of host
697 anemone bleaching on anemonefish populations. *Coral Reefs*, 30, 497-506.

- 698 Salles, O.C., Maynard, J.A., Joannides, M., Barbu, C.M., Saenz-Agudelo, P., Almany, G.R. *et al.*
699 (2015). Coral reef fish populations can persist without immigration. *Proc. R. Soc. Lond. B.*
700 *Biol. Sci.*, 282, 20151311.
- 701 Salles, O.C., Pujol, B., Maynard, J.A., Almany, G.R., Berumen, M.L., Jones, G.P. *et al.* (2016a).
702 First genealogy for a wild marine fish population reveals multi-generational philopatry. *Proc.*
703 *Natl. Acad. Sci. USA*, 46, 13245-13250.
- 704 Salles, O.C., Saenz-Agudelo, P., Almany, G., Berumen, M.L., Thorrold, S.R., Jones, G.P. *et al.*
705 (2016b). Genetic tools link long-term demographic and life-history traits of clownfish to their
706 anemone hosts. *Coral Reefs*, 35, 1127-1138.
- 707 Schroeder, J., Burke, T., Mannarelli, M.E., Dawson, D.A. & Nakagawa, S. (2012). Maternal effects
708 and heritability of annual productivity. *J. Evol. Biol.*, 25, 149-156.
- 709 Shama, L.N. (2015). Bet hedging in a warming ocean: predictability of maternal environment
710 shapes offspring size variation in marine sticklebacks. *Glob. Chang. Biol.*, 21, 4387-4400.
- 711 Sheldon, B.C. (2000). Lifetime reproductive success and heritability in nature. *Amer. Nat.*, 155,
712 301-310.
- 713 Spiegelhalter, D.J., Best, N.G., Carlin, B.P., & van der Linde, A. (2014). The deviance information
714 criterion: 12 years on. *J. R. Stat. Soc. B.*, 76, 485-493.
- 715 Swearer, S.E., Caselle, J.E., Lea, D.W. & Warner, R.R. (1999) Larval retention and recruitment in
716 an island population of a coral-reef fish. *Nature* 402, 799-802.
- 717 Swearer, S.E., Shima, J.S., Hellberg, M.E., Thorrold, S.R., Jones, G.P., Robertson, D.R. *et al.*
718 (2002). Evidence of self-recruitment in demersal marine populations. *B. Mar. Sci.*, 70, 251-
719 271.
- 720 van Hooijdonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadi, G., Raymundo, L. *et al.* (2016).
721 Local-scale projections of coral reef futures and implications of the Paris Agreement. *Sci.*
722 *Rep.*, 6, 39666.

- 723 Wagner, G.P. & Altenberg L. (1996). Complex adaptations and the evolution of evolvability.
724 *Evolution*, 50, 967-976.
- 725 Wheelwright, N.T., Keller, L.K. & Postma, E. (2014). The effect of trait type and strength of
726 selection on heritability and evolvability in an island bird population. *Evolution* 68-11, 3325-
727 3336.
- 728 Wilson, A.J., Réale, D., Clements, M.N., Morrissey, M.M., Postma, E., Walling, C.A. *et al.* (2010).
729 An ecologist's guide to the animal model. *J. Anim. Ecol.*, 79, 13-26.
- 730 Wilson, S.K., Graham, N.A., Pratchett, M.S., Jones, G.P. & Polunin, N.V. (2006). Multiple
731 disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Glob.*
732 *Chang. Biol.*, 12, 2220-2234.
- 733 Wolak, M.E., Arcese, P., Keller, L.F., Nietlisbach, P. & Reid, J.M. (2018). Sex-specific additive
734 genetic variances and correlations for fitness in a song sparrow (*Melospiza melodia*)
735 population subject to natural immigration and inbreeding. *Evolution* 72-10, 2057-2075.

736 **SUPPORTING INFORMATION**

737 Additional Supporting Information may be found in the online version of this article.

738 The Additional Supporting Information file contains:

- 739 • **Table S1.** Previous estimates of fitness heritability and maternal effects on fitness in 15 wild
740 populations.
- 741 • **Figure S1.** Pedigree data and power analysis for the Kimbe Island orange clownfish
742 population.
- 743 • **Supplementary methods, results and discussion** on De-lifing measures.

744

1 **Supporting Information**

2 **Habitat variation of wild clownfish population shapes self-recruitment more**
3 **than genetic effects**

4 Océane C. Salles, Glenn R. Almany, Michael L. Berumen, Geoffrey P. Jones, Pablo Saenz-
5 Agudelo, Maya Srinivasan, Simon R. Thorrold, Benoit Pujol*, and Serge Planes*

6
7 **Both authors share senior authorship of this article*

8 **Correspondence:** Océane Salles and Benoit Pujol; Emails: oceane.salles@gmail.com and
9 benoit.pujol@univ-perp.fr

10 **This file includes:**

11 **Table S1.** Previous estimates of fitness heritability and maternal effects on fitness in wild
12 populations.

13 **Fig. S1.** Pedigree data and power analysis for the Kimbe Island orange clownfish population.

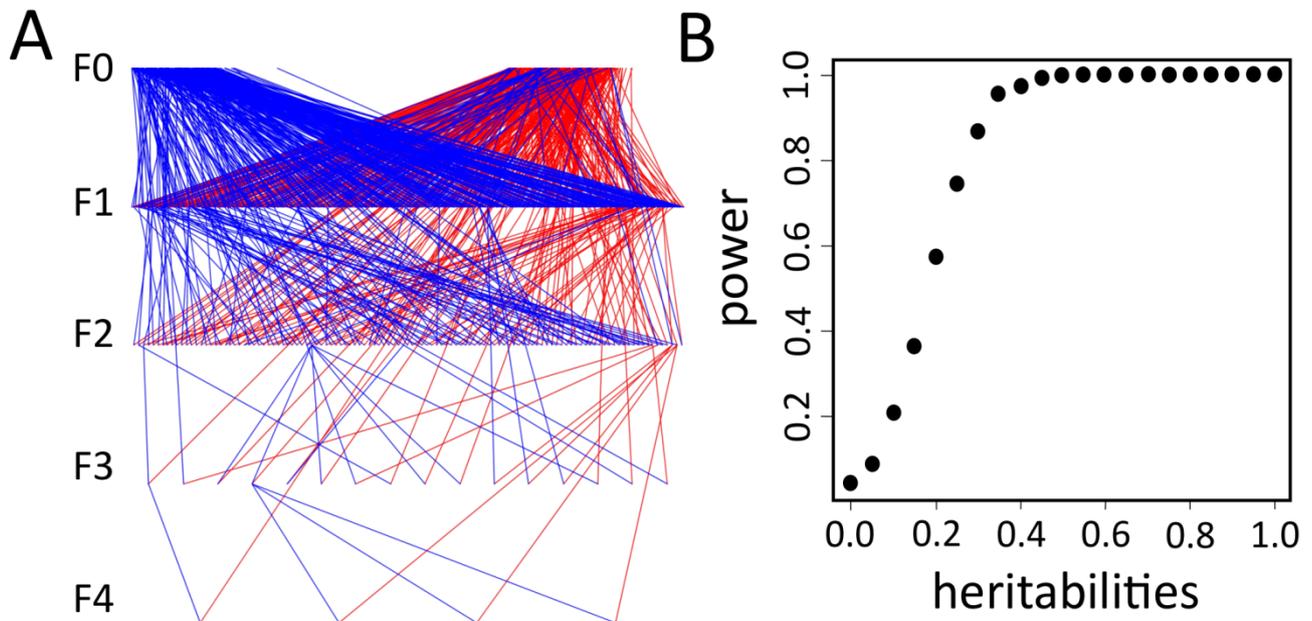
14 **Table S1. Previous estimates of fitness heritability and maternal effects on fitness in wild populations.** Different fitness measures are denoted as
 15 lifetime reproductive success (LRS), De-lifing or relative RS (LRS/mean of LRS in the population). ♀ corresponds to female, ♂ corresponds to male
 16 and ♀♂ corresponds to female and male confounded. NA indicates that maternal effects were not estimated or dropped from the quantitative genetic
 17 models.

Study organism	Location	Years of monitoring	Heritability estimate ± SE or 95%SI	Maternal effects estimate	Fitness measure	Reference
Collared flycatcher	Gotland Is.	1980 to 1984	♀ 0.01 ± 0.16 ♂ 0.01 ± 0.13	NA NA	LRS	(Gustafsson 1986)
Red deer	Isle of Rum	1971 to 1999	♀ 0.00 ± 0.05 ♂ 0.02 ± 0.06	0.16 ± 0.041 NA	LRS	(Kruuk <i>et al.</i> 2000)
		1971 to 2005	♀ 0.21 ± 0.06 ♂ 0.07 ± 0.06	0.0021 0.0045	De-lifing	(Foerster <i>et al.</i> 2007)
Collared flycatcher	Gotland Is.	1980 to 1997	♀ 0.21 ± 0.06 ♂ 0.07 ± 0.06	NA NA	LRS	(Merila & Sheldon 2000)
Bighorn sheep	Ram Mountain	1973 to 1998	♀ 0.66 ± 0.32	NA	LRS	(Réale & Festa-Bianchet 2000)
	Sheep River	1981 to 1998	♀ 0.19 ± (0.50)	NA	LRS	
Cheetahs	Serengeti park	1970 to 1994	♀ 0.88 ± ?	NA	LRS	(Kelly 2001)
Great tit	Wytham Wood	1960 to 1998	♀ 0.00 ± 0.04 ♂ 0.02 ± 0.04	NA NA	LRS	(McCleery <i>et al.</i> 2004)
Bighorn sheep	Ram Mountain	1971 to 2003	♀ 0.00 ± 0.00 ♂ 0.00 ± 0.00	NA NA	LRS	(Coltman <i>et al.</i> 2005)
Red billed gulls	Kaikoura	1958 to 2004	♀ 0.36 ± 0.29 ♂ 0.00 ± 0.00	NA NA	LRS	(Teplitsky <i>et al.</i> 2009)
Rhesus macaques	Cayo Is.	1959 to 1990	♀ 0.36 ± 0.081	NA	LRS	(Blomquist 2010)
House sparrow	Lundy Is.	2000 to 2011	♀ 0.09 (0.03 to 0.18)	0.33 (0.14 to 0.51)	De-lifing	(Schroeder <i>et al.</i> 2012)
Soay sheep	St Kilda	1985 to 2002	♀ 0.03 ± 0.01	NA	Relative RS	(Morrissey <i>et al.</i> 2012)
Red squirrels	Yukon	1987 to 2011	♀ 4.90x10 ⁻⁰⁴ (3.0x10 ⁻⁰⁸ to 0.07) ♂ 6.80 x10 ⁻⁰⁴ (8.5x10 ⁻¹¹ to 0.10) ♂ 4.90 x10 ⁻⁰⁴ (1.1x10 ⁻⁰³ to 0.39)	0.07 (0.02 to 0.14) 0.08 (0.01 to 0.14) 0.10 (0.10 to 0.37)	LRS	(McFarlane <i>et al.</i> 2014)
Savannah sparrow	Kent Is.	1987 to 2005	♀ 0.002 ± 0.036 ♂ 0.000 ± 0.036	NA NA	LRS LRS	(Wheelwright <i>et al.</i> 2014)
Brown anole lizard	Kidd Cay	2005 to 2008	♀ 1.40 (8.0x10 ⁻¹⁰ to 0.023)	NA	RS	(Calsbeek <i>et al.</i> 2015)
Song sparrow	Mandarte Island	1993-2015	♀ 0.5 ± 0.21	NA	LRS	(Wolak <i>et al.</i> 2018)

♂ 0.44 ± 0.74

NA

18 Blomquist, G.E. (2010). *Evol Ecol*, 24, 657-669; Calsbeek, R. *et al.* (2015). *J. Evol. Biol.*, 28, 1975-1985; Coltman, D.W. *et al.* (2005). *Evolution*, 59, 1372-1382; Foerster, K. *et al.* (2007). *Nature*, 447,
19 1107-U1109; Gustafsson, L. (1986). *Amer. Nat.*, 128, 761-764; Kelly, M.J. (2001). *Cons. Biol.*, 15, 137-147; Kruuk, L.E.B. *et al.* (2000). *Proc. Natl. Acad. Sci. USA*, 97, 698-703; McCleery, R.H. *et al.*
20 (2004). *Amer. Nat.*, 164, E62-E72; McFarlane, S.E. *et al.* (2014). *Ecol. and Evol.*, 4, 1729-1738; Merila, J. & Sheldon, B.C. (2000). *Amer Nat*, 155, 301-310; Morrissey, M.B. *et al.* (2012). *Evolution*,
21 66, 2399-2410; Réale, D. & Festa-Bianchet, M. (2000). *Heredity*, 85, 593-603. Schroeder, J. *et al.* (2012). *J. Evol. Biol.*, 25, 149-156; Teplitsky, C. *et al.* (2009). *Evolution*, 63, 716-726; Wheelwright,
22 N. T., (2014). *Evolution*, 68, 3325-3336. Wolak, M.E. *et al.* (2018). *Evolution*. doi.org/10.1111/evo.13575.



23

24 **Fig. S1. Pedigree data of the Kimbe Island orange clownfish population.** (A) Pedigree
 25 representation of the orange clownfish *Amphiprion percula* in Kimbe Island (n= 1735, excluding
 26 new-recruits). Each line connects a parent with one of its offspring (blue and red lines represent
 27 respectively paternal and maternal links). It is important to note that an individual can be father then
 28 mother. The generation is indicated on the left from first generation (F0, n=502) to fifth generation
 29 (F4). (B) Power analysis of the pedigree.