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Strong habitat and weak genetic effects shape the lifetime reproductive success in a wild clownfish population

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ECOLOGY LETTERS

Strong habitat and weak genetic effects shape the lifetime reproductive success in a wild clownfish population

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4 1 **Strong habitat and weak genetic effects shape the lifetime**
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7 2 **reproductive success in a wild clownfish population**
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4
5 22 MLB contributed new reagents/analytic tools; OCS and BP analyzed data; OCS, BP and SP wrote
6
7 23 the manuscript and all authors contributed substantially to revise the paper.
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11
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13
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3 45 **Summary:** The relative contributions of environmental, maternal and additive genetic factors to the
4
5 46 Lifetime reproductive success (LRS) determine whether species can adapt to rapid environmental
6
7 47 change. Yet to date, studies quantifying LRS across multiple generations in marine species in the wild
8
9 48 are non-existent. Here we used 10-year pedigrees resolved for a wild orange clownfish population
10
11 49 from Kimbe Island (PNG) and a quantitative genetic linear mixed model approach to quantify the
12
13 50 additive genetic, maternal and environmental contributions to variation in LRS for the self-recruiting
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15 51 portion of the population. We found that the habitat of the breeder, including the anemone species
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17 52 and geographic location, made the greatest contribution to LRS. There were low to negligible
18
19 53 contributions of genetic and maternal factors equating with low heritability and evolvability. Our
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21 54 findings imply that our population will be susceptible to short-term, small-scale changes in habitat
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23 55 structure and may have limited capacity to adapt to these changes.
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57 **Introduction**

58 Lifetime reproductive success (LRS) – the number of successful offspring an individual contributes
59 to the next generation – is a critical variable underpinning ecological and evolutionary responses to
60 the environment (Clutton-Brock 1988). Several factors including different environmental, parental,
61 and additive genetic effects can influence LRS (Hendry *et al.* 2018). If LRS is exclusively a
62 phenotypic response to the conditions experienced by individuals, populations will be severely
63 impacted by rapid environmental change and there is no prospect of adaptive microevolution.
64 Maternally transmitted responses to environmental conditions can mediate the effect of those changes
65 on the next generation (Mousseau & Fox 1998). However, it is the additive genetic variation in LRS
66 that determines the rate of adaptation of a population to the environmental demand (Fisher 1930). To
67 date, few studies have distinguished these relative contributions to LRS over multiple generations in
68 wild populations (Hendry *et al.* 2018). This situation is changing as long-term, individual-based
69 ecological studies with multi-generational pedigrees provide the necessary longitudinal information
70 to quantify the different components of LRS (Pemberton 2008). Such studies are imperative as we
71 seek to understand the ability of species to withstand or adapt to accelerating climate change (Munday
72 *et al.* 2017).

73
74 Intergenerational responses to selection are a product of the interplay between evolutionary and
75 ecological mechanisms that ultimately shape inherited variation in fitness-related traits.
76 Environmentally driven mechanisms (*e.g.*, phenotypic plasticity, genetic assimilation) can facilitate
77 (Ghalambor *et al.* 2007; Danchin *et al.* 2019) or constrain the microevolutionary response to selection
78 (Pujol *et al.* 2018). However, in the absence of genetic variation for LRS, these mechanisms will
79 likely have little effect on a negligible rate of adaptive evolution. In quantifying additive genetic
80 variation, it is important to distinguish between *heritability* and *evolvability* (Wheelwright *et al.*
81 2014). Narrow sense heritability is widely used as a measurement of the population potential to
82 respond to selection (Mousseau & Roff 1987). It is the additive genetic variance standardized by the

1
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3 83 total phenotypic variance. Low heritability values can either reflect low additive genetic variance or
4
5 84 large environmental, or residual effects. Evolvability is the mean-standardized additive genetic
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8 85 variance (Houle 1992). Environmental or maternal effects do not affect it, which makes it a more
9
10 86 appropriate metric in the comparison of evolutionary potential between traits, populations and
11
12 87 species. When measured for a surrogate of fitness like LRS, it estimates the expected proportional
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14 88 change per generation in population mean fitness given a unit strength of selection. Heritability for
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16 89 LRS reveals whether its additive genetic variance represents a non-trivial proportion of its total
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18 90 variance in the actual environmental context of a given wild population. Together, evolvability and
19
20 91 heritability inform us about how much environmental change a wild population can withstand on the
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22 92 basis of its evolutionary potential.
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28 94 The few ($n=15$) long-term, individual-based studies that have quantified additive genetic variation,
29
30 95 heritability and evolvability of LRS in wild populations have all focused on terrestrial species (Postma
31
32 96 2014; Hendry *et al.* 2018; Table S1). They have largely confirmed low additive genetic variation and
33
34 97 evolvability (~ 0.08) for LRS, which nevertheless reflects some evolutionary potential (Hendry *et al.*
35
36 98 2018). Whether marine fish and terrestrial species reveal the same patterns remains unknown to date.
37
38 99 Until recently, quantifying LRS in marine organisms with a pelagic larval stage has been considered
39
40 100 impossible because of the difficulties in following the fate of offspring from one generation to the
41
42 101 next. However, there is increasing evidence of some degree of natal philopatry or self-recruitment in
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44 102 local marine populations (Jones *et al.* 2009). Genetic parentage analysis is making it possible to assign
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46 103 a significant proportion of offspring to their parents (Planes *et al.* 2009) and construct
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48 104 multigenerational pedigrees for the offspring that return to their natal population (Salles *et al.* 2016).
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50 105 As in most quantitative genetic studies of LRS, it is impossible to measure the recruitment of marine
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52 106 fish dispersing juveniles at other locations. The regional component of LRS, which would inform us
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54 107 on fitness variation beyond the local scale is impossible to obtain. Measuring the local component of
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3 108 LRS in marine fish is nevertheless an opportunity as in any other species because it estimates the
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5 109 relative contribution of local fish to the population self-recruitment and replenishment.
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10 111 For coral reef fishes, quantifying environmental and genetic components of LRS and assessing its
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12 112 evolvability in wild populations is of great contemporary importance. Between 30 to 50% of the
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14 113 world's coral reefs have been lost and those remaining are considered highly vulnerable (van
15
16 114 Hooidonk *et al.* 2016). The rapid loss of suitable habitat is widely acknowledged to be contributing
17
18 115 to a decline in reef fish populations and biodiversity (Jones *et al.* 2004). The potential for adaptation
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20 116 of reef fish is uncertain and near future environmental conditions predicted under climate change
21
22 117 should have a dramatic effect on their reproductive success (Munday *et al.* 2013). To date,
23
24 118 environmental, maternal and additive genetic contributions to LRS in wild coral reef fish populations
25
26 119 have not been assessed. However, recent work establishing high levels of natal philopatry in some
27
28 120 coral reef fishes (Jones *et al.* 2005) that allowed for resolving their pedigree across multiple
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30 121 generations (Salles *et al.* 2016) opened the way for quantifying the local component of LRS for the
31
32 122 first time in coral reef fishes.
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40 124 Here, we focus on the entire local population of the orange clownfish *Amphiprion percula* at Kimbe
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42 125 Island, Papua New Guinea where each year ~half the juveniles successfully recruiting are progeny of
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44 126 local breeding pairs (Salles *et al.* 2016). We use multi-generational pedigrees of up to 5 generations
45
46 127 obtained from biennial DNA sampling over 10 years (Salles *et al.* 2016) and apply a quantitative
47
48 128 genetic linear mixed model approach (Kruuk & Hill 2008) to quantify the additive genetic, maternal
49
50 129 and environmental components of variation in LRS for the self-recruiting portion of the population.
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52 130 Habitat effects were quantified by examining this local LRS for individuals resident in two different
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54 131 anemone species and from different geographic locations around the island. By integrating habitat
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56 132 data with the pedigree information in a quantitative genetic generalized linear mixed model, we were
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58 133 able to assess the relative contribution of additive genetic, maternal and habitat effects to local LRS.
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3 134 We also calculated the evolvability and heritability of local LRS to evaluate its evolutionary potential
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5 135 to respond to selection at the scale of the Kimbe island population.
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10 137 **Material and methods**

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12 138 *Study population and data collection*

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14 139 A natural population of orange clownfish (*A. percula*) living in the reef surrounding Kimbe Island
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16 140 (Fig. 1a; 5°12'22.56" S, 150°22'35.58" E), West New Britain Province of Papua New Guinea, was
17
18 141 surveyed every second year from 2003 to 2013. Here, *A. percula* lives in a mutualistic association
19
20 142 with one of two host sea anemone species, *Heteractis magnifica* (Fig. 1b) and *Stichodactyla gigantea*
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22 143 (Fig. 1c). We geographically located and tagged a total of 310 anemones (176 *H. magnifica* and 134
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24 144 *S. gigantea*) that were occupied by *A. percula* on the entire reef surrounding the island.
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30 146 These two anemone species are remarkably different in terms of the micro-habitat they provide,
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32 147 including a wide range of shapes, sizes, depth distributions and surrounding substrata (Dunn 1981).
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34 148 Although we did not directly measure these variables (other than depth), the combination of host
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36 149 anemone species (*H. magnifica* or *S. gigantea*) with one of the three geographical areas covering the
37
38 150 entire reef around the island (northern, western or eastern areas, Figure 1a) where it is located
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40 151 describes a 'habitat' variable for each fish that encompasses a suite of biotic and abiotic
41
42 152 environmental conditions. These geographical areas correspond to the different coasts of the island
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44 153 that reflect possible environmental effects of the geographic location. In total, the combination of the
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46 154 two host anemone species with the three geographical areas allowed us to describe six different
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48 155 habitats.
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56 157 Clownfish within one anemone live in group of typically three to five individuals in the Kimbe Island
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58 158 population. The size-based dominance hierarchy in *Amphiprion* allows us to determine the
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60 159 reproductive status of each individual (Fricke 1979). The female is the largest, the male is the second

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3 160 largest, and the non-breeders rank progressively lower in the hierarchy as they decrease in size. If the
4
5 161 single female adult of a group dies, then the male changes sex to female, and the largest non-breeder
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7 162 from the anemone becomes sexually mature as male. Reproduction occurs year round, with females
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9 163 laying several hundred eggs in a clutch near the pedal disk of the host anemone each lunar month.
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11 164 The eggs hatch after ~7 days of paternal care into larvae that spend ~10 days in the pelagic
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13 165 environment (Berumen *et al.* 2010) before settling settling to an anemone, either at their natal location
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15 166 (Kimbe Island) or elsewhere (Planes *et al.* 2009).
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21 168 Divers captured fish by using hand nets. Individuals were measured *in situ* using calipers, fin-clipped
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23 169 (size > 35mm) or collected whole (size < 35mm) for genetic analysis and then released back on the
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25 170 same anemone. Small pieces of fin tissue were preserved in 95% ethanol in 2-mL vials. The biggest
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27 171 fish in each anemone was identified as the female, the second largest individual was assumed to be
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29 172 the male, and all other individuals were classified as non-breeders. We extracted DNA from all
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31 173 samples and genotyped them at 22 polymorphic microsatellite loci (Bonin *et al.* 2015). Then, we
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33 174 identified the individuals sampled multiple times over the years by using the Excel macro GenAlex
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35 175 v6.5 (Peakall & Smouse 2012) to compare multilocus genotypes from 2003, 2005, 2007, 2009, 2011
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37 176 and 2013. Individuals were in average sampled 2.88 ± 0.04 times (mean \pm SE) over the six surveys (1%
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39 177 of individuals persisted over the 10-yr period, Salles *et al.* 2016). The 2-yr sampling scheme
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41 178 precluded calculating a precise measurement of the age of individuals, in particular for fish sampled
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43 179 in 2003 during the first sampling period, which age was unknown. The total duration of this long term
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45 180 survey did not allow us to obtain many replicated measurements within individuals before and after
46
47 181 sex change (n=41 individuals). Estimating sex dependent additive genetic variance is precluded in
48
49 182 this case because some effects cannot be disentangled as the clownfish only changes sex in one
50
51 183 direction (from male to female). This change is always associated with a change of sexual partner and
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53 184 with an increase in female body size, which we expect to generate a confounding effect between a
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3 185 female condition and its genetic quality. We therefore did not consider sex in our model as a result of
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5 186 data and analytical limitations.
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10 188 *Pedigree used for quantitative genetic analysis*
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12 189 Pedigree reconstruction was conducted by assigning juvenile fish to parental pairs on the basis of
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14 190 their multilocus genotypes (Salles *et al.* 2016). We used the software FaMoz (Gerber *et al.* 2003).
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16 191 This approach is based on the calculation of LOD scores (Log of the odd-ratio comparison) for any
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18 192 potential parentage relationship. It determined critical thresholds to accept or reject assignments by
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20 193 simulating true and false parent-offspring pairs. Further details on parentage analyses and pedigree
21
22 194 reconstruction are given in Salles *et al.* (2016a). We kept assignments to known parental pairs, but
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24 195 rejected assignments to single adults. In the context of overlapping generations, we used the year of
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26 196 first sampling and the anemone of each parental couple as information to avoid possible false
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28 197 assignments. As a result, sibship links could not be confused with parental links. The same individual
29
30 198 can be related to its offspring with either a paternal or maternal link because of sex changes. We
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32 199 identified the mother and the father based on the size of the two parents on the year of first capture.
33
34 200 The original population pedigree includes 2927 clownfish over five generations including 121
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36 201 families, 987 paternal, 987 maternal, 1809 full-sib, 412 maternal half-sibs, 248 paternal half-sib, 135
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38 202 maternal grandmothers, 135 maternal grandfathers, 278 paternal grandmothers, 278 paternal
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40 203 grandfathers and 218 cousins (Salles *et al.* 2016). For this study, we excluded from the original
41
42 204 pedigree the 1192 individuals that were removed from the habitat at the juvenile stage (size < 35mm,
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44 205 10 to 458 days old). The final pedigree used for this study includes 1735 individuals from five
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46 206 generations (Fig. S1). We used the R package 'pedantics' (Morrissey & Wilson 2010) to assess the
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48 207 power of the resolved pedigree to detect significant quantitative genetic parameters (Fig. S1).
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58 209 *LRS: the individual contribution to self-recruitment*
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3 210 LRS, which when measured at the scale of the local population is also the contribution of an individual
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5 211 to self-recruitment, corresponds to the total number of offspring produced during its lifetime and
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7 212 recruiting into Kimbe Island (*e.g.*, the local breeder population). We used biennial measurements of
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9 213 their reproductive success (using field-data from 2003, 2005, 2007, 2009, 2011 and 2013) to compare
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11 214 LRS between individuals because some fish were still alive at the end of sampling and others might
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13 215 have already reproduced before the first sampling year. The LRS corresponds here to the total number
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15 216 of descendants produced on a biennial basis that successfully recruited into Kimbe Island population,
16
17 217 which provided us with repeated measures over the period of the survey from 2003 to 2013. In the
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19 218 Supplementary information we present results from an alternative approach based on the De-lifing
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21 219 method (DL). The calculation of DL takes into account the temporal variation of the population
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23 220 growth and estimates the contribution of every clownfish to biennial changes in population size
24
25 221 through both reproduction and survival (Coulson *et al.* 2016). Statistical problems with the use of
26
27 222 DL, potentially leading to precision issues, have been pointed out (Dupont *et al.* 2017). DL was used
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29 223 in two of the 15 studies where the genetic variation of fitness was quantified in wild populations
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31 224 (Table S1), which limits our ability to discuss its properties. We therefore also provided DL results
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33 225 in this study in the supplementary section.
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42 227 *Quantitative genetic generalized linear mixed model approach*

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44 228 Similarities between relatives living in contrasted micro-habitats allowed us to evaluate
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46 229 simultaneously the genetic and habitat components of LRS. Repeated ‘records’ on individuals made
47
48 230 it possible to estimate permanent environmental effects, and therefore account for intra-individual
49
50 231 and unmeasured environmental trait variation across time. Permanent environmental effects also
51
52 232 account for a part of non-additive genetic effects (Wilson *et al.* 2010). LRS variance was partitioned
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54 233 into six random effects: Additive genetic (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat
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56 234 (V_{RH}), Permanent Environment (V_{PE}) and Residual (V_R) variances by using the ‘animal model’
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58
59 235 quantitative genetic approach (Kruuk 2004). This Linear Mixed Model (LMM) approach uses
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3 236 pedigree information to extract the additive genetic component. This approach is more powerful than
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5 237 traditional analyses (e.g., parent–offspring regressions) because it takes into account every
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8 238 relationship link in a pedigree. Maternal variance was modeled using the mother’s identity as a
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10 239 random effect, allowing maternal effects to include both genetic and environmental maternal effects.
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12 240 Permanent environmental effects were modeled by including the identity of individuals as a random
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14 241 effect. The LRS variance is the sum of six variance components:

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

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19 243 Quantitative genetic models were computed as univariate GLMMs using the ‘MCMCglmm’ package
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21 244 (Hadfield 2010) in R version 3.5.1 (R.Core.Team 2018), with LRS as a Poisson response variable.
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24 245 Using this Bayesian framework facilitates parameter estimation for non-Gaussian traits. We used
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26 246 parameter expanded priors for all analyses ($V=1$, $nu=0.02$), which are often referred to as ‘non
27
28 247 informative’ priors although such denomination can be debated, as we wanted posterior estimates to
29
30 248 be determined from the data and not from the priors (Morrissey *et al.* 2014). We ran model MCMC
31
32 249 chains over 1,000,000 iterations with initial burning of 10,000 iterations and a thinning of 1,000
33
34 250 iterations. Historically, the Deviance Information Criterion (DIC) was often used to compare models
35
36 251 and assess the significance of the random variance components in this type of approach. However, it
37
38 252 is becoming less commonly used since it was recognized as an inappropriate tool for model
39
40 253 comparisons of the same type than quantitative genetic GLMM analyses (Spiegelhalter *et al.* 2014).
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42 254 Effects of variance components were considered statistically supported if their posterior distributions
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44 255 did not overlap zero (Wilson *et al.* 2010).
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51 257 *Variance Components*

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53 258 Variance components were estimated as the mode of the posterior distributions established on the
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55 259 MCMC sample and we reported lower and upper limits of the 95% credible intervals. For the six
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57 260 variance components, we calculated their relative contribution to the sum of all variance components,
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59 261 thereby expressing their effects as percentages of the total phenotypic variance (V_{LRS}). As a result,

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3 262 we obtained standard narrow sense heritability estimates for LRS (h^2) by applying the basic formula
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5 263 ($h^2 = V_A / V_P$), and similarly maternal effects by estimating the proportion of total phenotypic variance
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7 264 explained by the maternal variance ($m^2 = V_M / V_P$). Evolvability (I_A) of LRS is the additive genetic
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9 265 variance divided by the squared mean of the LRS (Houle 1992). Analyses assumed a Poisson
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11 266 distribution and provided parameter estimates on a statistically convenient latent scale for non-
12
13 267 Gaussian traits. We therefore back-transformed these estimates onto the observed data scale to
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15 268 improve our inferences by using the 'QGImm' package (de Villemereuil *et al.* 2016). We used the
16
17 269 function 'QGparams' to estimate additive components such as V_A and h^2 , and 'QGicc' to estimate
18
19 270 broader sense components such as V_M and m^2 , V_{NH} , V_{RH} , V_{PE} and V_R . Although parameter estimates
20
21 271 transformed back on the data-scale are expected to be upward biased, their ratio is reliable, and hence
22
23 272 the estimators derived from their relative proportions such as h^2 . It is necessary to point out two
24
25 273 specific aspects of this back transformation on the observed data scale. First, V_R is estimated on the
26
27 274 basis of the additive over-dispersion term in the nonlinear model and its value cannot be interpreted
28
29 275 similarly to the usual residual variance term estimated by classical quantitative genetic linear mixed
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31 276 models. Second, the sum of the variance components estimated on the data scale are not additive and
32
33 277 therefore not expected to sum up to the value of the phenotypic variance calculated directly on the
34
35 278 raw data. For the sake of clarity and comparison, we present the results on the latent scale and the
36
37 279 observed data scale. We calculated the 95% credibility intervals from the posterior distributions of
38
39 280 observed parameters for all the variance components and other estimates expressed on their basis by
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41 281 using the 'HDInterval' package (Meredith & Kruschke 2016).
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283 **Results**

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

285 Biennial estimates of the Lifetime Reproductive Success (LRS) measured inside the area of the
286 Kimbe island population ranged from 0 to 13, with a phenotypic variance $V_{LRS}=1.31$ and an average
287 value of 0.54 ± 0.05 (mean \pm SE) offspring per individual for a two-year period. Because clownfish live

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3 288 in strong association with their anemone, we were able to identify and geo-locate the precise position
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5 289 and habitat where breeders contributed more to the local replenishment of the population (Fig. 1a).
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8 290 Breeders that produced more self-recruiting offspring lived in Kimbe Island's eastern area and mostly
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10 291 in *S. gigantea* anemones. Our analysis also revealed fish that did not contribute at all to the local
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12 292 replenishment of the population over the 10-year monitoring period. These fish represented 25% of
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14 293 the pairs of local breeders and were located in 48 *H. magnifica* and 30 *S. gigantea* of the 310 anemones
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16 294 monitored in both deep and shallow waters (Fig. 1a).
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21 296 Quantitative genetic generalized linear mixed models on the latent and the observed data scale gave
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23 297 very close results. Our results on the scale of observed data showed that Natal Habitat and Resident
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25 298 Habitat explained respectively 19.1% and 5.7% of the variance in local LRS, furthermore, residual
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27 299 and permanent environment explained respectively 41.0% and 31.0%, whereas additive genetic
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29 300 effects and maternal effects were very weak and explained 1.3% and 1.9% respectively (Fig. 2a,
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31 301 variances on observed data-scale). Similar results were obtained for DL (see Supplementary
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33 302 Information for more details).
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39 304 *Low evolvability and low heritability for LRS*

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41 305 The modes of the posterior distributions estimating the additive genetic variance for LRS, expressed
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43 306 on the latent and observed data-scales, were extremely small (Table 1). On the observed data-scale,
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45 307 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
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47 308 pedigree (Fig. S1). Our model nevertheless placed fairly restricted bands on the 95% credible
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49 309 intervals (Table 1). Credible intervals did not overlap the zero but were close. The extent to which
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51 310 these very low values of genetic estimates are not null must therefore be considered with caution.
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54 311 LRS evolvability estimated on the observed data-scale, which evaluated the micro-evolutionary
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56 312 change of the number of self-recruiting offspring that can be reached by the population, was equal to
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59 313 0.103 ($CI_{95\%}$ 1.661×10^{-3} to 0.511). In other words, 0.103 additional juveniles were added to the
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3 314 average number of juveniles originating and recruiting in the population per generation. The
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5 315 heritability estimate expressed on the observed data-scale was $h^2=0.013$ (CI_{95%} 4.951×10^{-5} to
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7 316 1.227×10^{-2}) for LRS (Table 1). We can therefore estimate the maximum response (R) to selection (S),
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9 317 expected in theory, in the presence of strong selection pressures acting on the Kimbe Island orange
10 318 clownfish population by using the Breeder's equation $R=h^2\times S$ (Lush 2008). The low to negligible
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12 319 value of the LRS heritability means that the maximum genetic change of the population average LRS
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14 320 would never exceed ~ 0.020 offspring per generation. Similar results were obtained for DL (see
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16 321 Supplementary Information for more details).
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23 323 *Weak maternal effects for LRS*

24 324 Our analysis detected maternal variance for the LRS but it was also extremely small to the extent that
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26 325 it might be considered as null (Table 1): $V_M=0.019$ (CI_{95%} 2.966×10^{-5} to 2.044×10^{-2}). It made very
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28 326 little contribution to the total variance in LRS ($m^2=1.9\%$, expressed on observed data-scale, Fig. 2).
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30 327 The habitat occupied by the mother (Natal Habitat) had a stronger effect on LRS than the mother
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32 328 herself. The relative contribution of individuals to the population replenishment was indeed
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34 329 influenced by the Natal Habitat to an extent of 19.1% for LRS. Similar results were obtained for DL
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36 330 (see Supplementary Information for more details).
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44 332 **Discussion**

45 333 *Strong habitat and weak genetic effects on LRS*

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47 334 Our study revealed that biennial LRS in the Kimbe Island orange clownfish population quantified
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49 335 over five generations was largely explained by ecological factors. Host anemone species, depth and
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51 336 geographical location explained $\sim 25\%$, and permanent environmental effects $\sim 30\%$ of its variation,
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53 337 with only weak maternal (1.9%) and additive genetic effects (1.3%). Intrinsic biological
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55 338 characteristics of anemone species (*e.g.*, size, shape and toxicity) affecting the life-history traits of
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57 339 their resident clownfish might explain strong habitat effects (Chausson *et al.* 2018). In addition, the
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3 340 higher toxicity of *S. gigantea* (Nedosyko *et al.* 2014) might provide better protection against predators
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5 341 of eggs attached to the host anemone, but this hypothesis remains to be tested. The geographical
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7 342 location also appears to be important. Most successful individuals were close to the land in shallow
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9 343 water on *S. gigantea* and in deeper lagoons for *H. magnifica*, which might promote greater local
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11 344 retention of larvae. Mechanisms responsible for geographical differences in LRS around Kimbe
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13 345 Island remain unknown (Berumen *et al.* 2010). Some breeders likely have a different reproductive
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15 346 success beyond the sampled population, through dispersers rather than self-recruiters. Inside the
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17 347 Kimbe island clownfish population, weak genetic effects on LRS indicate a low to negligible rate of
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19 348 adaptive evolution in progress and raise concern about the ability of this population to adapt to rapid
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21 349 climate change.
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28 351 *Susceptibility to habitat change*

30 352 Habitat largely drove LRS variation. Individuals that happen to settle on particular anemones and
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32 353 places do well. The dependence on habitat quality of LRS inside the Kimbe island population suggests
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34 354 this species will be extremely susceptible to habitat degradation over ecological time scales.
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36 355 Detrimental direct and indirect anthropogenic impacts on reef anemones habitats are already affecting
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38 356 numerous clownfish species (Saenz-Agudelo *et al.* 2011). *S. gigantea* anemones located in shallow
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40 357 waters are likely to be disproportionately more impacted by increasing water temperatures and
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42 358 irradiance (Hobbs *et al.* 2013). If these habitats are differentially impacted, this will affect clownfish
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44 359 contributions to the local replenishment of the population and compromise population persistence.
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51 361 *Low to negligible evolutionary potential*

53 362 Our findings provide the first empirical support for a wild marine population to Fisher's fundamental
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55 363 theorem of selection that additive genetic variance in fitness is depleted under selection and tends
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57 364 towards zero in a population reaching evolutionary equilibrium (Gustafsson 1986). Although normal
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59 365 and expected, low heritability and evolvability in LRS is concerning giving the increasing rate of
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3 366 environmental change. The low to negligible scope for adaptive evolution (estimated by evolvability)
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5 367 and the low to negligible genetic potential for responding to selection (estimated by heritability) may
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8 368 not be a problem for gradual environmental change. At this rate, it would take around at least 10
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10 369 generations for the population average LRS to increase by one juvenile, which highlights the stability
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12 370 of the demographic rate of self-recruitment in this population. Our results therefore support the
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14 371 hypothesis that the population is at evolutionary equilibrium (no genetic changes) in a context of
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16
17 372 environmental stability over the timescale of the survey.
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21 374 *Connectivity as a plausible cause*

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24 375 Our findings were at first surprising because immigration accounts for on average 44% of the juvenile
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26 376 recruitment (Salles *et al.* 2016). Average dispersal distance in Kimbe Bay is between 10 and 20km,
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28 377 providing substantial connectivity among adjacent reefs and potential dispersal of up to 100km
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30 378 (Pinsky *et al.* 2017). The associated gene flow would be expected to bring new genetic variants and
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33 379 thereby increase genetic variation (Facon *et al.* 2008). Under such scenario, selection for self-
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35 380 recruitment, and thereby against migrants, has to be strong to keep the population at evolutionary
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37 381 equilibrium. An alternative scenario is that homogenization by gene flow results in most immigrants
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39 382 sharing a similar genetic background. As a result, no new genetic variants are brought in the
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41 383 population by gene flow and low genetic variation is maintained (Pujol *et al.* 2010). Low genetic
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43 384 variation for LRS implies that evolution by selection at the local scale is extremely limited in its
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45 385 current state. However, this does not imply a dead end for adaptive evolution in this clownfish
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47 386 population because several mechanisms can provide adaptive evolutionary potential over the long
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49 387 term (Pujol *et al.* 2018).
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54 389 *Slight but probably negligible maternal genetic effect*

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56 390 Additional adaptive evolutionary potential can in theory be provided to a population by maternal
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58 391 effects (Räsänen & Kruuk 2007). In the Kimbe Island orange clownfish, we found that maternal

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3 392 effects explained 1.9% of the LRS variance, which is quite small, even if it was more than additive
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5 393 genetic effects. Maternal effects therefore increased slightly the low to negligible rate of LRS change
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7 394 by adaptive evolution. One must note that this increase is nearly negligible. It is likely that this small
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9 395 value reflects the genetic component of the maternal effect. The habitat of birth, which is also the
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11 396 maternal habitat, probably encompassed a non-negligible part of the maternal environmental effects
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13 397 (Germain & Gilbert 2014). There is growing awareness that maternal environmental effects can
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15 398 contribute to adaptation in natural populations, especially when maternal and offspring environments
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17 399 are positively correlated (Shama 2015). It might even buy some time for adaptive evolution through
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19 400 slow genetic change to occur (Levis & Pfenning 2016).
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26 402 *Towards a wider sample of contemporary rates of adaptive evolution in the wild*

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28 403 In our study, LRS estimated local fish contribution to the local population replenishment. As with
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30 404 most wild population pedigrees, this excludes the dispersal fitness because the amount of offspring
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32 405 that successfully dispersed somewhere else is unknown (Kruuk *et al.* 2000). Its genetic variation
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34 406 evaluates the rate of adaptive evolution inside the Kimbe island population. While there are no
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36 407 comparable data from marine systems, 15 studies conducted on terrestrial vertebrates have also
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38 408 estimated the additive genetic variation and the heritability of LRS (Table S1). The number of
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40 409 estimates of maternal effects on LRS variation are extremely rare (McFarlane *et al.* 2014 and
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42 410 references therein). A majority of these studies similarly found low to negligible contributions of
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44 411 additive genetic effects in the wild. Marine fish, mammals and birds revealed the same patterns. There
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46 412 is little evidence of additive genetic variance for LRS in studies conducted in the wild. This situation
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48 413 is less clear for maternal effects, partly because studies remain scarce. Very low but significant
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50 414 additive and maternal genetic variations for fitness indicate that there was some genetic change over
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52 415 the course of the survey but very limited potential for short-term adaptive evolution.
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417 *A wider use of LRS does not preclude caution*

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3 418 LRS studies in wild populations with a known pedigree have multiplied during the last thirty years.
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5 419 Although useful insights were gained, one must note that the use of LRS as a surrogate for fitness is
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7 420 not well suited for iteroparous species (Grafen 1988). This is particularly true when population growth
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9 421 varies between reproductive seasons (Coulson *et al.*, 2006). Furthermore, although quantitative
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11 422 genetic approaches decomposing the genetic and environmental components of LRS are theoretically
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13 423 correct, they might provide imprecise parameter estimates in the wild because temporal and spatial
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15 424 environmental effects (e.g., condition dependent LRS, cohort effects) might not have been adequately
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17 425 corrected for. Caution must therefore be taken when interpreting the additive genetic variance of LRS
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19 426 as adaptive evolutionary rate or evolutionary potential in wild populations where it might in fact
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21 427 reflect other ecological parameters. Our quantitative genetic model explained a large amount of
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23 428 environmental variation in LRS in the Kimbe island clownfish population, which supports the
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25 429 reliability of our genetic estimates.
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33 431 **Conclusion**

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35 432 The major outcome of this study is that the heterogeneity of the habitat of the Kimbe Island orange
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37 433 clownfish had a profound influence on the individual contribution to the local population
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39 434 replenishment over five generations. This finding implies that habitat ecology is crucial for this
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41 435 clownfish population. In terms of future persistence, expected changes in habitat quality and
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43 436 configuration over relatively short time scales might affect the ability of fish to self-recruit. This
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45 437 ability harbored low to negligible additive genetic and maternal genetic variation. As a consequence,
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47 438 this population potential for rapid evolutionary change of LRS by selection, and therefore its rate of
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49 439 adaptive evolution, can be considered negligible in the current state of the population. This finding,
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51 440 which is in line with other studies on the topic, stresses the importance of environmental mechanisms
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53 441 (*e.g.*, plasticity) that have the potential to enable rapid adaptive responses. From the perspective of
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55 442 management, our results caution against hoping for local adaptive evolutionary responses and lend
56
57 443 support to focusing conservation efforts on maintaining habitat quality.
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460

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468 **Conflict of interest:** Authors declare no conflict of interests

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3 470 **Supplementary material**
4

5 471 Additional Supporting Information may be found in the online version 3 of this preprint on the Zenodo
6
7 472 repository: <https://doi.org/10.5281/zenodo.3476529>.

9
10 473 The Additional Supporting Information file contains:

11
12 474 **Table S1.** Previous estimates of fitness heritability and maternal effects on fitness in 15 wild
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14 475 populations.

15
16 476 **Figure S1.** Pedigree data and power analysis for the Kimbe Island orange clownfish population.

17
18 477 **Supplementary methods, results and discussion** on De-lifing measures.
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23 479 **References**

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

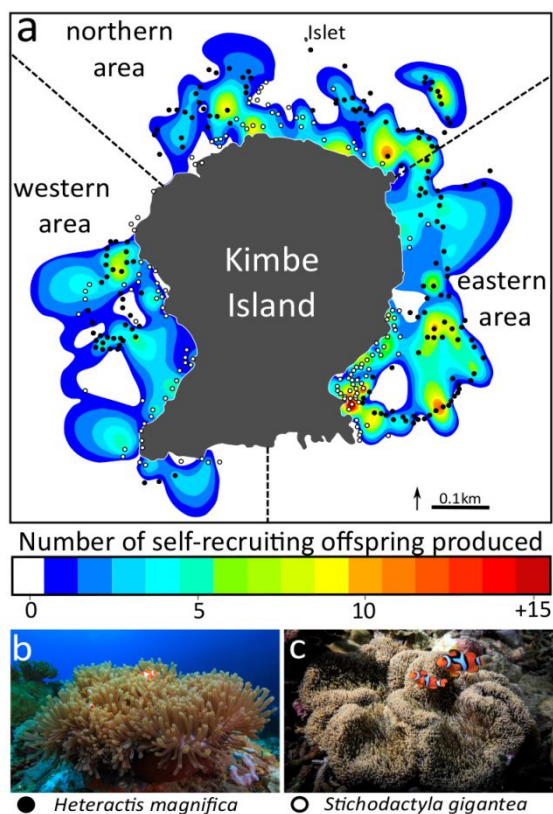
Here we reported variance component estimates quantified by using the animal model approach: Additive genetic (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environmental (V_{PE}) and Residual (V_R) Variances. We also report size effects as proportions of explained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

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3	(CI)	(1.71 to 3.65)	(0.65 to 8.05)
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6	h^2	0.019	0.013
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8	(CI)	(6.827×10^{-4} to 0.057)	(4.951×10^{-5} to 1.227×10^{-2})
9			
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11	m^2	0.027	0.019
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13	(CI)	(9.157×10^{-4} to 0.083)	(2.966×10^{-5} to 2.044×10^{-2})
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15	I_A	0.154	0.103
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17	(CI)	(4.643×10^{-4} to 0.492)	(1.661×10^{-3} to 0.511)
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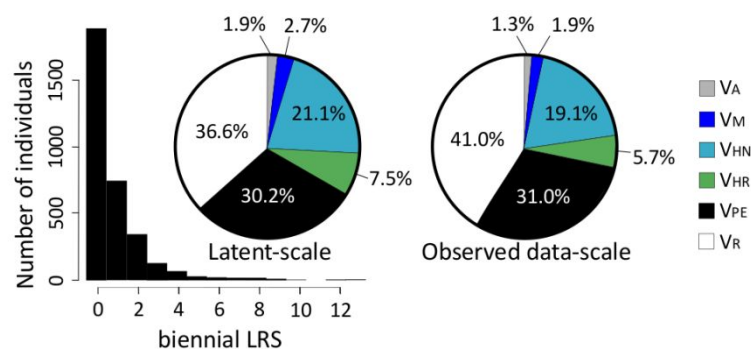


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617 **Figure 1. Variation of the total number of offspring orange clownfish produced on each**
 618 **anemone around Kimbe Island between 2003 and 2013.**

619 (a) The studied region was divided in three areas (northern, eastern and western areas). Colors
 620 correspond to the variation of the total number of juveniles locally self-recruited that were produced
 621 on each anemone (varying from 0 to 27) over a 10-year period. The expected value is interpolated
 622 from those around it (using default algorithms implemented in *Origin* software). Dots correspond
 623 respectively to the location of the two host anemones species: (b) *Heteractis magnifica* (black dots)
 624 and (c) *Stichodactyla gigantea* (white dots). Photos by Tane Sinclair-Taylor.

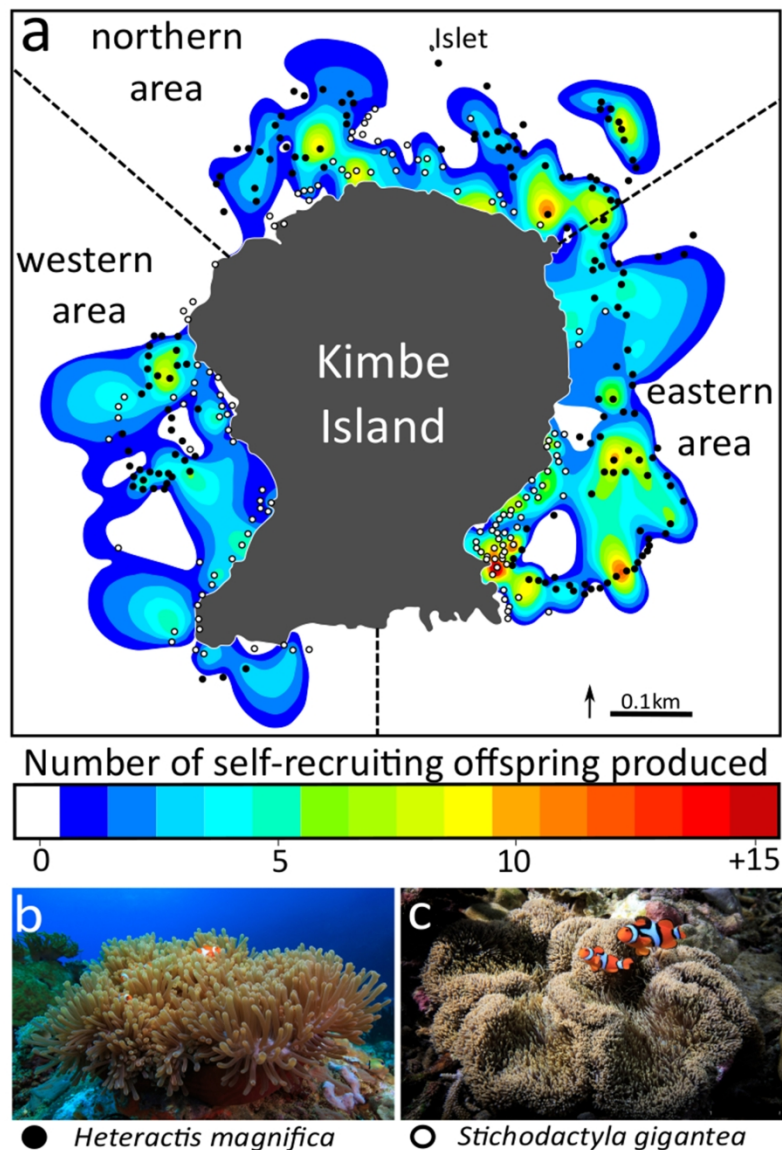
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627 **Figure 2. Sources of variation in the biennial estimate of the local Lifetime Reproductive**
 628 **Success (LRS) of the Kimbe Island orange clownfish.**

629 Distribution of the biennial estimate of the LRS (histograms). Variance components on both latent-
 630 scale and observed data-scale (pie charts) for the biennial estimate of the LRS explained by
 631 Additive genetic (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent
 632 Environmental (V_{PE}) and Residual (V_R) variances. These proportions were calculated from the
 633 values of the posterior modes of a quantitative genetics generalized linear mixed model analysis (for
 634 details see Table 1).



45 Figure 1. Variation of the total number of offspring orange clownfish produced on each anemone around
46 Kimbe Island between 2003 and 2013.
47 (a) The studied region was divided in three areas (northern, eastern and western areas). Colors correspond
48 to the variation of the total number of juveniles locally self-recruited that were produced on each anemone
49 (varying from 0 to 27) over a 10-year period. The expected value is interpolated from those around it (using
50 default algorithms implemented in Origin software). Dots correspond respectively to the location of the two
51 host anemones species: (b) *Heteractis magnifica* (black dots) and (c) *Stichodactyla gigantea* (white dots).
52 Photos by Tane Sinclair-Taylor.

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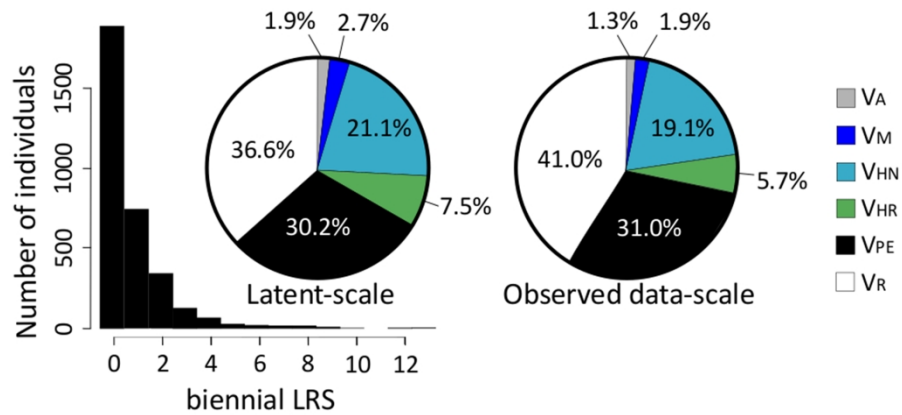


Figure 2. Sources of variation in the biennial estimate of the local Lifetime Reproductive Success (LRS) of the Kimbe Island orange clownfish. Distribution of the biennial estimate of the LRS (histograms). Variance components on both latent-scale and observed data-scale (pie charts) for the biennial estimate of the LRS explained by Additive genetic (VA), Maternal (VM), Natal Habitat (VNH), Resident Habitat (VRH), Permanent Environmental (VPE) and Residual (VR) variances. These proportions were calculated from the values of the posterior modes of a quantitative genetics generalized linear mixed model analysis (for details see Table 1).