

# 1 Coral reef fish populations can persist without immigration

## 2 Running Title: Reef fish population persistence

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23 **Abstract**

24 Determining the conditions under which populations may persist requires accurate estimates of  
25 demographic parameters, including immigration, local reproductive success, and mortality rates. In  
26 marine populations, empirical estimates of these parameters are rare, due at least in part to the  
27 pelagic dispersal stage common to most marine organisms. Here, we evaluate population  
28 persistence and turnover for a population of orange clownfish, *Amphiprion percula*, at Kimbe Island  
29 in Papua New Guinea. All fish in the population were sampled and genotyped on five occasions at  
30 2-year intervals spanning eight years. The genetic data enabled estimates of reproductive success  
31 retained in the same population (reproductive success to self-recruitment), reproductive success  
32 exported to other subpopulations (reproductive success to local connectivity), and immigration and  
33 mortality rates of sub-adults and adults. Approximately 50% of the recruits were assigned to parents  
34 from the Kimbe Island population and this was stable through the sampling period. Stability in the  
35 proportion of local and immigrant settlers is likely due to: low annual mortality rates and stable egg  
36 production rates, and the short larval stages and sensory capacities of reef fish larvae. Biannual  
37 mortality rates ranged from 0.09 to 0.55 and varied significantly spatially. We used these data to  
38 parameterize a model that estimated the probability of the Kimbe Island population persisting in the  
39 absence of immigration. The Kimbe Island population was found to persist without significant  
40 immigration. Model results suggest the island population persists because the largest of the  
41 subpopulations are maintained due to having low mortality and high self-recruitment rates. Our  
42 results enable managers to appropriately target and scale actions to maximize persistence likelihood  
43 as disturbance frequencies increase.

44 **Keywords:** *Amphiprion percula* | long-term monitoring | parentage analysis | self-recruitment |  
45 population demography | persistence

## 46 **1. Introduction**

47 Understanding and identifying biotic and abiotic conditions under which wild populations can  
48 persist over space and through time is a formidable theoretical and practical challenge in population  
49 ecology [1,2]. Identifying the spatial scale at which populations are influenced by these conditions  
50 allows us to define conservation management units and implement appropriately targeted and  
51 scaled actions. Wild populations of many species are fragmented and function as metapopulations,  
52 comprised of local populations linked by migration [3]. Within metapopulations, local population  
53 size is driven by four fundamental  
54 demographic rates: recruitment and immigration, which increase the population size, as well as  
55 mortality and emigration, which decrease the population size [4]. Local populations within  
56 metapopulations can only persist when recruitment and immigration equals or exceeds mortality  
57 and emigration [5,6]. However, these demographic rates may equalize as populations approach  
58 carrying capacity, a theoretical upper limit on the population size [7,8].

59 Population models provide a useful way of examining the influence of demographic parameters on  
60 population persistence [2,9,10]. These models can be used to generate projections of how the size of  
61 a population may change under different environmental conditions, movement patterns of  
62 individuals within populations, and mortality rates. Demographic models may also include some  
63 level of density dependence, although such processes are hard to estimate in wild populations [11].  
64 However, the reliability of demographic models depends on the accuracy of parameters that are  
65 often estimated indirectly due to logistical sampling constraints [12–14]. Evaluating demographic  
66 parameters is challenging because it is often difficult or impossible to follow a large number of  
67 individuals in situ over a time period sufficiently long enough to accurately estimate rates of  
68 population turnover [15]. This is particularly the case for organisms that are not sessile, with  
69 complex life cycles that include dispersal, ontogenetic movements, hibernation, or cryptic phases.

70 Building demographic models is especially challenging for marine species as they often have  
71 complex life cycles that may include a dispersive larval phase and/or a mobile adult phase.  
72 Consequently, it is often difficult to distinguish between losses due to emigration and losses due to  
73 mortality [16]. Many studies have been forced to assume that emigration equals immigration, but it  
74 is then impossible to quantify the relative contributions of these two processes to the dynamics of  
75 local populations within metapopulations [17,18]. This assumption can bias models towards  
76 overestimating the contribution of local populations to the persistence of the metapopulation.  
77 Identifying the natal origins of larvae recruiting to marine populations has also represented a  
78 significant challenge to the development of accurate demographic models. Larval recruitment to  
79 subpopulations comes from two potential sources. Individuals may return to their natal  
80 subpopulation (typically termed self-recruitment), or may disperse to other subpopulations within  
81 the metapopulation (typically termed connectivity). Both self-recruitment and connectivity may be  
82 critical for the persistence of subpopulations, but the means to determine their relative importance  
83 has not been available until recently.

84 The development of several methods to determine the natal origins of juveniles has provided new  
85 insights into the spatial scale of larval dispersal (e.g. physical oceanography [19,20], artificial  
86 tagging [10], trace-elemental fingerprinting of fish otoliths [21] and invertebrate larval shells [22],  
87 and molecular genetics [23,24]). For instance, parentage analysis based on DNA genotyping  
88 provides a means to distinguish natal origins as it allows for detection of parent–child relationships  
89 [24]. We have used this approach to estimate larval dispersal of orange clownfish in Kimbe Bay  
90 from samples collected in 2005 and 2007 [24,25]. When applied regularly to all individuals in a  
91 population, DNA fingerprinting using microsatellite loci also provides a powerful tool for  
92 measuring mortality and population turnover. Orange clownfish (*Amphiprion percula*) form  
93 obligate associations with sea anemones, where they remain for the rest of their lives. Mortality and  
94 population turnover rates can be quantified by tracking individuals from each subpopulation  
95 through time. Previous results from such studies showed a high self-recruitment rate (approx. 50%

96 of recruitment) for the *A. percula* of Kimbe Island in 2005 and 2007 [24,25] and a very low adult  
97 mortality rate (approx. 12.9% per year, [26]) for the same species in Madang, Papua New Guinea.  
98 Based on these findings, we hypothesized that levels of self-recruitment may be high enough to  
99 ensure the self-persistence of the *A. percula* population in Kimbe Island without immigration. We  
100 test this hypothesis using parentage analysis and DNA identification of all of the individuals in the  
101 orange clownfish population in Kimbe Island, Papua New Guinea over an 8-year sampling period.  
102 We used the resulting demographic data to parameterize a demographic model of Kimbe Island  
103 subpopulations to address a specific question: can the orange clownfish population of Kimbe Island  
104 and any of its subpopulations persist in the absence of larval connectivity from other locations in  
105 the region?

## 106 **2. Material and methods**

### 107 *(a) The study system*

108 *Amphiprion percula* typically lives in groups and occurs in obligate association with sea anemones  
109 [27,28]. Groups are usually composed of a dominant breeding pair and between 0 and 6  
110 juveniles[29]. Within each group, there is a size-based dominance hierarchy: the female is largest,  
111 the male is second largest and the non-breeders rank progressively lower in the hierarchy as they  
112 decrease in size. If the single female adult (i.e. rank 1) of a group dies, then the male (i.e. rank 2)  
113 changes sex and the largest juvenile (i.e. rank 3) from the anemone becomes male [30,31].  
114 Reproduction occurs year round, and breeders hatch hundreds of eggs each lunar month but the  
115 importance of the lunar cycle on larval settlement is poorly understood [32,33]. Then, eggs hatch  
116 into pelagic larvae that spend approximately two weeks in the pelagic environment before settling  
117 on an anemone [10,24,34], which may or may not be on the natal reef. Because adult clownfish  
118 rarely move among anemones, persistence at the scale of a single anemone (and hence the larger  
119 scale) is determined by whether the rate of settling larvae can offset the mortality of juveniles and  
120 adults.

121 ***(b) Study site and field collections***

122 The study was conducted every two years from 2005 to 2013 during April in Kimbe Island  
123 (5°12'22.56" S, 150°22'35.58" E), a small island located in Kimbe Bay, Papua New Guinea  
124 (electronic supplementary material, figure S1). We subdivided the island into seven geographical  
125 areas (A–G). In this study, these geographical areas are described as subpopulations. We located  
126 and tagged a total of 210 anemones that were present during the five periods of sampling, all of  
127 which were occupied by *A. percula* (electronic supplementary material, figure S1). All fish at each  
128 anemone were captured by divers using hand nets and processed in situ. Individuals were measured  
129 using calipers (total length TL, mm), fin-clipped for genetic analysis and then released back on the  
130 same anemone. The biggest fish in each anemone was identified as the female, the second largest  
131 individual was assumed to be the male and all other individuals were classified as juveniles. In 2005  
132 and 2007, juveniles (non-breeders) with TL > 35 mm were not fin-clipped but were recorded for  
133 2007. The small pieces of fin tissue were preserved in 95% ethanol in 0.2 ml vials. The smallest  
134 non-breeders (TL < 35 mm, hereafter referred to as ‘new-recruits’) were removed from their  
135 anemones and the whole fish were preserved in vials with 95% ethanol.

136 Resident clownfish may prevent recruitment of new individuals at high densities [32]. Therefore,  
137 removal of the small individuals homogenized conditions for larval settlement among all anemones.  
138 All details related to capture numbers for each stage, subpopulation and year of sampling are  
139 provided within the electronic supplementary material, table S1. DNA from a total of 3 890  
140 collected samples (including 1 067 new-recruits) were extracted and screened at 22 polymorphic  
141 microsatellite loci (electronic supplementary material, table S2) that satisfied Hardy–Weinberg  
142 equilibrium and linkage disequilibrium assumptions.

143 ***(c) Demographic parameters***

144 *Mortality measurement (biannual).*

145 The package GenAlex v6.5 [35] was used to compare each of the individual genotypes from fish  
146 sampled in 2009, 2011, and 2013 (2005 and 2007 are excluded because juveniles with TL > 35 mm  
147 were not fin-clipped in those years) to identify all unique multilocus genotypes [36]. The combined  
148 probability of identity (i.e. the probability of two samples having the same multilocus genotype by  
149 chance) for this set of markers in this population was small ( $1.7 \times 10^{-24}$ ). Therefore, if fin clips from  
150 different sampling years had the same genotype, they were assumed to be from the same individual.  
151 To account for possible genotyping errors, mismatches of up to two loci between genotypes were  
152 allowed in pair-wise genotype comparisons. In this way, we were able to measure mortality for each  
153 stage (i.e. average mortality of females, males, and juveniles) for each of the seven subpopulations  
154 of Kimbe Island for two time steps (i.e. 2009–2011 and 2011–2013). We used  $\chi^2$ -test to compare  
155 the mortality rates observed among the seven subpopulations and between the various life stages  
156 (i.e. juvenile, male, and female stages). We then used the Fisher-test to evaluate whether the  
157 mortality rate calculated for 2009–2011 was significantly different than the mortality rate calculated  
158 for 2011–2013.

159 *Reproductive success to self-recruitment and to local connectivity, and immigration measurements*  
160 *(biannual).*

161 For every sampling year (2005, 2007, 2009, 2011, and 2013) and for each subpopulation of Kimbe  
162 Island (A–G), we used assignment/exclusion tests to estimate an index of reproductive success to  
163 self-recruitment, reproductive success to local connectivity, and immigration. Reproductive success  
164 to self-recruitment is calculated as the number of juveniles with parents from the same  
165 subpopulation divided by the number of females in this population. Reproductive success to local  
166 connectivity is calculated as the number of juveniles in a subpopulation that were offspring of  
167 parents from another Kimbe Island subpopulation, divided by the number of females in the focal  
168 population. Immigration is defined as the number of juveniles that were not assigned to any parent  
169 from Kimbe Island. To assign one individual to a breeding pair, we used individual genotypes and  
170 the platform FaMoz [37]. We then compared the percentages of self- and local-recruits and

171 immigrants within Kimbe Island among all sampling years using a Kruskal–Wallis test. In this  
172 analysis, local-recruitment is the percentage of self-recruitment, defined by Burgess et al. [15] as  
173 the fraction of recruitment to a site comprised of individuals born in that site and the percentage of  
174 local connectivity. We used the Pettitt homogeneity test to evaluate differences in the presence of  
175 connections among subpopulations (i.e. exchange of recruits) and the number of recruits being  
176 exchanged among (local recruits) and within (self-recruits) subpopulations among years.

#### 177 *Carrying capacity.*

178 The number of female and male clownfish per anemone cannot exceed one since anemones only  
179 host one breeding pair. Therefore, the carrying capacity for adult males and females in a given  
180 subpopulation cannot exceed the number of anemones present in that subpopulation. The number of  
181 juveniles per anemone may vary between the different subpopulations. We calculated the mean  
182 number of clownfish observed per anemone in the seven subpopulations at four sampling periods  
183 (2007, 2009, 2011, and 2013, excluding 2005 because non-breeders more than 35 mm were not  
184 counted and sampled). For each subpopulation, we obtained a set of four values of mean number of  
185 clownfish per anemone and we used the highest values of mean number of clownfish per anemone  
186 as the juvenile carrying capacity per anemone. The juvenile carrying capacity per subpopulation is  
187 equal to the maximum number of clownfish observed per anemone multiplied by the total number  
188 of anemones in that subpopulation. Mortality rates, and rates for reproductive success to self-  
189 recruitment, reproductive success to local connectivity, and immigration are exact measures from  
190 the field observations (rather estimation) so are not presented with error bars. All statistical analyses  
191 were performed using R v3.0.2 [38] and significance was interpreted using a p-value of  $>0.05$ .

#### 192 *(d) Demographic model*

193 The system is based on a loss-input principle using recurrence equations [39]. The number of  
194 larvae, juveniles, males, and females in subpopulation at period  $t + h$  (with the time step  
195 resolution of the dynamic) is by  $L_{t+h}^i, J_{t+h}^i, M_{t+h}^i$  and  $F_{t+h}^i$ . The dynamics of each subpopulation

196 are described using these four recurrence equations:

$$L_{t+h}^i = h \left[ b^{ii} w_t^i + \sum_{j=1}^{sP} b^{ji} w_t^j + \theta^i \right], \quad (2.1)$$

$$J_{t+h}^i - J_t^i = h [(-d_j^i - t_M) J_t^i + s_L L_t^i], \quad (2.2)$$

$$M_{t+h}^i - M_t^i = h [(-d_M^i - t_F) M_t^i + t_M J_t^i], \quad (2.3)$$

$$F_{t+h}^i - F_t^i = h [-d_F^i F_t^i + t_F M_t^i], \quad (2.4)$$

197 where  $w_t^i$  and  $w_t^j$  are the number of breeding pair in the subpopulation  $i$  and  $j$  at time  $t$  and (eq.  
 198 2.1),  $d_j^i$ ,  $d_M^i$  and  $d_F^i$  are the mortality rates per capita and by unit of time of juveniles, males and  
 199 females in subpopulation  $i$  (eq. 2.2 to 2.4). The parameter  $b^{ii}$  represents the number per unit of time  
 200 of self-recruits and breeding pair ( $w_t^i$ ) in subpopulation  $i$  (i.e., reproductive success to self-  
 201 recruitment), while  $b^{ji}$  is the number per unit of time of juveniles produced per breeding pair in  
 202 subpopulation  $j$  ( $w_t^j$ ) at time  $t$  that disperse and recruit into subpopulation  $i$  (i.e. reproductive  
 203 success to local connectivity).  $\sum_{j=1}^{sP} b^{ji} w_t^j$  is the sum of the connectivity from the six other  
 204 subpopulations ( $sP=6$ )  $j$  to subpopulation  $i$ . The parameter  $\theta^i$  denotes the constant number per unit  
 205 of time of migrants recruiting to subpopulation  $i$  who were spawned outside of Kimbe Island. In  
 206 equation 2.2,  $s_L$  corresponds to settlement rate per unit of time of larvae arriving at subpopulation  $i$ .  
 207 The number of larvae that can enter the juvenile population on reef  $i$  is limited by the amount of  
 208 free space,  $(n^i K^i - J_t^i)$ :

$$s_L = s_l \frac{n^i K^i - J_t^i}{n^i K^i} \quad (2.5)$$

209 where  $n^i$  is the maximal number of juveniles per anemone in subpopulation  $i$  and  $K^i$  is the number  
 210 of anemones in the subpopulation  $i$ .

211 In equations 2.2 and 2.3,  $t_M$  measures the rate of transition function from juveniles to males per unit  
 212 of time:

$$t_M = t_m \frac{K^i - M_t^i}{K^i} \quad (2.6)$$

213 where  $(K^i - M_t^i)$  denotes the space available space for new males (i.e., male mortality or males  
 214 changing into females following female mortality) taking into account that we cannot observed  
 215 more than one male per anemone.

216 In equations 2.3 and 2.4,  $t_F$  corresponds to transition function from males to females per unit of  
 217 time:

$$t_F = t_f \frac{K^i - F_t^i}{K^i} \quad (2.7)$$

218 where  $K^i - F_t^i$  denotes the female turnover due to available space for females in anemones due to  
 219 female mortality taking into account that we cannot observe more than one adult female per  
 220 anemone.

### 221 **(e) Hypotheses, model fitting, and simulations**

222 Rates of mortality, self-recruitment, and local connectivity were all assumed to be known  
 223 parameters, deduced from the parentage analysis, which was entirely independent of the model. The  
 224 parameters  $s_i$ ,  $t_m$ , and  $t_f$  in equations (2.5)–(2.7) appear as adjustment parameters that fit the model  
 225 to the observed data (electronic supplementary material, figure S2). Their estimated values are  
 226 obtained by minimizing the least-square criterion measuring the distance between observed data  
 227 and their values predicted by the model [40], using the procedure outlined by Nelder & Mead [41].

228 Reproductive success rates of self- and local-recruitment, and immigration used in the demographic  
 229 model were the averages among all five sampling periods for each subpopulation (table 1).

230 Mortality rates used as inputs to the demography model are the averages between 2009–2011 and

231 2011–2013 for each life stage of each subpopulation (table 1). Demographic parameters are  
232 rescaled to equivalent monthly rates to increase resolution of the model dynamics. The model was  
233 initialized from 2007 with a monthly time step. The population dynamics were evaluated  
234 considering three different recruitment and immigration scenarios: (i) with all inputs; (ii) removing  
235 immigration; and (iii) removing local recruitment and immigration. The numerical solution for the  
236 demographic model was programmed into R v3.0.2 [38].

### 237 *(f) Sensitivity analysis*

238 Sensitivity analyses were used to determine which demographic parameters most greatly influence  
239 population dynamics and persistence among: mortality rate of females, males, and juveniles, self-  
240 recruitment and local-recruitment rates, immigration, and juvenile and adult carrying capacity. We  
241 independently varied each parameter by 30% and plotted the resulting trajectory of population size  
242 through time.

243 Further details on the demographic parameters and sensitivity analysis (figure S2b,f) are provided  
244 in the electronic supplementary material.

## 245 **3. Results**

### 246 *(a) Population demography*

#### 247 *Mortality measurements (biannual).*

248 In total, 1 706 fins were collected and genotyped between 2009 and 2013. Genetic similarity  
249 analyses revealed that 561 individuals were observed only once, 334 individuals were found in two  
250 successive sampling years (i.e. 2009 and 2011 or 2011 and 2013) and 159 individuals survived  
251 during the three years of sampling. From these data, we calculated the mortality rate between the  
252 periods 2009–2011 and 2011–2013 (electronic supplementary material, figure S3 and table S3).

253 We excluded two cases of survival assignments (i.e. similar genotypes with three mismatches on 44  
254 alleles from fins clipped in two consecutive periods) because fins came from females which were  
255 sampled in different subpopulations separated by more than 350 m. During the period 2009–2011,

256 the mortality rates differed significantly among the seven subpopulations and for the various life  
257 stages (Chi square test,  $p < 0.001$ ). During the period 2011-2013, the mortality rates among the seven  
258 subpopulations and for the various life stages were significantly different only for males and  
259 females (Chi square test,  $p_J = 0.120$ ,  $p_{M,F} < 0.001$ ). The average mortality rate varied among  
260 subpopulations between 0.18 and 0.49 for juveniles, 0.09 and 0.44 for males, and 0.19 and 0.55 for  
261 females (Table 1). The mortality rates were higher in subpopulation G than in the other  
262 subpopulations ( $d_G > d_D > d_C > d_F > d_A > d_E > d_B$ ). However, when all life stages  
263 and subpopulations were aggregated, differences in mortality rates between 2009-2011 and 2011-  
264 2013 were not significantly different (Fisher test,  $p = 0.703$ ). Further, when the development stage  
265 and subpopulations were considered separately, differences among mortality rates between the 2  
266 periods were only significant for males and females from subpopulation A (Fisher test,  $p < 0.001$ ).

267 *Recruitment measurements (biannual).*

268 Parentage analysis was used to establish the natal origin of all *A. percula* offspring spawned by  
269 females in the seven Kimbe Island subpopulations. The analysis quantified self-recruitment  
270 (fraction of recruitment to a subpopulation comprised of new-recruits born in that subpopulation),  
271 local connectivity (fraction of recruitment to a subpopulation comprised of new-recruits born in  
272 other Kimbe Island subpopulations), and immigration from other reefs outside Kimbe Island from  
273 2005–2013 (figure 1). From a total of 1 067 new-recruits collected over five sampling events, less  
274 than half were immigrants (489 new-recruit immigrants, 45.8%); 222 (20.9%) were self-recruits and  
275 356 (33.3%) were local recruits). The percentages of self-recruits, local-recruits, and immigrants  
276 among sampling years did not vary significantly among years (Kruskal–Wallis test,  $p = 0.877$ ).  
277 Further, levels of self-recruitment and local connectivity among subpopulations were all consistent  
278 among the five sample years. Differences in the presence of connections among subpopulations (i.e.  
279 exchange of recruits) and the number of recruits being exchanged among (local recruits) and within  
280 (self-recruits) subpopulations were not significantly different among years (Pettitt homogeneity test,  
281  $p = 0.702$ ). The average reproductive success to self-recruitment varied among subpopulations

282 between 0.06 and 0.45 juveniles per female (electronic supplementary material, table S4). The  
283 reproductive success to self-recruitment was higher in subpopulation A than in the other  
284 subpopulations ( $b_A > b_E > b_G > b_F > b_C > b_D > b_B$ ). The average number of juveniles per  
285 female in the subpopulation A represented ~40% of the total inputs coming from Kimbe Island.  
286 Further details on the mortality and reproductive success results are provided in the electronic  
287 supplementary material.

### 288 **(b) Modeling population dynamics**

289 The demographic parameters calculated from the field data and used in the model included the  
290 reproductive success to self-recruitment, reproductive success to local connectivity, mortality and  
291 the carrying capacity. The carrying capacity is the average number of juveniles per anemone for  
292 juveniles and is the number of anemones (K) for adult males and females. Although the number of  
293 juveniles per anemone was as high as 5 (figure. S4), the average number of juveniles per anemone  
294 varied between 1.14 and 2.19 among subpopulations (table 1). The optimum parameter values for  
295 fitting our demographic model to the observed data were  $s_l = 0.196$  (larval settlement),  $t_m = 0.310$   
296 (transition from juvenile to male),  $t_f = 1.950$  (transition from male to female).

297 We found that all subpopulations and the Kimbe Island population were stable and persisted when  
298 all connections were maintained (self-recruitment, local-recruitment, and immigration, figure 2  
299 black points). The subpopulations A, B, C, D, E, and G and the integrated Kimbe Island population  
300 were also stable and persisted when immigration was removed (figure 2, grey points). The number  
301 of juveniles in the subpopulation F was null after 5 years (figure 2, grey points). When immigration  
302 was removed, the presence of both a male and female on each anemone were maintained, but the  
303 number of recruits/juveniles was halved meaning the available habitat was no longer saturated. The  
304 global Kimbe Island population was also stable and persisted if all local connections and  
305 immigration were removed, though the habitat became less saturated through a 25% decline in  
306 females. In this scenario only subpopulations A, B, and E persisted (figure 2, blue points), albeit  
307 with reductions in juvenile densities of ~50% (A and E) and ~75% (B). The juvenile stage in the

308 subpopulations C, D, F, and G disappeared after ~5 years. Mortality rates for these subpopulations  
309 were all higher than for A, B, and E and thus C, D, F, and G were more dependent on local  
310 connectivity and immigration. Subpopulations C, D, F, and G were smaller than A, B, and E, which  
311 is why the overall Kimbe Island population persisted when only subpopulations A, B, and E  
312 persisted. The declines in the subpopulations C, D, F and G started as reductions in the number of  
313 juvenile followed by a decrease in the number of males and then total loss due to the absence of  
314 females (electronic supplementary material, figure S5).

315 A sensitivity analysis was conducted to determine which parameters most influence subpopulation  
316 dynamics. The sensitivity analysis revealed that for subpopulations C, D, and F the time of  
317 extinction stayed the same irrespective of whether the other demographic parameters are modified  
318 by 30% (electronic supplementary material, figure S6a and b). For these three subpopulations, self-  
319 recruitment, local-recruitment, and immigration were equally important. Considering the entire  
320 population of females in Kimbe Island, the mortality rate of females and the carrying capacity were  
321 the most influential demographic parameters driving persistence (electronic supplementary  
322 material, figure S6a and b). The sensitivity analysis demonstrates the robustness of our main  
323 finding: the orange clownfish population from Kimbe Island can persist without immigration. In  
324 fact, we observed the persistence of the orange clownfish population even after increasing or  
325 decreasing by 30% the different demographic parameters.

## 326 **4. Discussion**

327 We followed an entire population of a coral reef fish through eight years to quantify demographic  
328 parameters used in assessments of population dynamics. Our results indicate that the overall Kimbe  
329 Island population of clownfish was stable with consistent patterns of self-recruitment and larval  
330 immigration, and model results suggest that the population can persist without immigration from  
331 other sources. Model results also suggest several smaller lagoonal subpopulations within Kimbe  
332 Island were also stable and likely to persist if only populated from self-recruitment. The high level

333 of demographic stability demonstrated at a small spatial scale is a novel and unexpected result for a  
334 marine population that includes a dispersive larval stage. The conclusion that the population can be  
335 sustained through self-recruitment is likely to be robust for two primary reasons. Firstly, our  
336 demographic model was based on genetic identification of every individual and their progeny over  
337 an 8-year period. The primary input variables to the model were therefore based directly on  
338 sampling of all individuals in the population and parent–offspring relationships, rather than use of  
339 indirect methods as is the case in other studies [12,42–44]. Further, the study was long enough to  
340 see a near-complete population turnover, with only 18% of adults persisting over the 8-year  
341 sampling period. Secondly, mortality, self-recruitment and connectivity patterns were stable over  
342 the 8-year sampling period, suggesting that the demographic importance of self-recruitment was not  
343 a transitory phenomenon. Although larval connectivity is not necessary for the persistence of  
344 relatively undisturbed populations, it is likely to be of great demographic significance via a rescue  
345 effect [45] should extrinsic disturbances extirpate a subpopulation.

346 The power of longitudinal genetic monitoring of each individual was that we can distinguish  
347 between death and emigration to generate an accurate estimate of mortality. Our data indicated that  
348 a small number of adult individuals moved short distances during the study period from their  
349 anemone to another anemone within the same lagoon (approx. 2%), which meant we could adjust  
350 mortality rates accordingly and calculate the true mortality rate. We calculated average biannual  
351 mortality rates of 31–36% for juveniles, and adult males and females with a global mortality rate  
352 that was constant across two 2-year periods. There was no significant difference between the  
353 mortality rate of adults (either sex) and juveniles, though most juveniles sampled were large and  
354 positioned first in the queue for access to reproduction in the colony hierarchy ( juveniles named as  
355 ‘rank 3’ by Buston [26,32] represent approximately 83% of total juveniles sampled). Buston [26,32]  
356 used visual censuses to estimate mortality for the same species in another part of Papua New  
357 Guinea (Madang), and also concluded that adults (named by the authors ‘rank 1 and 2’ to refer to  
358 female and male, respectively) and juveniles (named ‘rank 3’) had similar mortality [26]. However,

359 the mortality rate we found was higher (approx. 16.5% versus approx. 12.9%) than Buston [26,32]  
360 observed following conversion of our biannual and his monthly mortality rates to annual rates.  
361 Also, differences among subpopulations were as great as approximately 25%, all of which speaks to  
362 the value of longitudinal genetic monitoring of each individual and to the importance of local-scale  
363 differences in the environment (abiotic and/or biotic) for survival.

364 Differences among subpopulations in mortality rates probably reflect a rapid turnover as a result of  
365 intense competition for reproductive status on anemones (related to the number of fish in the queue  
366 within an anemone), which are clearly a limiting resource. Only the dominant pair of clownfish  
367 breeds and non-breeding subordinates queue for breeding positions. The highest-ranking individuals  
368 are the most likely to inherit breeding positions so competition for rank may be intense, which  
369 results in high stress for some juveniles and competition for food resources within anemones  
370 [26,30]. The extent to which competition for rank plays out probably varies among subpopulations  
371 resulting in more rapid turnover where competition is most intense, which might be the case for our  
372 subpopulations C, D, and G, where mortality rates are highest.

373 For marine populations, recruitment is often a highly stochastic process with great inter-annual  
374 variation [46,47]. In our study, longitudinal genetic monitoring of each individual allowed us to  
375 distinguish between individuals that were offspring of parents from Kimbe Island subpopulations  
376 and those that were spawned by adults on other reefs (i.e. located more than 10 km from Kimbe  
377 Island). We found that local connectivity and self-recruitment combined to provide approximately  
378 50% of recruits each year during the five sampling periods. Importantly, the stability we see  
379 through time is a result of several settlement events because new-recruits sampled are between 10  
380 and 281 days old (Salles O.C., 2015) and we are therefore integrating a number of settlement events  
381 through the year. Stability in the proportion of local and immigrant settlers over time is likely due to  
382 a combination of biological and physical factors. Population numbers are fairly consistent through  
383 time with low annual mortality rates (approx. 15%), suggesting that egg production rates were also

384 likely to be relatively stable when averaged over the year in question. Also, the duration of the  
385 larval stage for this species is relatively short (10–12 days on average [34]) and therefore capacity  
386 for dispersal will be significantly less than for species with longer pelagic larval durations. Larval  
387 behaviour may also play a role in stabilizing self- and local-recruitment over time. Coral reef fish  
388 larvae are now known to have well-developed sensory systems and reef sounds [48–50] and  
389 olfactory cues [51–53] may be used as means to locate and orient towards home to a suitable habitat  
390 [54,55]. For instance, Dixon *et al.* [56] provided evidence that *A. percula* use olfactory cues to  
391 locate their natal reefs, providing a mechanism for the relatively high and consistent levels of self-  
392 recruitment documented for Kimbe Island.

393 Results obtained from our demographic model showed that the three subpopulations with the lowest  
394 mortality rates (A, B, and E) are capable of persisting without immigration. Two of these  
395 subpopulations (A and E) also have the largest anemone abundance and correspondingly have the  
396 highest number of clownfish and the highest self-recruitment rates. Yet, the female reproductive  
397 success for self-recruitment was quite different between subpopulations A and E despite their  
398 numbers differing by only 2%. The biannual production of self-recruiting juveniles per females  
399 from subpopulation A was more than twice that documented for E (approx. 0.38 versus approx.  
400 0.16), perhaps due to local water movement, ability of larvae to sense the shallower anemones here,  
401 or a combination of these. Two different demographic strategies can ensure the persistence of  
402 subpopulations in the absence of immigration. The first strategy relies upon high self-recruitment to  
403 compensate for high mortality (subpopulation A). The second is the inverse; female mortality rates  
404 may be low so self-recruitment rates can be low as well (subpopulations B and E). In contrast to A,  
405 B, and E, subpopulations C, D, F, and G disappeared quickly without immigration. Subpopulation F  
406 consisted of only seven inhabited anemones in total. For the three other subpopulations (C, D, and  
407 G) persistence was not assured once isolated due to higher mortality rates and lower self-  
408 recruitment rates in comparison to subpopulations A, B, and E. The persistence of the island

409 population as a whole was driven by the low mortality rates of females and the high self-  
410 recruitment rates characteristic of the largest subpopulations at Kimbe Island (i.e. A, B, and E).

411 In conclusion, longitudinal genetic monitoring of each individual within a population is a powerful  
412 approach for understanding the local drivers of population persistence. It can provide accurate  
413 measurements of demographic rates that often cannot be reliably estimated by traditional  
414 approaches. Our use of longitudinal genetic monitoring is why we are confident it is possible for the  
415 Kimbe Island population to persist without immigration; i.e. that our primary result is robust. While  
416 we cannot be absolutely certain as to whether the Kimbe Island clownfish population will persist  
417 without immigration, all of the evidence presented suggests it is possible. We were also able to  
418 reliably determine the demographic parameters driving local-scale spatial variation in persistence  
419 likelihood, which, with further work, could be used to examine how and whether local adaptation  
420 develops and manifests. The approach outlined here will also be of help to managers in developing  
421 appropriately targeted and scaled actions that maximize persistence likelihood in this era of climate  
422 change and increasing disturbance frequencies. For example, our results indicate that protecting  
423 Kimbe Island may be sufficient to preserve the local *A. percula* population over time even without  
424 immigration from surrounding populations.

425 **Ethics statement.** The research accomplished in this project was conducted under James Cook  
426 University ethics approval number A1264 and followed all guidelines for the country in which it  
427 took place.

428 **Authors' contributions.** SP, GPJ, and SRT conceived the study; OCS, PSA, GRA, GPJ, MLB,  
429 SRT, and SP collected field data; OCS and PSA carried out the molecular lab work and parentage  
430 analysis, OCS, JAM, and SP drafted the manuscript; GRA, SRT, GPJ, and MLB helped to draft the  
431 manuscript; OCS carried out the statistical analyses; OCS, CMB and MJ developed and analyzed  
432 the demographic model. All authors gave final approval for publication.

433 **Acknowledgements.** We thank all those that assisted in the field. N. Tolou and S. Baksay assisted  
434 with genetic analysis. Mahonia Na Dari R and CC and the crew of M.V. FeBrina provided essential  
435 logistic support. We are grateful to the traditional owners of the reefs near Kimbe Island, PNG, for  
436 allowing us access to their reefs.

437 **Funding statement.** This research was supported by LABEX Corail, ERC, CRISP, the GEF CRTR  
438 Connectivity Working Group, NSF, the ARC CoE Coral Reef Studies, TNC, Total Foundation,  
439 JCU, KAUST, and WHOI.

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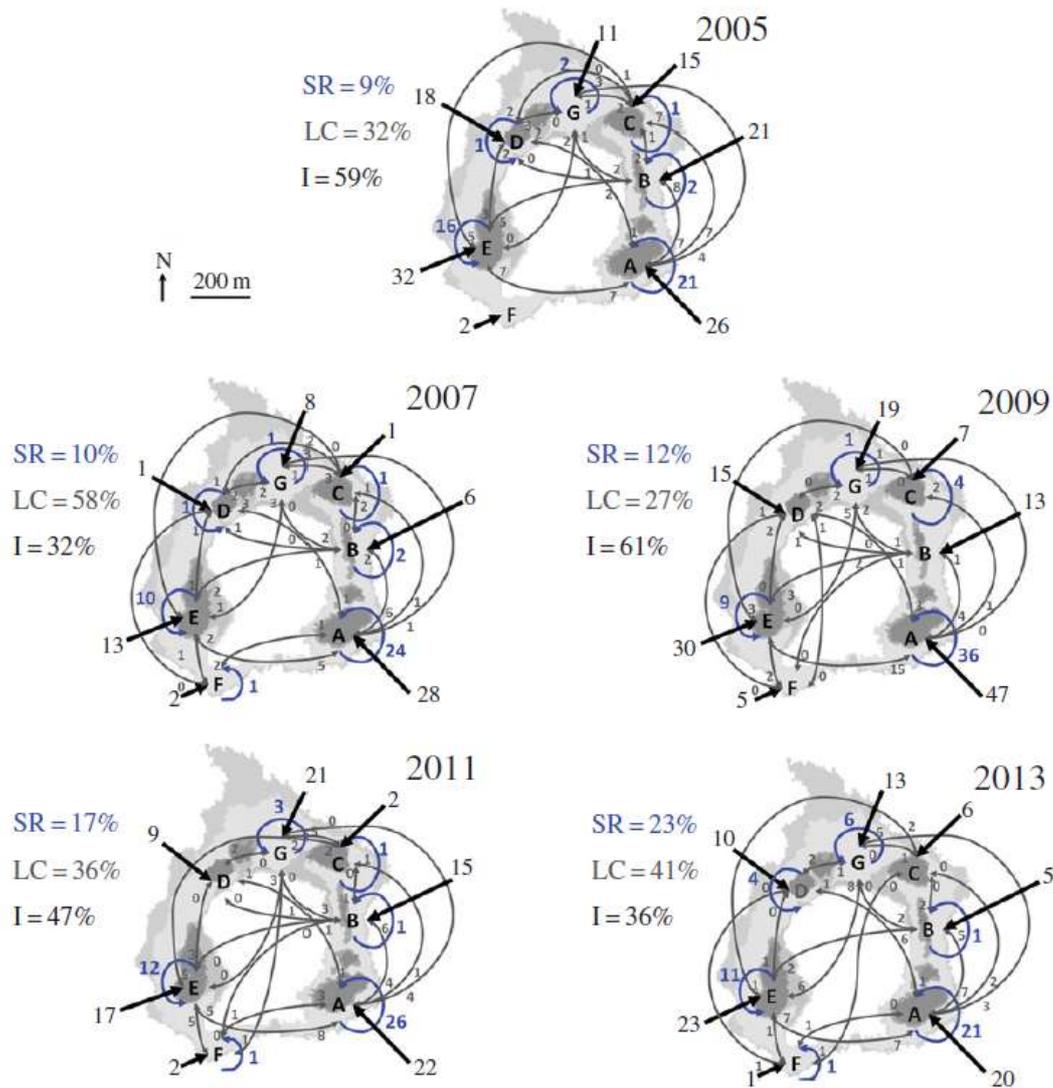
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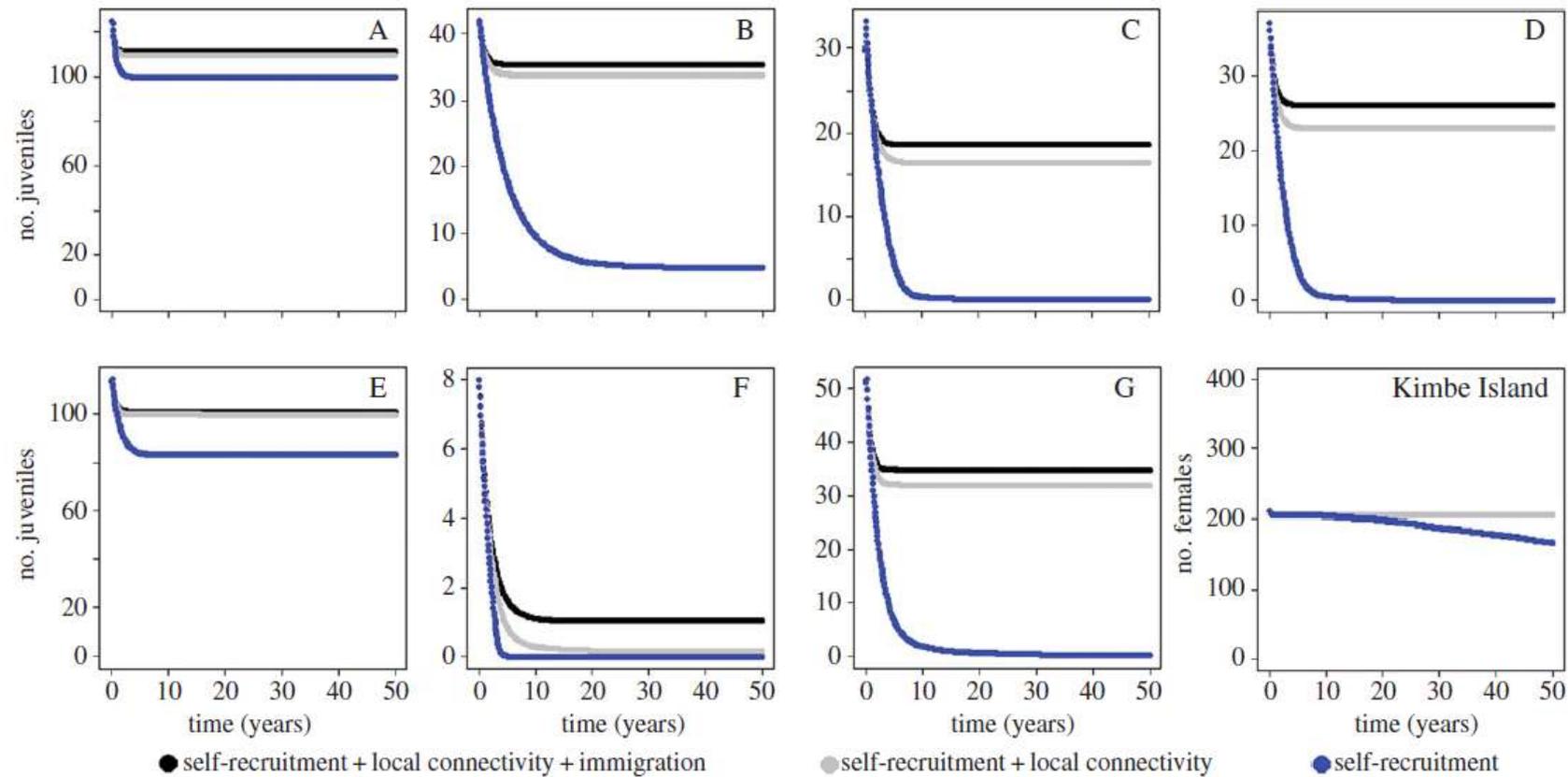
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577 **Figure captions**

578

579 **Figure 1.** Self-recruitment (SR, blue arrows), local connectivity (LC, grey arrows), and  
 580 immigration (I, black arrows) calculated on the natural *Amphiprion percula* populations from  
 581 parentage analysis from 2005 to 2013 in Kimbe Island, Papua New Guinea. Subpopulations are  
 582 indicated with letters A-G. The numbers correspond to new-recruits and the arrows show the  
 583 sources of these inputs (i.e. self-recruitment, local connectivity, or immigration).



585 **Figure 2.** Demographic model projections of numbers of juvenile *Amphiprion percula* within each of the subpopulations (A - G) and the whole  
 586 population of Kimbe Island (subpopulations A-G combined) for three different recruitment and immigration scenarios. The model was initialized  
 587 with data of total juvenile captures during 2007 (set as time[year] =0). The model temporal resolution is one month and the results are plotted here  
 588 every six months for 50 years. Self-recruitment and local connectivity refer to reproductive success to self-recruitment and reproductive success to  
 589 local connectivity, respectively, in the demographic model.

590 **Table**591 **Table 1.** Demographic parameters from empirical values of natural population of *A. percula*.

592  $d_{J,M,F}^i$  refers to average biannual mortality rate per capita of juvenile, and adult males and females  
 593 for each subpopulation between two periods 2009-2011 and 2011-2013 (see Table S1 for mortality  
 594 rates for each of the two 2-year periods).  $n^i$  is the maximal average number of juvenile per  
 595 anemone in the subpopulation  $i$  between 2007 and 2013 and  $K^i$  is the total number of anemones in  
 596 the subpopulation  $i$  (equal to the maximal number of male or female per subpopulation).

Parameters	A	B	C	D	E	F	G
$d_J^i$	0.296	0.270	0.269	0.477	0.179	0.500	0.487
$d_M^i$	0.373	0.095	0.393	0.400	0.198	0.286	0.440
$d_F^i$	0.397	0.190	0.382	0.350	0.243	0.357	0.552
$n^i$	2.19	2.00	1.58	1.85	2.03	1.14	1.70
$K^i$	57	21	19	20	56	7	30

597