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1 **Spatial autocorrelation and host anemone species drive variation in local components of**  
2 **fitness in a wild clownfish population**

3

4 Pascal Marrot<sup>1,2</sup>, Cécile Fauvelot<sup>2,3</sup>, Michael L. Berumen<sup>4</sup>, Maya Srinivasan<sup>5</sup>, Geoffrey P.  
5 Jones<sup>5</sup>, Serge Planes<sup>1,2</sup>, Benoit Pujol<sup>1,2</sup>

6

7 **Authors' affiliations:**

8 <sup>1</sup> PSL Université Paris: EPHE-UPVD-CNRS, UAR 3278 CRIOBE, Université de Perpignan,  
9 52 Avenue Paul Alduy, 66860 Perpignan Cedex, France.

10 <sup>2</sup> Laboratoire d'Excellence 'CORAIL', 58 avenue Paul Alduy, F-66360 Perpignan, France.

11 <sup>3</sup> UMR ENTROPIE (IRD, UR, UNC, IFREMER, CNRS), Laboratoire d'Océanographie de  
12 Villefranche, Villefranche-sur-Mer, France

13 <sup>4</sup> Red Sea Research Center, Division of Biological and Environmental Sciences and  
14 Engineering, King Abdullah University of Science and Technology, Thuwal, 23955, Saudi  
15 Arabia.

16 <sup>5</sup> ARC Centre of Excellence for Coral Reef Studies, and College of Science and Engineering,  
17 James Cook University, Townsville, Queensland 4811, Australia.

18

19 **Authors' contributions:** CF, PM and BP designed the research program of this study; GPJ,  
20 MLB, MS and SP designed the monitoring program and long-term research program on  
21 Kimbe island wild clownfish; PM analysed data; BP and PM wrote the manuscript, and all  
22 authors contributed substantially to revise the paper.

23

24 **Data accessibility statement:** R programming protocols, script and codes, and data from this  
25 study can be obtained on the Zenodo repository: <https://doi.org/10.5281/zenodo.13806778>

26

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28

29 **Keywords:** clownfish, lifetime reproductive success, self-recruitment, spatial autocorrelation,  
30 PCNM

31

32 Person to whom correspondence should be sent: Benoit Pujol, UAR 3278 CRIOBE,  
33 Université de Perpignan, 52 Av. Paul Alduy, 66860 Perpignan cedex, France. Tel: +33 (0)4  
34 30 19 23 24. Fax: +33(0)4 68 50 36 86. Email: benoit.pujol@univ-perp.fr

35

36 **Summary:** The susceptibility of species to habitat changes depends on which ecological  
37 drivers shape individual fitness components. To date, only a few studies have quantified  
38 fitness components such as the Lifetime Reproductive Success across multiple generations in  
39 wild marine species. Because of a long-term sampling effort, such information is available for  
40 the for the population of wild orange clownfish, *Amphiprion percula*, from Kimbe Island  
41 (Papua New Guinea). Previous work on the wild orange clownfish near Kimbe Island  
42 suggests that there is little adaptive potential and that variation in LRS is mainly driven by a  
43 breeder's habitat. Whether the host anemone species, geographic location, density or depth  
44 contributed to LRS remains however unknown because they were combined into a unique  
45 variable. We tested whether it is the ecology or the spatial distribution of clownfish that  
46 shaped the individual variation of a local fitness component, which would affect the  
47 population self-recruitment process and ultimately the maintenance of this wild population.  
48 Our spatially explicit analysis disentangled the role of these factors. We found that the host  
49 anemone species had an impact on wild clownfish LRS independently from their spatial  
50 distribution. The spatial distribution nevertheless had an impact on its own, as reflected by the  
51 spatial autocorrelation of LRS. Depth and density of anemones did not show a significant  
52 impact. Our findings imply that this clownfish population is susceptible to modifications of  
53 the spatial distribution and local assembly of anemone species.

54

## 55 **Introduction**

56 The resilience of wild populations to environmental change is closely linked to their ability to  
57 adapt (Eizaguirre and Baltazar-Soares 2014). Several taxa show such ability in response to  
58 climate related changes of their environment, e.g., in plants (Jordan et al. 2017), birds  
59 (Gienapp et al. 2008), mammals (Boutin and Lane 2014), fish (Muñoz et al. 2015) and corals

60 (Matz et al. 2020). Effective evaluation of this ability is successfully integrated in  
61 conservation strategies (Funk et al. 2019). For instance, the efficiency of coral reef restoration  
62 is logically maximized when the ability of species to adapt is known and high (Baums et al.  
63 2019). Assessing the relative environmental vs. genetic contribution to fitness variation,  
64 allows identifying the mechanisms shaping the ability of wild populations to adapt because  
65 the genetic variation of fitness is a prerequisite for adaptive evolution. This assessment is  
66 typically done by using quantitative genetic approaches to estimate genetic and environmental  
67 variance components for fitness proxies (Kruuk 2004). Experimental evidence in the wild  
68 showed that the Lifetime Reproductive Success (LRS) is a good proxy for the real fitness of  
69 individuals in wild populations (Brommer et al. 2004). LRS is the total number of offspring  
70 captured on site in a given monitored population recorded as breeders produced by individuals  
71 over their lifetime (Hendry et al. 2018). However, it remains rarely used in wild populations  
72 because its measurement requires long-term datasets (Bonnet et al. 2022). It was studied in  
73 birds and mammals (e.g. Kruuk et al. 2000, McCleery et al. 2004, Teplitsky et al. 2009,  
74 McFarlane et al. 2014), and only rarely in other taxa such as insects, fish and plants (Hendry et  
75 al. 2018, Salles et al. 2020). In our study, the LRS definition was slightly different because it  
76 was based on recruits defined as adults (or subadults) sampled and born on site rather than  
77 offspring produced by each individual and sampled as breeders on the following years (Salles  
78 et al. 2020). It is important to note that in long term surveys of a given wild population  
79 defined by its geographic perimeter, these two options are often equivalent.

80 Lack of knowledge on environmental and genetic variation of LRS in wild marine populations  
81 is obviously problematic when considering the stakes of their adaptation to global change.  
82 This is particularly true for coral reefs that are severely impacted and threatened by climate  
83 change (Hughes et al. 2003, van Hooidonk et al. 2016). The degradation and loss of coral reef  
84 habitats affects many fish species (Jones et al. 2004). Coral reef fish populations are  
85 experiencing a massive shift in selective forces that challenges their connectivity, self-  
86 recruitment, and therefore their conservation (Munday et al. 2008, 2009). Previous work in  
87 the long-term monitored wild population of the orange clownfish (*Amphiprion percula*) at  
88 Kimbe Island, Papua New Guinea, showed that the habitat of the breeders made the greatest  
89 contribution to LRS variation among individuals (Salles et al. 2020). Overall, this work  
90 demonstrated that there was little genetic variation in LRS (less than 2%) and therefore little  
91 microevolutionary adaptive change (Salles et al. 2020). Finally, the sustainability of this

92 population is therefore mostly under the control of the environment that the local breeders are  
93 experiencing.

94 Most studies investigating the genetic variation of fitness in monitored wild populations found  
95 that only a little proportion of this variation was attributable to genetic variation (Hendry et al.  
96 2018, Moiron et al. 2022), although Bonnet et al. (2022) found substantial genetic variation.  
97 This is expected from populations at evolutionary equilibrium when no adaptive evolution is  
98 ongoing over the rather limited timeframe of the survey as compared to the timeframe of the  
99 evolution of species. Ecological mechanisms driving fitness variation are rarely identified. In  
100 this study, we disentangle different ecological sources of variation in LRS that were  
101 previously combined into a unique notion of habitat (e.g., host anemone species, depth) and  
102 considered the role of spatial autocorrelation. These ecological effects may affect the  
103 contribution of individuals to recruitment through their LRS in this wild coral reef fish  
104 population. Our aim is also to improve the understanding of the capacity of wild clownfish to  
105 maintain self-recruitment above 50% in the population (Salles et al. 2016). This is crucial  
106 because the habitat of the clownfish is changing and self-recruitment has been shown as a key  
107 contribution for the population maintenance in the long term (Jones et al. 1999). In this  
108 system, most of the variation in LRS was explained by a breeder's habitat and the lagoon  
109 where they live (Salles et al. 2020). In the worldwide context of natural habitat degradation  
110 that also affects host anemones, it is crucial to separate the role of specific interactions from  
111 other ecological factors affecting clownfish survival. The relative contribution of the anemone  
112 species, its depth and the local density in anemones to the LRS of clownfish remains  
113 unknown to date. Knowledge of this relationship would improve our understanding of  
114 clownfish ecology and adaptation to their complex habitat. Moreover, the spatial distribution  
115 of anemones where the fish live is not homogeneous around Kimbe island. Because of this  
116 spatial heterogeneity, anemones are not spatially independent so that disentangling the effects  
117 of ecological conditions (density, depth, etc.) would be inappropriate if this spatial  
118 autocorrelation is unaccounted for.

119 Spatial autocorrelation of LRS is found if similarity in LRS exists amongst geographically  
120 close individuals (Legendre 1993). Although studies on this topic remain rare, they have  
121 mainly documented spatial variation in fitness proxies (Kalisz 1986, Stratton & Bennington  
122 1998, Wilkin et al. 2009). For example, Wilkin et al. (2009) found spatial variation for the  
123 average mass of great tit fledglings – which is a fitness proxy – in association with soil  
124 concentration in calcium in a woodland. Traditionally used in macro-ecological or population

125 genetic approaches, spatial autocorrelation recently gained interest for studies of fitness  
126 variation (Stopher et al. 2012, Marrot et al. 2015). This is because spatial autocorrelation  
127 causes pseudoreplication if not taken into account, which might strongly bias statistical  
128 estimates (Haining 2003). A meta-analysis conducted on 24 studies using linear regressions  
129 found that on average, model coefficients were biased by 25% when spatial autocorrelation  
130 was unaccounted for (Dormann 2007). For instance, heritability and selection can be  
131 overestimated if spatial dependency among sampling units is ignored (Stopher et al. 2012,  
132 Marrot et al. 2015, Gervais et al. 2022). Around Kimbe island, similar complications may  
133 arise from the spatial distribution of anemones associated with heterogeneity in depth and  
134 density by causing spatial dependency among clown fishes. This study has two aims: (i) to  
135 build a spatially explicit model estimating the effect of environmental features on the LRS of  
136 clownfish, and (ii) to compare this spatially explicit model to a spatially naïve model to  
137 quantify the potential bias induced by spatial dependency. To accomplish these aims, we used  
138 a geostatistical method that takes into account spatial autocorrelation at multiple scales to  
139 disentangle the relative contribution of environmental effects independently from spatial  
140 effects. Overall, we expected the effect of the host anemone species, local density, and depth  
141 to be overestimated when spatial autocorrelation is not taken into account.

142

## 143 **Material & Methods**

### 144 *Study system*

145 A natural population of orange clownfish (*A. percula*) living on the reef surrounding Kimbe  
146 Island (Fig. 1a; 5°12'22.56" S, 150°22'35.58" E), West New Britain Province of Papua New  
147 Guinea, was surveyed every second year from 2003 to 2013. *A. percula* lives in a mutualistic  
148 association with one of two host sea anemone species, *Heteractis magnifica* and *Stichodactyla*  
149 *gigantea*. All anemones occupied by a clownfish group have been geographically located,  
150 tagged for long term monitoring and sampled every second years for a total of 310 anemones  
151 (176 *H. magnifica* and 134 *S. gigantea*). A size-based dominance hierarchy exists within each  
152 clownfish group of typically three to five individuals: the female is the largest, the male is the  
153 second largest, and the immatures rank progressively lower in the hierarchy as they decrease  
154 in size. If the single female adult of a group dies, then the male changes sex to female, and the  
155 largest immature from the anemone moves up in the hierarchy to a sexually mature male.  
156 Reproduction occurs year-round, with females laying a few hundreds of eggs in a clutch near

157 the pedal disk of the host anemone each lunar month. The eggs hatch after c.a. 7 days of  
158 paternal care into larvae that spend c.a. 10 days in the pelagic environment (Roux et al. 2020)  
159 before settling into an anemone, either at their natal location (Kimbe Island) or elsewhere  
160 along a declining dispersal kernel (Planes et al. 2009). On the reefs around Kimbe Island,  
161 anemone positions were recorded with a GPS, and depth was measured using a dive  
162 computer. Anemones were surveyed during each biannual sampling period, and all clownfish  
163 individuals within the anemones were counted, captured using hand nets, measured using  
164 callipers (total length, TL), and fin-clipped underwater for genetic analysis. Each fish was  
165 processed on SCUBA in situ, with each individual caught, processed next to the anemone, and  
166 then released back on the same anemone. The biggest fish in each anemone was identified as  
167 the female, the second largest individual was assumed to be the male, and all other individuals  
168 were recorded as subadults (TL, >25 mm) or new recruits (TL, <25 mm). Every sampled fish  
169 was genotyped at 22 polymorphic microsatellite loci (Bonin et al. 2016) and the pedigree of  
170 the population has been constructed (see Salles et al. 2016 and Salles et al. 2020 for a  
171 complete description of the pedigree construction of this population). The pedigree revealed  
172 half of the juveniles successfully recruiting were progeny of local breeding pairs (Salles et al.  
173 2016).

174

#### 175 *LRS & Ecological drivers*

176 The high level of philopatry in this wild population of fish represents a rare opportunity to  
177 explore variation in LRS in a marine fish with a pelagic larval stage, given the fact that most  
178 estimations of LRS in the wild have been conducted in birds and mammals. Based on the  
179 pedigree, the LRS of an individual has been defined as the total number of descendants  
180 produced during its lifetime on a biannual basis that successfully recruited at Kimbe island.  
181 Note that, contrary to most studies using LRS, our LRS measure does not refer to the number  
182 of offspring produced by each individual and sampled as breeders on the following years. A  
183 recruit is defined as an adult (or subadult) sampled and born on the reef surrounding Kimbe  
184 island. This choice was made to adapt LRS to the group hierarchy of clownfish breeders and  
185 to be a sensible measurement of the relative ability of clownfish individuals to participate to  
186 the population self-recruitment. Our focus was made on the habitat of breeders and not on the  
187 habitat conditions where the larvae settle, which could have an effect on the LRS of their  
188 parents. The focus on the habitat of breeders rather than larvae should however not affect our  
189 results because clownfish offspring recruited in similar proportions in the two species of

190 anemones around Kimbe island (Salles et al. 2016). Furthermore, settlement habitat  
191 conditions were partially considered in the local density in anemone species within a 200m-  
192 radius around the focal anemone we investigated.

193 We chose to disentangle the effect of four ecological drivers: the anemone species where the  
194 parents are living (called after the “focal anemone”), the density in *H. magnifica* in a 200m-  
195 radius around the focal anemone, the density in *S. gigantea* in a 200m-radius around the focal  
196 anemone and the depth. The micro-habitat provided by the two anemone species is  
197 remarkably different in terms of shape, size and toxicity (Dunn 1981). Specifically, *H.*  
198 *magnifica* has larger and less toxic tentacles than *S. gigantea* (Nedosyko et al. 2014). We  
199 chose to measure the density of anemones in an area with a 200m-radius around the focal  
200 anemone because the spatial distribution of recruits is not heterogeneous around their parents  
201 in this population, and the mean distance between self-recruits and their parents was equal to  
202 254m ( $\pm$  189m), with 47% of recruits located at less than 200m from their parents  
203 (Supplementary information 1). This mean distance between recruits and their parents was  
204 significantly different (Wilcox test  $P$ -value  $<$  0.001) from the mean distance between each  
205 anemone occupied by a self-recruit and the other anemones in this population (388m  $\pm$  37m),  
206 suggesting a potential effect of the local environment around the focal anemone on the  
207 probability of self-recruiting (Jones et al., 2005; Buston et al., 2012). We chose to investigate  
208 depth as a potential driver because the two anemones species are not equally distributed  
209 across depth (Fig. 1B, 1C) with *H. magnifica* more likely found in deeper lagoon waters  
210 (4.10m  $\pm$  2.61) than *S. gigantea*, which is found closer to shore (1.34m  $\pm$  0.51). Moreover,  
211 because larvae may recruit on deeper anemones than their anemones of birth (Buston et al.  
212 2012), we expected that the probability to produce self-recruits increases as the depth of the  
213 anemone hosting the parents decreases, independently from the species of the anemone.

214

### 215 *Statistical analysis*

216 All statistical analyses were carried out using the R software (v. 4.0.3) (R Core Team, 2020).  
217 In this population, the mean of individual LRS was 1.27 ( $\pm$  2.32) and reached a maximum of  
218 20 self-recruits. Because the statistical distribution of individual LRS included an excess of  
219 zero (58% of individuals did not produce self-recruits in the population), we chose to test for  
220 the effect of ecological drivers by using a zero-inflated Poisson model. In this type of model,  
221 the excess of zero is analysed by a separate process (the probability that fish will not produce  
222 self-recruits, because in a zero-inflated model, it is the probability to have a zero that is



223 estimated, generally with a logit link function) from the count values (the number of self-  
224 recruits produced by breeders, generally with a log link function). This choice was  
225 corroborated by a smaller Akaike information criterion (AIC) of a null zero-inflated model  
226 (AIC=4246) than the AIC of a null generalized linear model following a Poisson distribution  
227 (AIC=5423). We included in the model the first year of sampling of each fish to take into  
228 account the effect of lifespan on LRS. Although this variable is an incomplete proxy of  
229 lifespan, it is equally spatially distributed in the population, preventing it from affecting the  
230 spatial distribution of LRS.

231

232 The explanatory variables included in the model were the species of the parental anemone (*S.*  
233 *gigantea* vs. *H. magnifica*), the depth and the density of the two species of anemone. This  
234 model is not spatially structured and we compared the estimates of responses variables to a  
235 spatially explicit model (see following section).

236

### 237 *Geostatistics*

238 The visualization of the spatial distribution of the LRS suggested that this variable is not  
239 homogeneous across space (Fig. 1A). Before conducting geostatistical analyses, we formally  
240 tested if LRS was significantly spatially autocorrelated around Kimbe island by using spatial  
241 correlograms. Our analysis revealed a significant and positive spatial autocorrelation at 230m  
242 and 460m and a significant negative spatial autocorrelation at 690m and 920m (Fig. 2A). This  
243 result indicated that LRS is not spatially independent and geostatistical modelling is required  
244 to disentangle the effect of the ecological drivers. Based on the abundant literature that  
245 compare the performance of different geostatistical methods (Dormann et al. 2007, Kissling  
246 and Carl 2008, Beguería and Pueyo 2009, Bini et al. 2009, Diniz-Filho et al. 2009, Beale et al.  
247 2010, Marrot et al. 2015), we chose to use the Principal Coordinates of Neighbourhood  
248 Matrix (PCNM) approach (Dray et al. 2006) because it is the best method to remove spatial  
249 autocorrelation, independently from its direction and its strength (relaxing the assumption of  
250 isotropy and stationary). The general principle of the PCNM is based on the extraction of  
251 eigenvectors from a truncated distance matrix among spatial units. Each of these eigenvectors  
252 (called after “Egs”) describes a specific spatial scale (regarding the spatial distribution of  
253 sampling units) and can be subsequently added as a covariate in any statistical model to model  
254 the spatial structure of the response variable (Borcard and Legendre 2002). The use of the  
255 PCNM approach can be decomposed in four steps: (i) compute a truncated pairwise Euclidean  
256 distance matrix between spatial units, (ii) perform principal coordinate analysis of the distance

257 matrix and extract the corresponding eigenvectors (Egs) for a total number of Egs equal to the  
258 number of sampling units (302 clownfish with non-null LRS at Kimbe island), (iii) select a  
259 subset of Egs to include as covariates in any model. Although the whole set of Egs describes  
260 the whole spatial structure of the dataset, it is not possible to include all Egs in any model  
261 without over-parameterizing it. This Egs selection part of the analysis is crucial and strategies  
262 to select Egs are diversified (Blanchet et al. 2008). We chose to conduct a backward-forward  
263 selection based on AIC (Ficetola and Padoa-schioppa 2009) to select the best set of Egs that  
264 explains spatial variation in LRS. This selection led us to keep 29 Egs. This set of Egs  
265 represented the minimum number of Egs necessary to describe spatial variation in LRS. (iv)  
266 Include the set of selected Egs in any model to take into account spatial autocorrelation  
267 between units of sampling. We included the set of 29 Egs as covariates in our model, and we  
268 compared the sign and the absolute value of ecological variables with a “naïve” model (not  
269 including the Egs). This approach allowed us to quantify the biased induced by spatial  
270 autocorrelation when it was ignored. In both models, all variables (ecological variables and  
271 Egs) have been standardized (o mean, unit variance).

272

## 273 **Results**

274

### 275 *Strong spatial autocorrelation*

276 Spatial autocorrelation detected in LRS (Fig. 2A) was totally removed by the set of 29 Egs  
277 selected by the PCNM method (Fig. 2B). We added this set of Egs as covariate in the zero-  
278 inflated model and we compared it with a naïve model. The estimates and their associated  
279 standard errors and *P*-values are summarised for the non-spatial and the spatially explicit  
280 model in Table 1. The inclusion of Egs altered the magnitude, the sign and the standard errors  
281 of estimates both in terms of probability of not self-recruiting and the count number of  
282 recruits produced (Table 1). Detailed results for each parameter are described below.

283

### 284 *Non spatial and spatially explicit model comparison*

285 The comparison between the non-spatial full model and a spatially explicit the model  
286 (including all variables and the set of 29 Egs) showed that the inclusion of Egs increased the  
287 degree of fit of the model with an improvement of adjusted  $R^2$  of 0.18 (the non-spatial and the  
288 spatially explicit model explained respectively 16% and 34% of the variance in LRS) and a

289 drop of AIC of 183. This AIC drop means that the inclusion of the 29 Eggs significantly  
290 improved the degree of fit of the model without over-parameterizing the model.

291

### 292 *Year of sampling effect*

293 In both non-spatial and spatially explicit models, the year of first sampling (first year  
294 sampling) increased the probability to not self-recruit and in the presence of self-recruitment  
295 decreased the number of recruits with the same magnitude (Table 1). This means that earliest  
296 sampled fish had the highest probability to produce at least one self-recruit and produced also  
297 more self-recruits than late sampled fish because mathematically, the monitoring period is  
298 more likely to overlap with the full lifespan of fish sampled earlier, which increases the  
299 probability to produce a self-recruit that we had the opportunity to sample.

300

### 301 *Ecological effect on LRS components*

302 The probability that fish will not produce a self-recruit (represented by the logarithm of the  
303 odds ratio; which estimate and 95% confidence interval are presented between brackets) was  
304 significantly affected by the focal anemone species (-0.693 [Standard Error: 0.248]) for  
305 breeders living on *S. gigantea*) in the spatially explicit model. Interestingly, this was also the  
306 case in the non-spatial model where the probability that fish will not produce a self-recruit  
307 was significantly affected by the focal anemone species (-0.527 [SE: 0.174]) for breeders  
308 living on *S. gigantea*, and the 200m-radius density in *H. magnifica* (-0.143 [SE: 0.070]).

309

310 We back transformed the results of the spatially explicit model from the latent (inferred  
311 through the model link function) to the observed scale for the sake of clarity. Fish living on *S.*  
312 *gigantea* had odds to not produce a self-recruit lowered by half ( $\exp(-0.693) = 0.553$ ), and  
313 therefore twice the odds to produce a self-recruit, in comparison to those living on *H.*  
314 *magnifica*. This means that, while our model estimated a probability to not self-recruiting of  
315 57% for all fishes, this probability was lowered by 17% for fishes living on *S. gigantea*.

316

317 The other component of LRS, which was the number of recruits produced by breeders, was  
318 not affected by the anemone species and was positively (but marginally significantly) affected  
319 by the density of *S. gigantea* in a 200m radius around the parental anemone (0.084 [SE:  
320 0.041]) in the spatially explicit model. It is interesting to note that it was significantly affected  
321 by the focal anemone species (0.383 [SE: 0.075]) for breeders living on *S. gigantea*) and the  
322 200m-radius density in both anemone species (0.125 [SE: 0.031]) and 0.126 [SE: 0.031] for

323 the density in *S. gigantea* and *H. magnifica* respectively) in the non-spatial model, again  
324 emphasizing some effect of spatial auto-correlation that is not taken into account in traditional  
325 analyses.

326

## 327 **Discussion**

328 Our spatially explicit analysis of long-term monitoring data from a wild clownfish population  
329 which pedigree and individual geographic location are known revealed two main results: (i)  
330 the spatially explicit model outperformed the non-spatially-explicit model, so that ignoring  
331 spatial autocorrelation affected the estimates of our zero-inflated model, (ii) breeders living on  
332 *S. gigantea* contributed to a larger extent to the self-recruitment of the population than those  
333 living on *H. magnifica*, and this effect was independent from the local density, the depth and  
334 the spatial structure.

335

336 *Why use a spatially explicit approach?*

337 Beyond taking into account the spatial structure of clownfish LRS to identify its ecological  
338 drivers independently from spatial effects, our study aimed at evaluating the consequences of  
339 not accounting for spatial autocorrelation. We successfully removed spatial dependency at all  
340 scales in LRS by using the PCNM approach. This method presents numerous advantages: it  
341 allows to control for spatial autocorrelation at any scale, it does not need the assumption of  
342 stationary (spatial autocorrelation does not depend on direction) and isotropy (spatial  
343 autocorrelation is constant across the study site), and it can be incorporated with any statistical  
344 models commonly used by ecologists (Borcard and Legendre 2002). The inclusion of Egs  
345 doubled the variance explained in the LRS at Kimbe island (the non-spatial and the spatially  
346 explicit model explained respectively 16% and 34% of the variance in LRS, Table 1),  
347 suggesting that unaccounted spatially autocorrelated variables affect the LRS. Note however  
348 that although the variance explained by a model including only the ecological variables  
349 explained 16% of the variation in LRS, it is incorrect to attribute 18% of variation explained  
350 by the Egs because ecological variables and Egs explained shared variation in LRS.  
351 Moreover, a model including only the set of Egs explained 27% of the variation in LRS (not  
352 shown in Table 1).

353

354 The comparison of the non-spatial and the spatially explicit models including the Egs revealed  
355 that, when unaccounted for, spatial autocorrelation biased the absolute values of estimates and

356 their confidence intervals. This result was not surprising and confirmed a large body of  
357 evidence, both on simulated and real data, showing the effect of spatial autocorrelation on  
358 estimates (e.g. Lennon 2000, Dormann 2007, Beale et al. 2010, Le Rest et al. 2013). As  
359 pseudoreplication, spatial autocorrelation decreases the precision (increasing the type 1 error)  
360 around estimates and alters (in a non-predictable way) their absolute values when  
361 unaccounted for if the response and the explicative variables are spatially autocorrelated  
362 (Beale et al. 2010). Among the ecological variables, three of them had their confidence  
363 intervals overlapping 0 (for both LRS components) when spatial autocorrelation was taken  
364 into account. Beyond statistical considerations, these results highlight how spatial  
365 autocorrelation may result in biological misinterpretations when unaccounted for. For  
366 example, while a non-spatial analysis would conclude that wild clownfish surrounded by a  
367 high density in anemone (within a 200m-radius) produce more recruits than those living in  
368 empty areas, our spatially explicit model did not detect any effect of the density in anemones.

369

#### 370 *Spatial autocorrelation of LRS*

371 Our results showed that there was a spatial structure of self-recruitment around Kimbe island.  
372 This is in line with a previous study conducted in the same clownfish population where it was  
373 suggested that the location of the lagoon could influence LRS (Salles et al. 2020). Our  
374 approach allowed us to go further and detected a strong spatial autocorrelation of LRS. As  
375 mentioned earlier, it would be inappropriate to try and to provide a precise estimate of its  
376 strength. This effect occurred over a relatively small spatial scale (less than 1km). This result  
377 is original because spatial autocorrelation is a property of ecosystems and can be found at any  
378 scale, from micrometres to the continental scale (Legendre 1993), but it was mainly  
379 investigated by ecologists interested in macro-ecological patterns at very large scales  
380 (Dormann 2007) and population geneticists estimating the limits of dispersal within and  
381 between populations (Sokal et al. 1989, Vekemans and Hardy 2004). It was in fact rarely  
382 investigated in studies exploring individual fitness variation. Only a few examples from wild  
383 plant and animal populations indicate that spatial autocorrelation can strongly impact the  
384 estimation of natural selection (Marrot et al. 2015, 2022), estimates of genetic variation for  
385 fitness-related traits (Stopher et al. 2012, Gervais et al. 2022) and now ecological drivers of  
386 LRS with this study. The biological mechanisms that underlie this pattern of spatial  
387 autocorrelation remain unknown to date. Yet, identifying them would improve our  
388 understanding of clownfish LRS and self-recruitment.

389 One limitation of our spatial analysis comes from the Euclidean distances that we used.  
390 Euclidean distances likely may not accurately represent connectivity in the ocean, where  
391 islands and currents can impede routes of travelling larvae (Tremblay et al. 2008). Oceanic  
392 distances accounting for actual currents around the island would be a good alternative to  
393 Euclidean distances (White et al. 2010, Truelove et al. 2017) because currents are generally  
394 predicted to have a strong effect on dispersal pattern (Cowen et al. 2000, but see Van  
395 Wynsberge et al. 2017). They would likely help to explain the variation of LRS more  
396 accurately. Our results have to be interpreted with caution since currents and the role of the  
397 island of Kimbe were not considered in our spatially-explicit analysis of LRS. One should  
398 note that a previous study showed that these currents were likely not influencing self-  
399 recruitment at short distances of about one kilometer around Kimbe island (Buston et al.  
400 2012) although at the broader scale of Kimbe bay, a direct relationship was found between  
401 geographic distance and genetic differentiation (Pinsky et al. 2017). Furthermore, although  
402 not explicitly modelled, the potential role of the island was at least partially taken into account  
403 by the PCNM method because it estimates patterns of spatial autocorrelation at any scale  
404 (Borcard and Legendre 2002).

405

#### 406 *The host anemone species affects clownfish LRS*

407 Our spatially explicit approach allowed us to identify some ecological drivers of wild *A.*  
408 *percula* clownfish LRS without potentially confounding their effect with spatial effects. Our  
409 results confirmed the findings from a previous study (Salles et al. 2020) conducted on the  
410 same clownfish population: an important part of variation in components of fitness linked to  
411 self-recruitment was explained by the ecological conditions of the habitat of breeders. Our  
412 approach allowed us to go further and disentangle the relative contribution of different  
413 ecological factors. Among them, we demonstrated that the anemone species is the only factor  
414 affecting the LRS. Specifically, we found a higher probability to produce at least one recruit  
415 for breeders living in *S. gigantea* than those living in *H. magnifica*. The spatially explicit  
416 approach showed that this effect was likely independent from the depth, the local density in  
417 anemones around the focal anemone, and the spatial structure of the population, suggesting a  
418 direct causal relationship between the anemone species and LRS.

419

420 Experiments will be necessary to identify the causal mechanism linking the anemone species  
421 to the variation in LRS that we observed in wild populations. Several hypotheses can be

422 assessed to explain our finding. First, one may push forward the lower clownfish fecundity  
423 caused by hormonal stress resulting from host anemone bleaching (Beldade et al. 2017) as a  
424 potential explanation of our results if anemone bleaching affected differentially the two  
425 anemone species. However, anemone bleaching cannot explain our results because evidence  
426 suggests that bleaching affects all anemone species with the same magnitude (Hobbs et al.  
427 2013) and no anemone bleaching event was reported over the duration of the survey. Second,  
428 one candidate hypothesis to explain the higher LRS of clownfish living on *S. gigantea* is that  
429 this anemone species is more toxic than *H. magnifica* (Nedosyko et al. 2014), which could  
430 offer more protection to clownfish, and ultimately affect positively its fitness because of a  
431 higher survival. Third, along with this difference in protection allocated to clownfish, female  
432 size may vary (Buston 2004) as it is mediated by the group size which has been shown to be  
433 driven by the size and shape of the anemone (Chausson et al. 2018). A direct link can be  
434 drawn to a recent study on *A. percula* (Barbasch et al. 2020), using both experimental design  
435 and field work data, which revealed a strong and positive relationship between anemone area,  
436 clownfish size, and reproductive success, driven by food availability. Whether *S. gigantea*  
437 provides clownfish with a higher food availability remains however to be tested. Observations  
438 in the field nevertheless suggest that clownfish spend more time feeding out and above *S.*  
439 *gigantea* anemones than clownfish hosted by *H. magnifica* (S. Planes personal observation).

440

441 The host anemone species, whether through their toxicity, size or available food, or other  
442 unknown features, directly influences wild clownfish self-recruitment, and thereby their  
443 ability to locally replenish the population around Kimbe island. Any changes to the ecology of  
444 the anemone species would therefore impact the sustainability of the clownfish population.  
445 The limits of the perspective on clownfish sustainability provided by our finding is restricted  
446 to the frontiers of the local population. Broader consequences cannot be revealed by our  
447 investigation of the local component of the clownfish lifetime reproductive success. Whether  
448 an integrative perspective considering long distance dispersal would reveal a trade-off  
449 between a breeder's ability to produce self-recruits and successful settlers on foreign  
450 anemones remains unknown to date.

451

## 452 *Conclusion*

453 Ecological conditions experienced by wild clownfish are impacting components fitness linked  
454 to self-recruitment such as the LRS. Our study showed that taking into account spatial

455 autocorrelation is efficient for disentangling ecological sources of variation from confounding  
456 spatial effects and prevents biological misinterpretation. Geostatistical models such as PCNM  
457 represent a powerful tool to identify the spatial autocorrelation of LRS, even at small spatial  
458 scale. In a context of worldwide threat on coral reefs (Hughes et al. 2003, van Hooidonk et al.  
459 2016), it is crucial to investigate the sources of individual variation in LRS to predict the  
460 resilience of wild coral reef fish populations. As part of a marine reserve (Almany et al.  
461 2007), the lagoons around Kimbe island where wild clownfish are monitored are protected  
462 from fishery or direct habitat degradation and this clownfish population has proven to persist  
463 in absence of migrants (Salles et al. 2015). However, our study revealed that the subsistence  
464 of the population could be altered if the proportion of *S. gigantea* was to change  
465 independently from density, depth and other environmental aspects and a similar concern  
466 could be raised if the spatial distribution of anemone species was to change.

467

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#### 481 **Conflict of interest disclosure**

482 The authors declare they have no conflict of interest relating to the content of this article.  
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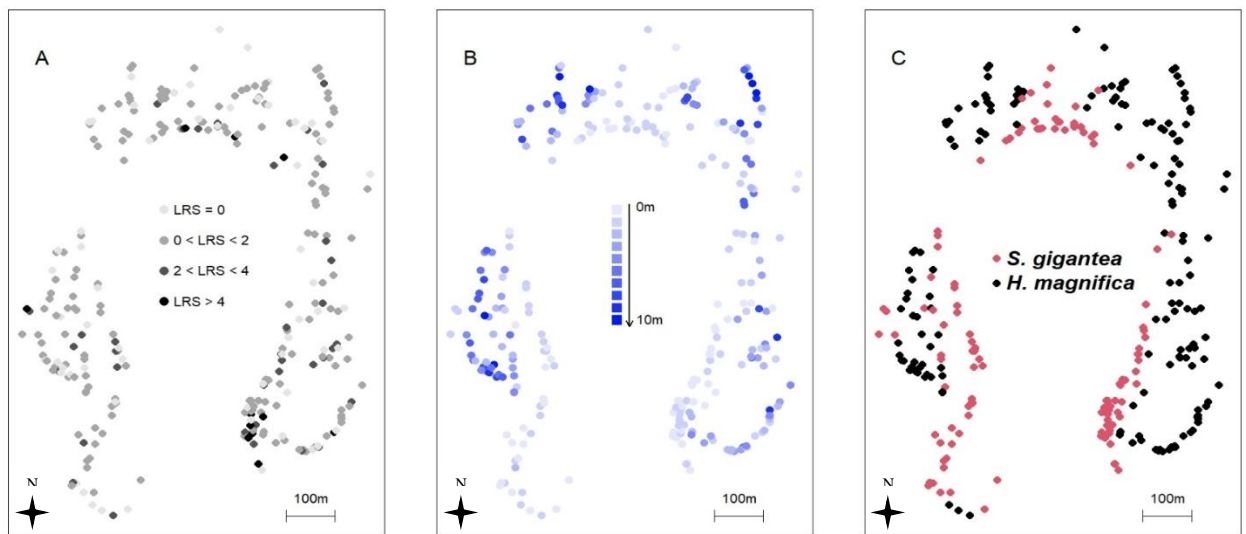


709 Table 1: Zero-inflated non-spatial vs. spatially explicit model estimates associated with their  
710 standard errors. The probability to not self-recruit is represented by the logarithms of the odds  
711 ratios. Anemone species: *S. gigantea* represents the effect of living on *S. gigantea* compared  
712 to *H. magnifica*. Density 200m *S. gigantea* and Density 200m *H. magnifica* represent  
713 respectively the effect of the density in *S. gigantea* and *H. magnifica* in a 200m-radius around  
714 the focal anemone. In bold the variables associated with P-values < 0.05.

715

	Non-spatial model			Spatial model (including Egs)		
	Estimates	Standard error	P-value	Estimates	Standard error	P-value
<i>Probability to not self-recruit</i>						
Intercept	<b>0.381</b>	<b>0.010</b>	<b>&lt;0.001</b>	<b>0.281</b>	<b>0.121</b>	<b>0.020</b>
First year sampling	<b>0.431</b>	<b>0.073</b>	<b>&lt;0.001</b>	<b>0.475</b>	<b>0.081</b>	<b>&lt;0.001</b>
Depth	0.026	0.082	0.750	-0.055	0.120	0.644
Anemone species: <i>S. gigantea</i>	<b>-0.527</b>	<b>0.174</b>	<b>&lt;0.01</b>	<b>-0.693</b>	<b>0.248</b>	<b>&lt;0.01</b>
Density 200m <i>S. gigantea</i>	0.060	0.070	0.400	0.074	0.095	0.434
Density 200m <i>H. magnifica</i>	<b>-0.143</b>	<b>0.070</b>	<b>0.040</b>	0.002	0.091	0.981
<i>Number of recruits produced</i>						
Intercept	<b>0.732</b>	<b>0.051</b>	<b>&lt;0.001</b>	<b>0.830</b>	<b>0.056</b>	<b>&lt;0.001</b>
First year sampling	<b>-0.312</b>	<b>0.039</b>	<b>&lt;0.001</b>	<b>-0.246</b>	<b>0.041</b>	<b>&lt;0.001</b>
Depth	0.029	0.040	0.471	0.001	0.050	0.989
Anemone species: <i>S. gigantea</i>	<b>0.383</b>	<b>0.075</b>	<b>&lt;0.001</b>	-0.047	0.101	0.642
Density 200m <i>S. gigantea</i>	<b>0.125</b>	<b>0.031</b>	<b>&lt;0.001</b>	<b>0.084</b>	<b>0.041</b>	<b>0.038</b>
Density 200m <i>H. magnifica</i>	<b>0.126</b>	<b>0.031</b>	<b>&lt;0.001</b>	0.071	0.040	0.075
<i>Degree of fit (including all variables)</i>						
Adjusted R <sup>2</sup>		0.16			0.34	
AIC		4042			3859	

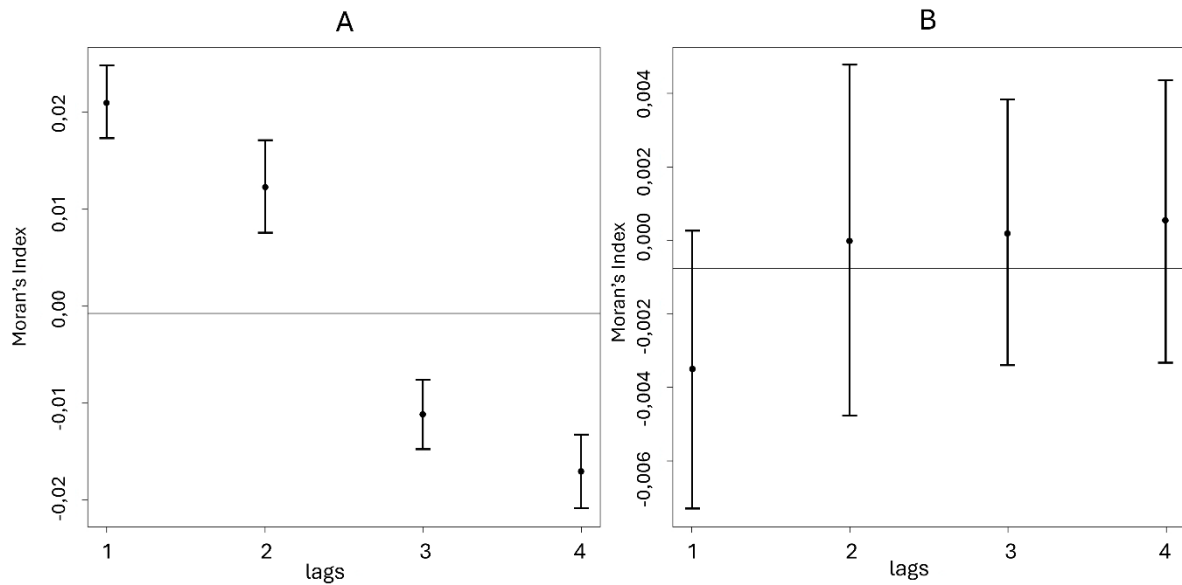
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717

718 Figure 1: Spatial distribution of the mean LRS (A, averaged among all breeding fishes living  
719 on the same anemone), the depth (B) and the anemone species (C). Each point represent an  
720 anemone for a total of 302 anemones sampled at Kimbe island.

721

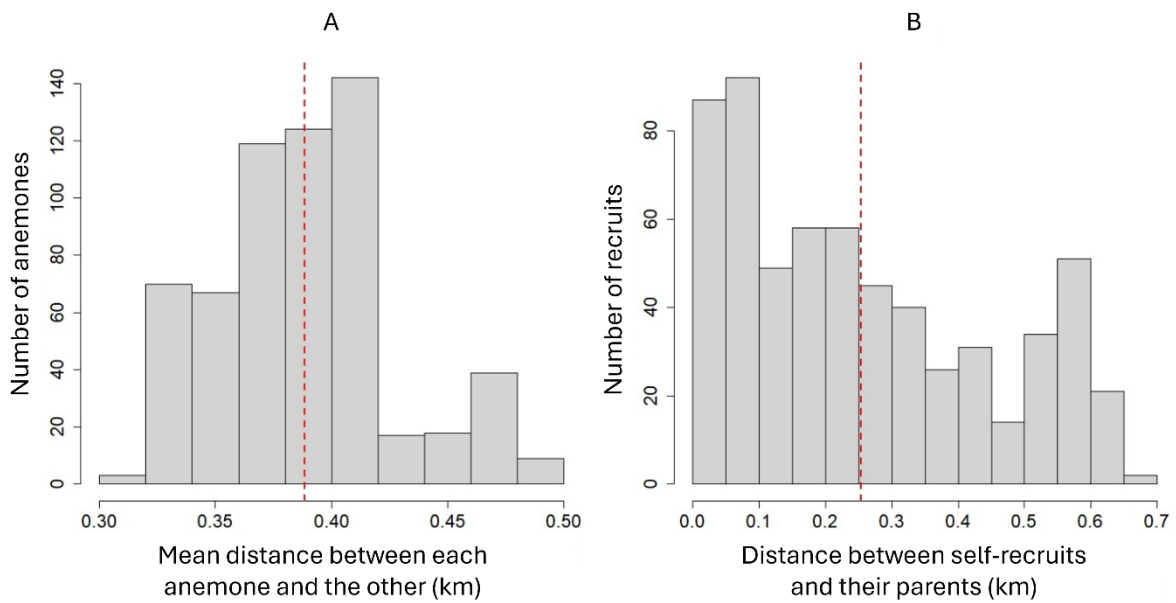


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723 Figure 2: Moran's I correlogram for LRS at Kimbe island (with associated standard  
 724 deviations) before (A) and after (B) correcting for spatial autocorrelation with the Egs  
 725 selected by the PCNM (see method). *For B, Moran's indexes have been estimated on the*  
 726 *residuals from a model linking the response variable (LRS) and the Egs only.* Moran's index  
 727 was calculated at 4 distance classes, from 230m to 920m, with a distance lag of 230m. There  
 728 is a significant and positive spatial autocorrelation at 230m and 460m and a significant  
 729 negative spatial autocorrelation at 690m and 920m in LRS before correcting for spatial  
 730 autocorrelation (A). Spatial autocorrelation was undetected in LRS after correcting with the  
 731 PCs (B).

732

733 Supplementary information 1: Statistical distribution of the mean distance between each  
734 anemone occupied by a self-recruit and the other anemones (A) and the distance between self-  
735 recruits and their parents (B) at Kimbe island. Red dotted lines represent the mean of each  
736 statistical distribution (A:  $388\text{m} \pm 37\text{m}$ ; B:  $254\text{m} \pm 189\text{m}$ ). Based on a Wilcoxon test, these  
737 two statistical distributions were significantly different ( $P < 0.001$ ). Note that 47% of self-  
738 recruits were located at less than 200m from their parents.



739

740