



HAL
open science

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

Pascal Marrot, Cécile Fauvelot, Michael L Berumen, Maya Srinivasan, Geoffrey P Jones, Serge Planes, Benoit Pujol

► To cite this version:

Pascal Marrot, Cécile Fauvelot, Michael L Berumen, Maya Srinivasan, Geoffrey P Jones, et al.. Spatial autocorrelation and host anemone species drive variation in local components of fitness in a wild clownfish population. 2024. <hal-04777386v1>

HAL Id: hal-04777386

<https://hal.science/hal-04777386v1>

Preprint submitted on 12 Nov 2024 (v1), last revised 14 Jan 2025 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

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

3

4 Pascal Marrot^{1,2}, Cécile Fauvelot^{2,3}, Michael L. Berumen⁴, Maya Srinivasan⁵, Geoffrey P.
5 Jones⁵, Serge Planes^{1,2}, Benoit Pujol^{1,2}

6

7 **Authors' affiliations:**

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

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

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

13 ⁴ 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 ⁵ 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

27 **Short running title:** Spatial autocorrelation of clownfish reproductive success

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 Hooidek 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 (Trembl 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

468 **Acknowledgements**

469 PM post-doc salary was funded by a grant from the Laboratoire d'Excellence CORAIL. This
470 research was supported by Laboratoire d'Excellence CORAIL, Expenditure Review
471 Committee, Coral Reef Initiatives for the Pacific, the Global Environment Facility Coral Reef,
472 Targeted Research Connectivity Working Group, National Science Foundation, the Australian
473 Research Council Centre of Excellence Coral Reef Studies, The Nature Conservancy, Total
474 Foundation, James Cook University, King Abdullah University of Science and Technology.
475 Research visas were approved by the Papua New Guinea (PNG) government and research
476 protocols were endorsed by the Board of Mahonia Na Dari Research and Conservation
477 Centre, Kimbe, PNG. We thank the large number of volunteers who assisted in the field and
478 collected tissue samples. Mahonia and FeBrina provided essential logistic support. We are
479 grateful to the traditional owners of the reefs near Kimbe Island for allowing us access to their
480 reefs.

481 **Conflict of interest disclosure**

482 The authors declare they have no conflict of interest relating to the content of this article.
483 Benoit Pujol is a recommender for PCI Evol Biol.

484 **References**

485 Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Automat.

486 Contr. 19:716–723.

487 Almany, G. R., M. L. Berumen, S. R. Thorrold, S. Planes, and G. P. Jones. 2007. Local
488 Replenishment of Coral Reef Fish Populations in a Marine Reserve. *Science* 316:742–
489 744.

490 Barbasch, T. A., T. Rueger, M. Srinivasan, M. Y. L. Wong, G. P. Jones, and P. M. Buston.
491 2020. Substantial plasticity of reproduction and parental care in response to local
492 resource availability in a wild clownfish population. *Oikos* 129:1844–1855.

493 Baums, I. B., A. C. Baker, S. W. Davies, A. G. Grottoli, C. D. Kenkel, S. A. Kitchen, I. B.
494 Kuffner, T. C. LaJeunesse, M. V Matz, M. W. Miller, J. E. Parkinson, and A. A. Shantz.
495 2019. Considerations for maximizing the adaptive potential of restored coral populations
496 in the western Atlantic. *Ecol. Appl.* 29:e01978.

497 Beale, C. M., J. J. Lennon, J. M. Yearsley, M. J. Brewer, and D. A. Elston. 2010. Regression
498 analysis of spatial data. *Ecol. Lett.* 13:246–264.

499 Beguería, S., and Y. Pueyo. 2009. A comparison of simultaneous autoregressive and
500 generalized least squares models for dealing with spatial autocorrelation. *Global Ecology*
501 and *Biogeography*. 18:273-279.

502 Beldade, R., A. Blandin, R. O'Donnell, and S. C. Mills. 2017. Cascading effects of thermally-
503 induced anemone bleaching on associated anemonefish hormonal stress response and
504 reproduction. *Nat. Commun.* 8:716.

505 Bini, L. M., J. A. F. Diniz-Filho, T. F. L. V. B. Rangel, T. S. B. Akre, R. G. Albaladejo, F. S.
506 Albuquerque, A. Aparicio, M. B. Araújo, A. Baselga, J. Beck, M. I. Belloq, K.
507 Böhning-Gaese, P. A. V. Borges, I. Castro-Parga, V. K. Chey, S. L. Chown, P. De
508 Marco, D. S. Dobkin, D. Ferrer-Castán, R. Field, J. Filloy, E. Fleishman, J. F. Gómez, J.
509 Hortal, J. B. Iverson, J. T. Kerr, W. D. Kissling, I. J. Kitching, J. L. León-Cortés, J. M.
510 Lobo, D. Montoya, I. Morales-Castilla, J. C. Moreno, T. Oberdorff, M. Á. Olalla-
511 Tárraga, J. G. Pausas, H. Qian, C. Rahbek, M. Á. Rodríguez, M. Rueda, A. Ruggiero, P.
512 Sackmann, N. J. Sanders, L. C. Terribile, O. R. Vetaas, and B. A. Hawkins. 2009.
513 Coefficient shifts in geographical ecology: An empirical evaluation of spatial and non-
514 spatial regression. *Ecography* 32:193–204.

515 Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Forward selection of explanatory
516 variables. *Ecology* 89:2623–2632.

517 Bonin, M. C., P. Saenz-Agudelo, H. B. Harrison, G. B. Nanninga, M. H. van der Meer, H.
518 Mansour, S. Perumal, G. P. Jones, and M. L. Berumen. 2016. Characterization and cross-
519 amplification of microsatellite markers in four species of anemonefish (Pomacentridae,
520 *Amphiprion spp.*). *Mar. Biodivers.* 46:135–140.

521 Bonnet, T., M. B. Morrissey, P. de Villemereuil, S. C. Alberts, P. Arcese, L. D. Bailey, S.
522 Boutin, P. Brekke, L. J. N. Brent, G. Camenisch, A. Charmantier, T. H. Clutton-Brock,
523 A. Cockburn, D. W. Coltman, A. Courtiol, E. Davidian, S. R. Evans, J. G. Ewen, M.
524 Festa-Bianchet, C. de Franceschi, L. Gustafsson, O. P. Höner, T. M. Houslay, L. F.
525 Keller, M. Manser, M. G. McAdam, E. McLean, P. Nietlisbach, H. L. Osmond, J. M.
526 Pemberton, E. Postma, J. M. Reid, A. Rutschmann, A. W. Santure, B. C. Sheldon, J.
527 Slate, C. Teplitsky, M. E. Visser, B. Wachter, and L. E. B. Kruuk. 2022. Genetic
528 variance in fitness indicates rapid contemporary adaptive evolution in wild animals.
529 *Science.* 376:1012-1016.

530 Borcard, D., and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of
531 principal coordinates of neighbour matrices. *Ecol. Modell.* 153:51–68.

532 Boutin, S., and J. E. Lane. 2014. Climate change and mammals: evolutionary versus plastic
533 responses. *Evol. Appl.* 7:29–41.

534 Brommer, J. E., L. Gustafsson, H. Pietiäinen, and J. Merilä. 2004. Single-generation estimates
535 of individual fitness as proxies for long-term genetic contribution. *Am. Nat.* 163:505–
536 517.

537 Buston, P. 2004. Does the presence of non-breeders enhance the fitness of breeders? An
538 experimental analysis in the clown anemonefish *Amphiprion percula*. *Behav. Ecol.*
539 *Sociobiol.* 57:23–31.

540 Buston, P. M., G. P. Jones, S. Planes, and S. R. Thorrold. 2012. Probability of successful
541 larval dispersal declines fivefold over 1 km in a coral reef fish. *Proc. R. Soc. B Biol. Sci.*
542 279:1883–1888.

543 Calsbeek, R., M. C. Duryea, D. Goedert, P. Bergeron, and R. M. Cox. 2015. Intralocus sexual
544 conflict, adaptive sex allocation, and the heritability of fitness. *J. Evol. Biol.* 28:1975–
545 1985.

546 Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000.
547 Connectivity of Marine Populations: Open or Closed? *Science* 287:857– 859.

548 Diniz-Filho, J. A. F., J. C. Nabout, M. Pires de Campos Telles, T. N. Soares, and T. F. L. V.
549 B. Rangel. 2009. A review of techniques for spatial modeling in geographical,
550 conservation and landscape genetics. *Genet. Mol. Biol.* 32:203–211.

551 Dormann, C. F. 2007. Effects of incorporating spatial autocorrelation into the analysis of
552 species distribution data. *Glob. Ecol. Biogeogr.* 16:129–138.

553 Dormann, C. F., J. M. Mcpherson, M. B. Arau, R. Bivand, J. Bolliger, G. Carl, R. G. Davies,
554 A. Hirzel, W. Jetz, W. D. Kissling, R. Ohlemu, P. R. Peres-neto, F. M. Schurr, and R.
555 Wilson. 2007. Methods to account for spatial autocorrelation in the analysis of species
556 distributional data : a review. *Ecography.* 30:609-628

557 Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive
558 framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol.*
559 *Modell.* 196:483–493.

560 Dunn, D. F. 1981. The Clownfish sea anemones: Stichodactylidae (Coelenterata: Actiniaria)
561 and other sea anemones symbiotic with Pomacentrid fishes. *Trans. Am. Philos. Soc.*
562 71:3–115.

563 Eizaguirre, C., and M. Baltazar-Soares. 2014. Evolutionary conservation—evaluating the
564 adaptive potential of species. *Evol. Appl.* 7:963–967.

565 Ficetola, G. F., and E. Padoa-schioppa. 2009. Human activities alter biogeographical patterns
566 of reptiles on Mediterranean islands. *Glob. Ecol. Biogeogr.* 18:214–222.

567 Fisher, R. A. 1930. *The genetical theory of natural selection*. The Clarendon Press.

568 Funk, W. C., B. R. Forester, S. J. Converse, C. Darst, and S. Morey. 2019. Improving
569 conservation policy with genomics: a guide to integrating adaptive potential into U.S.
570 Endangered Species Act decisions for conservation practitioners and geneticists.
571 *Conserv. Genet.* 20:115–134.

572 Galipaud, M., M. A. F. Gillingham, M. David, and F.-X. Dechaume-Moncharmont. 2014.
573 Ecologists overestimate the importance of predictor variables in model averaging: a plea
574 for cautious interpretations. *Methods Ecol. Evol.* 5:983–991.

575 Gervais, L., N. Morellet, I. David, M. Hewison, D. Réale, M. Goulard, Y. Chaval, B. Lourtet,
576 B. Cargnelutti, J. Merlet, E. Quéméré, and B. Pujol. 2022. Quantifying heritability and
577 estimating evolutionary potential in the wild when individuals that share genes also share

578 environments. *Evolution*. 91:1239-1250.

579 Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and
580 evolution: Disentangling environmental and genetic responses. *Mol. Ecol.* 17:167–178.

581 Grafen, A. T. H. 1988. *On the Uses of Data on Lifetime Reproductive Success*. University of
582 Chicago Press.

583 Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in
584 ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24:699–711.

585 Hendry, A. P., D. J. Schoen, M. E. Wolak, and J. M. Reid. 2018. The Contemporary
586 Evolution of Fitness. *Annu. Rev. Ecol. Evol. Syst.* 49:457–476.

587 Hobbs, J.-P. A., A. J. Frisch, B. M. Ford, M. Thums, P. Saenz-Agudelo, K. A. Furby, and M.
588 L. Berumen. 2013. Taxonomic, spatial and temporal patterns of bleaching in anemones
589 inhabited by anemonefishes. *PLoS One* 8:e70966.

590 Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world’s coral
591 reefs. *Mar. Freshw. Res.* 50:839–866.

592 Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connoly, C. Folke, R. Grosberg,
593 O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nyström,
594 S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change,
595 human impacts, and the resilience of coral reefs. *Science*. 301:929–933.

596 Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral
597 reef fish population. *Nature*. 402:802-804.

598 Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V Eagle. 2004. Coral decline threatens
599 fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA*. 101:8251– 8253.

600 Jones, G. P., S. Planes, and S. R. Thorrold. 2005. Coral reef fish larvae settle close to home.
601 *Curr. Biol.* 15:1314–1318.

602 Jordan, R., A. A. Hoffmann, S. K. Dillon, and S. M. Prober. 2017. Evidence of genomic
603 adaptation to climate in *Eucalyptus microcarpa*: Implications for adaptive potential to
604 projected climate change. *Mol. Ecol.* 26:6002–6020. J

605 Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna*
606 (Scrophulariaceae). *Evolution*. 40:479–491.

- 607 Kissling, W. D., and G. Carl. 2008. Spatial autocorrelation and the selection of simultaneous
608 autoregressive models. 59–71.
- 609 Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the “animal
610 model.” *Philos. Trans. R. Soc. B Biol. Sci.* 359:873–890.
- 611 Kruuk, L. E. B., T. H. Clutton-Brock, J. Slate, J. M. Pemberton, S. Brotherstone, and F. E.
612 Guinness. 2000. Heritability of fitness in a wild mammal population. *Proc. Natl. Acad.
613 Sci. USA.* 97:698–703.
- 614 Le Rest, K., D. Pinaud, and V. Bretagnolle. 2013. Accounting for spatial autocorrelation from
615 model selection to statistical inference: Application to a national survey of a diurnal
616 raptor. *Ecol. Inform.* 14:17–24.
- 617 Legendre, P. 1993. Spatial Autocorrelation: Trouble or New Paradigm? *Ecology* 74:1659–
618 1673.
- 619 Lennon, J. J. 2000. Red-shifts and red herrings in geographical ecology. *Ecography.* 23:101–
620 113.
- 621 Marrot, P., D. Garant, and A. Charmantier. 2015. Spatial autocorrelation in fitness affects the
622 estimation of natural selection in the wild. *Methods Ecol. Evol.* 6:1474–1483.
- 623 Marrot, P., M. Latutrie, J. Piquet, and B. Pujol. 2022. Natural selection fluctuates at an
624 extremely fine spatial scale inside a wild population of snapdragon plants. *Evolution.*
625 76:658–666.
- 626 Matz, M. V., E. A. Treml, and B. C. Haller. 2020. Estimating the potential for coral adaptation
627 to global warming across the Indo-West Pacific. *Glob. Chang. Biol.* 26:3473–3481.
- 628 Mccleery, R., R. Pettifor, P. Armbruster, K. Meyer, B. Sheldon, C. Perrins, and A. E. T. Price.
629 2004. Components of variance underlying fitness in a natural population of the great tit
630 *Parus major*. *Am. Nat.* 164:E62–E72.
- 631 Mcfarlane, S. E., J. C. Gorrell, D. W. Coltman, M. M. Humphries, S. Boutin, and A. G.
632 Mcadam. 2014. Very low levels of direct additive genetic variance in fitness and fitness
633 components in a red squirrel population. *Ecol. Evol.* 4:1729–1738.
- 634 Merilä, J., and A. P. Hendry. 2014. Climate change, adaptation, and phenotypic plasticity:
635 The problem and the evidence. *Evol. Appl.* 7:1–14.

636 Moiron, M., A. Charmantier, and S. Bouwhuis. 2022. The quantitative genetics of fitness in a
637 wild seabird. *Evolution*. 76:1443-1452.

638 Munday P. L., G. P. Jones, M. S. Pratchett, and A. J. Williams. 2008. Climate change and the
639 future for coral reef fishes. *Fish and Fisheries*. 9:261-285.

640 Munday P. L., J. M. Leis, J. M. Lough, C. B. Paris, M. J. Kingsford, M. L. Berumen, and J.
641 Lambrechts. 2009. Climate change and coral reef connectivity. *Coral Reefs*. 28:379-395.

642 Muñoz, N. J., A. P. Farrell, J. W. Heath, and B. D. Neff. 2015. Adaptive potential of a Pacific
643 salmon challenged by climate change. *Nat. Clim. Chang*. 5:163–166.

644 Nedosyko, A. M., J. E. Young, J. W. Edwards, and K. Burke da Silva. 2014. Searching for a
645 toxic key to unlock the mystery of anemonefish and anemone symbiosis. *PLoS One*
646 9:e98449.

647 Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu.*
648 *Rev. Ecol. Evol. Syst.* 37:637–669.

649 Pinsky, M. L., P. Saenz-Agudelo, G. R. Almany, M. Bode, G. P. Jones, S. Planes. 2017.
650 Equivalence of marine dispersal over evolutionary and ecological time. *Current Biol.*
651 27:149-154.

652 Planes, S., G. P. Jones, and S. R. Thorrold. 2009. Larval dispersal connects fish populations in
653 a network of marine protected areas. *Proc. Natl. Acad. Sci. USA*. 106:5693– 5697.

654 Price, G. R. 1970. Selection and Covariance. *Nature*. 227:520–521.

655 R Core Team. 2020. R: A language and environment for statistical computing. R Foundation
656 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

657 Roux, N., P. Salis, S.-H. Lee, L. Besseau, and V. Laudet. 2020. Anemonefish, a model for
658 Eco-Evo-Devo. *Evodevo* 11:20.

659 Salles, O. C., G. R. Almany, M. L. Berumen, G. P. Jones, P. Saenz-Agudelo, M. Srinivasan,
660 S. R. Thorrold, B. Pujol, and S. Planes. 2020. Strong habitat and weak genetic effects
661 shape the lifetime reproductive success in a wild clownfish population. *Ecol. Lett.*
662 23:265–273.

663 Salles, O. C., J. A. Maynard, M. Joannides, C. M. Barbu, P. Saenz-Agudelo, G. R. Almany,
664 M. L. Berumen, S. R. Thorrold, G. P. Jones, and S. Planes. 2015. Coral reef fish

665 populations can persist without immigration. *Proc. R. Soc. B.* 282:20151311.

666 Salles, O. C., B. Pujol, J. A. Maynard, G. R. Almany, M. L. Berumen, G. P. Jones, P. Saenz-
667 Agudelo, M. Srinivasan, S. R. Thorrold, and S. Planes. 2016. First genealogy for a wild
668 marine fish population reveals multigenerational philopatry. *Proc. Natl. Acad. Sci. USA.*
669 113:13245–13250.

670 Sokal, R. R., G. M. Jacquez, and M. C. Wooten. 1989. Spatial autocorrelation analysis of
671 migration and selection. *Genetics* 121:845–855.

672 Stopher, K. V, C. A. Walling, A. Morris, F. E. Guinness, T. H. Clutton-brock, J. M.
673 Pemberton, and D. H. Nussey. 2012. Shared spatial effects on quantitative genetics
674 parameters: accounting for spatial autocorrelation and home range overlap reduces
675 estimates of heritability in wild red deer. *Evolution.* 66:2411-26.

676 Stratton, D. A., and C. C. Bennington. 1998. Fine-grained spatial and temporal variation in
677 selection does not maintain genetic variation in *Erigeron annuus*. *Evolution.* 52:678-691.

678 Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel
679 inference and model averaging in behavioural ecology using Akaike's information
680 criterion. *Behav. Ecol. Sociobiol.* 65:13–21.

681 Teplitsky, C., J. A. Mills, J. W. Yarrall, and J. Merilä. 2009. Heritability of fitness
682 components in a wild bird population. *Evolution.* 63:716–726.

683 Thayn, J. B., and J. M. Simanis. 2013. Accounting for spatial autocorrelation in linear
684 regression models using spatial filtering with eigenvectors. *Ann. Assoc. Am. Geogr.*
685 103:47–66.

686 Treml, E. A., P. N. Halpin, D. L. Urban, and L. F. Pratson. 2008. Modeling population
687 connectivity by ocean currents, a graph-theoretic approach for marine conservation.
688 *Landsc. Ecol.* 23:19–36.

689 Truelove, N. K., S. J. Box, K. A. Aiken, A. Blythe-Mallett, E. M. Boman, C. J. Booker, T. T.
690 Byfield, C. E. Cox, M. H. Davis, G. A. Delgado, B. A. Glazer, S. M. Griffiths, K.
691 Kitson-Walters, A. S. Kough, R. Pérez Enríquez, R. F. Preziosi, M. E. Roy, I. Segura-
692 García, M. K. Webber, and A. W. Stoner. 2017. Isolation by oceanic distance and spatial
693 genetic structure in an overharvested international fishery. *Divers. Distrib.* 23:1292–
694 1300.

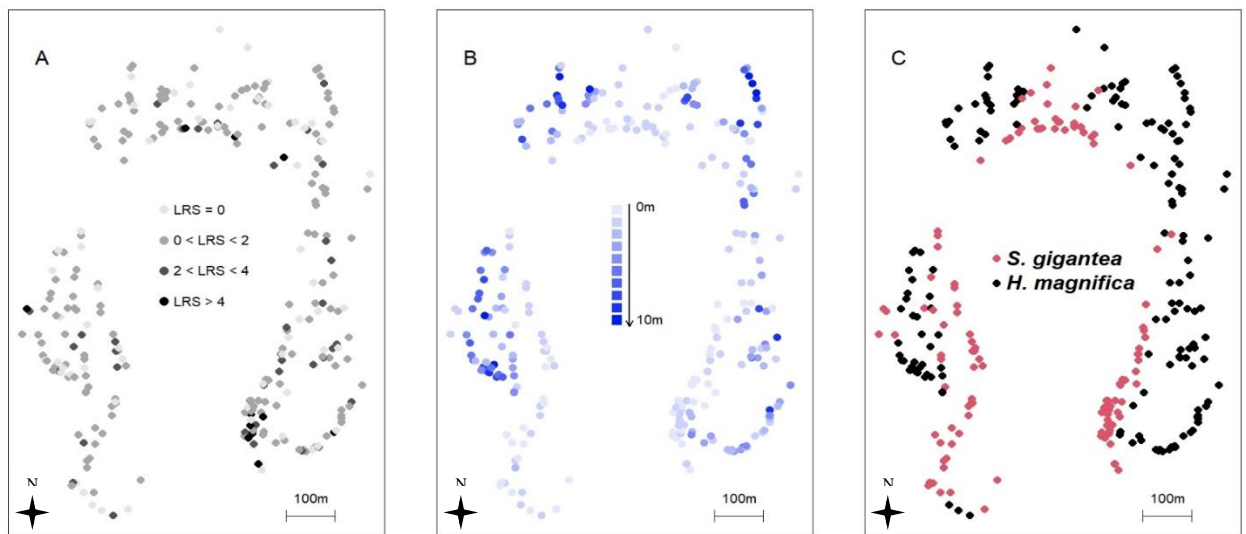
- 695 Vekemans, X., and O. Hardy. 2004. New insights from fine-scale spatial genetic structure
696 analyses in plant populations. *Mol. Ecol.* 13:921-935.
- 697 van Hooidek, R., J. Maynard, J. Tamelander, J. Gove, G. Ahmadi, L. Raymundo, G.
698 Williams, S. F. Heron, and S. Planes. 2016. Local-scale projections of coral reef futures
699 and implications of the Paris Agreement. *Sci. Rep.* 6:39666.
- 700 Van Wynsberge, S., S. Andréfouët, N. Gaertner-Mazouni, J. Tiavouane, D. Grulois, J.
701 Lefèvre, M. L. Pinsky, and C. Fauvelot. 2017. Considering reefscape configuration and
702 composition in biophysical models advance seascape genetics. *PLoS ONE* 12: e0178239.
- 703 White, C., K. A. Selkoe, J. Watson, D. A. Siegel, D. C. Zacherl, R. J. Toonen. 2010. Ocean
704 currents help explain population genetic structure. *Proc. R. Soc. B.* 277:1685–1694.
- 705 Wilkin, T. A., A. G. Gosler, D. Garant, S. J. Reynolds, and B. C. Sheldon. 2009. Calcium
706 effects on life-history traits in a wild population of the great tit (*Parus major*): Analysis
707 of long-term data at several spatial scales. *Oecologia* 159:463–472.
- 708

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	0.381	0.010	<0.001	0.281	0.121	0.020
First year sampling	0.431	0.073	<0.001	0.475	0.081	<0.001
Depth	0.026	0.082	0.750	-0.055	0.120	0.644
Anemone species: <i>S. gigantea</i>	-0.527	0.174	<0.01	-0.693	0.248	<0.01
Density 200m <i>S. gigantea</i>	0.060	0.070	0.400	0.074	0.095	0.434
Density 200m <i>H. magnifica</i>	-0.143	0.070	0.040	0.002	0.091	0.981
<i>Number of recruits produced</i>						
Intercept	0.732	0.051	<0.001	0.830	0.056	<0.001
First year sampling	-0.312	0.039	<0.001	-0.246	0.041	<0.001
Depth	0.029	0.040	0.471	0.001	0.050	0.989
Anemone species: <i>S. gigantea</i>	0.383	0.075	<0.001	-0.047	0.101	0.642
Density 200m <i>S. gigantea</i>	0.125	0.031	<0.001	0.084	0.041	0.038
Density 200m <i>H. magnifica</i>	0.126	0.031	<0.001	0.071	0.040	0.075
<i>Degree of fit (including all variables)</i>						
Adjusted R ²	0.16			0.34		
AIC	4042			3859		

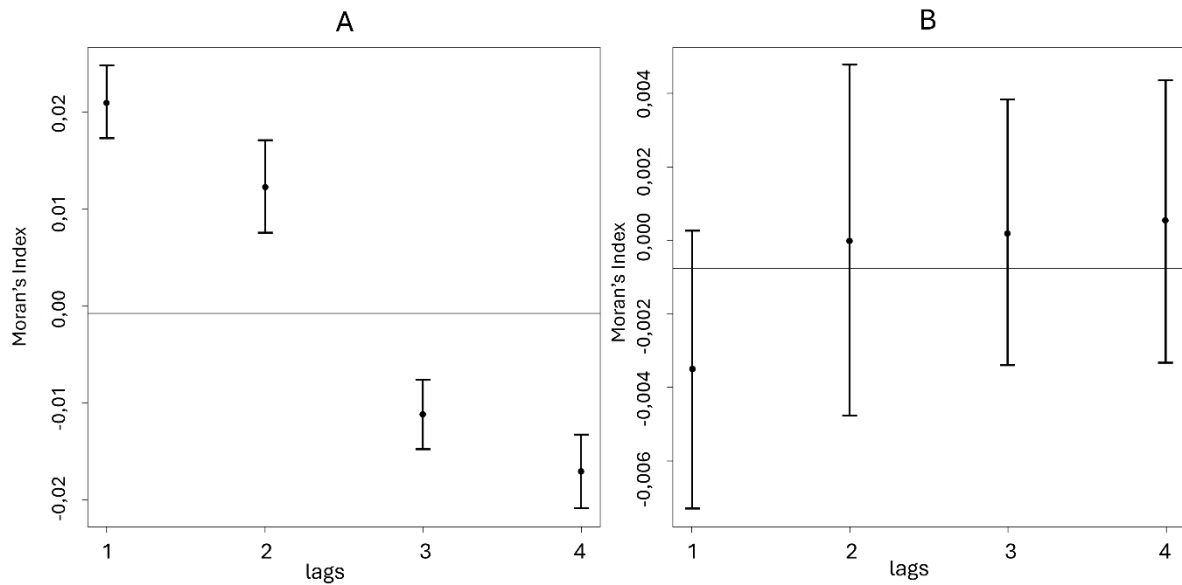
716



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

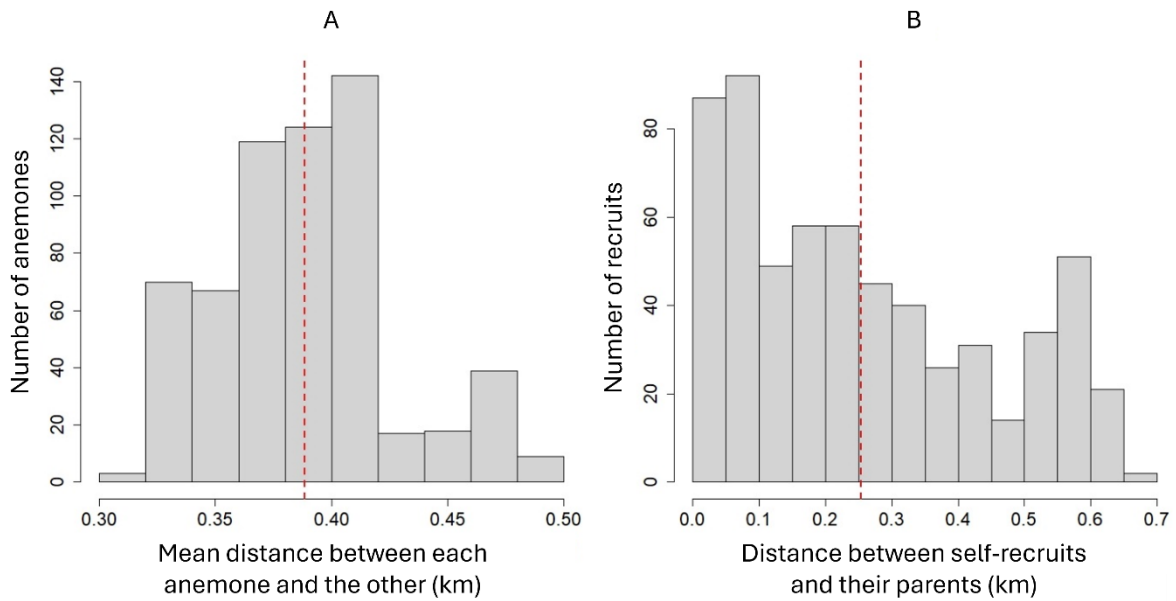


722

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: 388m \pm 37m; B: 254m \pm 189m). 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