

1 **Marine dispersal scales are congruent over**  
2 **evolutionary and ecological time**

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31  
32 **Article type:** Report  
33

34 **Summary**

35         The degree to which offspring remain near their parents or disperse widely is critical for  
36 understanding population dynamics, evolution, and biogeography, and for designing  
37 conservation actions. In the ocean, most estimates suggesting short-distance dispersal are based  
38 on direct ecological observations of dispersing individuals, while indirect evolutionary estimates  
39 often suggest substantially greater homogeneity among populations. Reconciling these two  
40 approaches and their seemingly competing perspectives on dispersal has been a major challenge.  
41 However, here we show for the first time that evolutionary and ecological measures of larval  
42 dispersal can closely agree by using both to estimate the distribution of dispersal distances. In  
43 orange clownfish (*Amphiprion percula*) populations in Kimbe Bay, Papua New Guinea, we  
44 found that evolutionary dispersal kernels were 17 [95% CI: 12–24] km wide, while an exhaustive  
45 set of direct larval dispersal observations suggested kernel widths of 27 [19–36] km or 19 [15–  
46 27] km across two years. The similarity between these two approaches suggests that ecological  
47 and evolutionary dispersal kernels can be equivalent, and that the apparent disagreement between  
48 direct and indirect measurements can be overcome. Our results suggest that carefully applied  
49 evolutionary methods, which are often less expensive, can be broadly relevant for understanding  
50 ecological dispersal across the tree of life.

51  
52 **Keywords:** population genetics, connectivity, isolation by distance, metapopulation, reef fish,  
53 larvae

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## 56 **Results**

57       The extent to which offspring disperse from natal locations remains a key uncertainty in  
58 ecology and evolution, particularly in the ocean. Dispersal distances are often represented as  
59 probability distributions, with some offspring providing demographically significant local  
60 recruitment and other larvae contributing to gene flow over longer distances. However, the width  
61 of these kernels has been difficult to determine. Evidence for the spatial scales of marine larval  
62 dispersal falls into two broad types: direct observations of individuals that have dispersed over  
63 ecological timescales, or measurements of genetic patterns that indirectly reveal dispersal over  
64 evolutionary timescales. Direct observations have been important for revealing short-distance  
65 dispersal [1, 2]. In contrast, indirect methods have often suggested long-distance dispersal and  
66 dramatic homogeneity among populations across large areas [3, 4]. Explanations for this  
67 apparent disparity include differences in the time scales and dispersal metrics measured with the  
68 two approaches [1, 5, 6], a potential bias towards direct measurements in species with short-  
69 distance dispersal [1, 3, 7], as well as a potential lack of statistical power [8], assumptions of  
70 equilibrium and simplistic demography [9, 10], and a potential influence from historical events  
71 [11] for many indirect approaches. Reconciling these seemingly contradictory results has become  
72 an important goal in ecology and oceanography [4, 12]. However, no explicit comparison of  
73 direct ecological and indirect evolutionary methods using equivalent dispersal metrics has been  
74 undertaken for any marine species.

75       Here, we reconcile evolutionary and ecological perspectives on dispersal in the orange  
76 clownfish (*Amphiprion percula*). This is a genus for which both long-distance gene flow over  
77 1000 km [13] and short-distance self-recruitment over 100 m has been reported [1, 14]. We  
78 compare dispersal measured from the direct detection of parent-offspring relationships [15]  
79 against an indirect approach based on isolation by distance (IBD) genetic patterns [16]. Patterns  
80 of IBD are common in marine organisms, occurring in at least half of all species examined [17,  
81 18].

### 82 ***Isolation by distance (IBD) patterns***

83       For our indirect evolutionary approach, we analyzed 21 microsatellites genotyped in 467  
84 clownfish collected from ten sites in Kimbe Bay, Papua New Guinea (Fig. 1, Table 1). Genetic  
85 divergence between populations was generally low (pairwise  $F_{ST}$ s < 0.03), suggesting extensive  
86 gene flow among populations. However, a strong IBD pattern was also apparent, and genetic  
87 distance between populations increased with geographic distance (Fig. 2, slope = 0.00014 [95%  
88 CI, 0.00010–0.00018],  $r^2 = 0.54$ , Mantel test  $p = 0.0013$ ). We also detected two moderate  
89 deviations from the overall IBD pattern: comparisons to the Muli site generally showed more  
90 divergence than would be expected from distance alone (Fig. 2 open circles), while comparisons  
91 to Tarobi generally showed less divergence than expected from distance alone (Fig. 2 squares).  
92 Muli is further offshore and more isolated, while Tarobi is close to shore and surrounded by  
93 extensive reef (Fig. 1). Jackknifing revealed relatively little sensitivity of the slope estimate to  
94 individual loci or populations (slopes ranged 0.00013–0.00015 over loci and 0.00012–0.00015  
95 over populations).

### 96 ***Effective density***

97       Estimating dispersal distances from IBD patterns requires measurements of the strength  
98 of genetic drift. The effective population size for Kimbe Bay was 1,363 individuals [95% CI,  
99 783–2834 individuals], or 6.1 individuals/km [95% CI, 3.5–12.6 individuals/km] over the 225  
100 km length of the bay, as estimated from gametic disequilibrium patterns in the cohort of new

101 recruits (Table 1) and corrected for overlapping generations. As expected, this is considerably  
102 lower than the number and density of adults estimated from visual surveys:  $42,300 \pm 10,100$   
103 individuals ( $\pm 1$  SEM), or  $188 \pm 45$  adults/km ( $\pm 1$  SEM). These estimates put the  $N_e/N$  ratio at  
104 3.4% [95% CI, 1.6–8.5%].

### 105 ***Dispersal kernel measurements from IBD***

106 Using IBD theory, we then used the slope of the IBD relationship and the effective  
107 density to estimate the spread (measured as the standard deviation) of the dispersal kernel while  
108 accounting for the uncertainty in each parameter (Table S2). The kernel is a probability  
109 distribution and the height of the kernel provides the probability of larvae dispersing to each  
110 position (Fig. 3d). The dispersal spread ( $\sigma$ ) for *A. percula* in Kimbe Bay was 17.2 km [95% CI,  
111 11.7–23.6 km]. An alternative, maximum likelihood method using Wright's neighborhood size  
112 instead of the IBD slope calculated a very similar dispersal spread of 17.9 km [95% CI, 12.2–  
113 24.1 km].

114 In contrast, using erroneous values for effective population density led to substantially  
115 different dispersal kernels (Fig. 3). For example, if we substituted census density from visual  
116 surveys (a severe overestimate) into the IBD equations, the results suggested a very narrow  
117 kernel with a dispersal spread ( $\sigma$ ) of 3.0 km [95% CI, 2.4–4.3 km]. Alternatively, results would  
118 also have been very different if we had used census density and a literature value for the  $N_e/N$   
119 ratio, instead of measuring  $N_e$  directly.  $N_e/N$  ratios are often near 0.001 in marine fishes, but this  
120 value would have produced a very wide kernel with a spread ( $\sigma$ ) of 95.6 km [95% CI, 75.7–136  
121 km].

### 122 ***Comparison of direct and indirect approaches***

123 We then compared our evolutionary dispersal estimates to kernels that had been fit to  
124 directly detected larval dispersal events [15]. In 2009, 407 of 1,447 sampled recruits (28%) were  
125 assigned to one or both parents from a pool of 2,546 potential parents. In 2011, 437 of 1,547  
126 recruits (28%) were assigned to parents from a pool of 2,913 adults. Both of the indirect  
127 dispersal spread values compared well to, but were slightly lower than, the direct ecological  
128 estimates of 26.5 [95% CI, 19.1–35.8] km in 2009 and 18.9 [95% CI, 15.5–26.8] km in 2011  
129 (Fig. 3a, d). Comparison of these kernels suggested that the 2009 kernel was 38% larger, with a  
130 95% CI of 1% smaller to 61% larger, than the IBD kernel. The 2011 kernel was only 11% larger,  
131 with a 95% CI of 34% smaller to 44% larger. Compared to the range of potential scales, from  
132 100s of m to 100s of km, these differences were slight.

133 The direct parent-offspring data indicated that a Laplacian dispersal kernel provided the  
134 best fit to the data [15]. Applying this kernel suggested an average dispersal distance of 12.1 km  
135 [95% CI, 8.2–16.7 km] from the IBD estimate, compared with 18.9 km [95% CI, 13.4–25.4 km]  
136 and 13.3 km [95% CI, 11.1–19.1 km] from direct methods in 2009 and 2011, respectively (Fig.  
137 3b). These estimates also suggested moderate levels of larval retention near their natal site. For  
138 individuals on the edge of small habitat patches 500 m wide, only 2% of larvae would be  
139 retained, while 17% would be retained on patches 5 km wide (Fig. 3c). Stated differently, 50% of  
140 larvae were expected to settle within 8 km and 95% to settle within 36 km. Indirect evolutionary  
141 retention values were slightly higher than those from the wider ecological dispersal kernels (Fig.  
142 3c). Retention with an alternative Gaussian kernel would be slightly lower (Fig. S1).

143

## 144 Discussion

145 Our investigation revealed agreement between long-term, indirect measurements of  
146 dispersal and short-term, direct measurements for *A. percula* populations in Kimbe Bay. The  
147 congruence helps reconcile the historically large gap between measurements of dispersal over  
148 ecological and evolutionary timescales, and between direct and indirect methods [4]. These  
149 results also suggest that micro-evolutionary methods based on isolation by distance patterns can  
150 be broadly useful for measuring ecologically relevant dispersal in the ocean.

151 A number of factors may help explain this congruence. First, we compared equivalent  
152 metrics (dispersal kernel spread), rather than qualitative conclusions about high or low dispersal.  
153 Second, we used appropriate spatial scales for both methods. Micro-evolutionary patterns of IBD  
154 reach a stationary phase within several generations over local spatial scales less than 50 times the  
155 dispersal spread [19, 20]. Our indirect estimates were therefore relatively less influenced by  
156 historical events. Similarly, our sampling for direct estimates was conducted over a relatively  
157 large spatial expanse and was better able to detect long-distance but rare dispersal. Finally,  
158 previous studies using IBD methods have faced consistent challenges measuring the strength of  
159 genetic drift, which usually requires a time-consuming demographic study [21-24], uncertain  
160 genetic methods [25-28], or a range of guesses [17, 29]. We overcame this limitation with a  
161 newly developed method for species with overlapping generations [30]. Our example erroneous  
162 values for effective density showed that guessing at effective density can produce substantially  
163 different dispersal estimates.

164 If used more broadly, care must be taken to appropriately apply and interpret IBD  
165 approaches. Sampling for IBD patterns needs to be spread over scales of  $10-50\sigma$ , since these are  
166 the scales at which genetic patterns are dominated by recent drift and dispersal [19, 20]. When  
167 appropriate scales are unknown, sampling a range of distances can identify the scale of IBD [31].  
168 Minimum age of reproduction and length of reproductive lifespan is also helpful to apply Waples  
169 et al.'s correction to effective population size for overlapping generations [30]. However, the  
170 correction was minor in clownfish (from  $\hat{N}_b = 1427$  to  $\hat{N}_e = 1363$ ), and will generally be minor  
171 in species with early maturity and long lifespans. Accurately estimating effective population size  
172 is important, and a 10x error in effective population size translates to a ~3x error in the dispersal  
173 estimate (see *Supplemental Experimental Procedures*). In general, uncertainty about effective  
174 population size is more important than uncertainty in the IBD pattern [27]. Because IBD  
175 methods measure a long-term average, they will be most meaningful in systems without  
176 persistent changes in dispersal or abundance (in contrast, variance around a stationary mean is  
177 less concerning). Direct methods will continue to be important for research that requires finer  
178 temporal or spatial resolutions.

179 The more widespread use of IBD methods creates an exciting opportunity to understand  
180 how dispersal varies across species and regions. IBD signals are common in marine species, with  
181 30 of 62 tests (48%) revealing isolation by distance in a recent metaanalysis [18], a figure that  
182 may even be an underestimate because study design often impedes IBD detection. Understanding  
183 patterns of dispersal across species and regions has been difficult, in part because many genetic  
184 measures do not separate the effects of genetic drift from gene flow [32]. For example, a widely  
185 cited meta-analysis had to make the strong assumption that all species had the same population  
186 density [33]. There remain important questions about how dispersal varies among marine  
187 species, including the relative importance of larval vs. adult traits [34] and oceanography vs.  
188 behavior [35]. Measurements of larval dispersal across a wide range of species using IBD could  
189 help answer these questions.

190 The degree to which marine larvae stay close to home or travel long distances has been a  
191 debate for decades. Our estimates of dispersal spread in a clownfish suggest that typical dispersal  
192 distances are neither hundreds of meters nor hundreds of kilometers, both of which have been  
193 suggested [13, 36]. Evidence that the probability of recruitment declines quickly over the first  
194 kilometer in clownfish [14], in combination with our measurements of slower rates of decline  
195 over dozens of kilometers, suggests that different dispersal processes may operate at different  
196 spatial scales. This conclusion would be consistent with differences between the hydrodynamics  
197 immediately over and around reefs and the regional eddies, jets, and currents that act between  
198 reefs. There may be a hierarchy of processes, with one set of larvae settling on their natal reef  
199 after experiencing only near-shore hydrodynamics, and a second set of larvae that are swept off-  
200 shore and transported dozens of kilometers.

201 Our results also contribute to fundamental questions about metapopulation persistence  
202 [37]. For a population to persist, it needs to meet the replacement criterion, namely  $F \times S \times$   
203  $LR > 1$ , where  $F$  is per capita lifetime fecundity,  $S$  is survival of recruits to adulthood, and  $LR$  is  
204 the proportion of locally retained larvae [37]. We can combine existing measurements of  
205 clownfish fecundity, lifespan, and survival [37-40] for a rough estimate of  $F \times S =$   
206  $0.08 \frac{\text{recruits}}{\text{adult-month}} \times 150 \frac{\text{months}}{\text{adult}} \times 0.4 \frac{\text{adults}}{\text{recruit}} = 4.8 \frac{\text{adults}}{\text{adult}}$ . Therefore, populations with  $LR > 20\%$   
207 should be persistent. With Laplacian dispersal kernels, habitat patches 6 km or wider meet this  
208 criterion, suggesting that even small populations can be self-persistent despite extensive larval  
209 settlement beyond their bounds. This fact is a boon for marine reserves, which often aim to  
210 benefit both conservation within and fisheries beyond their boundaries.

211 We have found remarkable similarity in scales of larval dispersal over evolutionary and  
212 ecological time, suggesting that indirect genetic methods can provide ecologically relevant  
213 information. While individual seasons are stochastic realizations from a theme, estimation of  
214 mean dispersal kernels now appears feasible for a wide range of species. Marine reserve  
215 networks, for example, have typically been designed with very limited information on the scales  
216 of dispersal for the species involved. Our results suggest that even small marine reserves can  
217 both be self-persistent and provide substantial spillover for some species.

218

### 219 **Supplemental Information**

220 Supplemental Information includes Supplemental Experimental Procedures and one  
221 figure and can be found with this article online. Data and R scripts are available from  
222 <https://dx.doi.org/10.6084/m9.figshare.4042881.v1>.

223

### 224 **Author contributions**

225 MLP conceived the study; GRA, PSA, MLB, SRT, GPJ, SP, and MLP conducted  
226 fieldwork; PSA, OS, and MLB led the lab work; SA contributed environmental data; MLP and  
227 MB conducted analyses; MLP wrote the paper; and all authors contributed to revisions.

228

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342

343 **Figure Legends**

344

345 **Figure 1. Sampling locations in Kimbe Bay, West New Britain, Papua New Guinea.** Red  
346 dots indicate samples used for population genetic analysis (see Table 1). Blue polygons indicate  
347 reef and green polygons indicate land. Scale bar shows 20 km. Inset map data courtesy of Google  
348 Maps.

349

350 **Figure 2. Isolation by distance pattern among orange clownfish populations.** Points indicate  
351 pairwise comparisons among  $N=10$  populations. Comparisons involving Muli are plotted as open  
352 circles, those involving Tarobi are plotted as squares, and the rest as dots. The linear regression  
353 is shown as a dashed line with shaded 95% CIs ( $r^2 = 0.54$ , Mantel test  $p = 0.0013$ ). Thin lines  
354 show regressions after jackknifing across populations. See also Table S1.

355

356 **Figure 3. Congruence among dispersal kernels from indirect methods over evolutionary**  
357 **timescales and from direct methods over ecological timescales.** Colors indicate indirect (dark  
358 grey), direct in 2009 (green) or direct in 2011 (blue). For contrast, we also show indirect kernels  
359 calculated using erroneous estimates of effective population densities (light grey) using census  
360 densities (Indirect Alt1) and using 0.1% of census densities (Indirect Alt2). (A) Estimates of the  
361 dispersal kernel spread ( $\sigma$ ), (B) Estimates of the mean dispersal distance, (C) Fraction of larvae  
362 retained on a habitat patch of a given width under the conservative assumption that larvae are  
363 released from the patch edge, and (D) Plot of the dispersal kernel shapes. Subfigure (A) does not  
364 assume a particular kernel shape, while calculations for (B) through (D) use a Laplacian kernel  
365 following [15]. Kernel shape in (B) through (C) was not estimated from isolation by distance  
366 patterns. In (D), only one side of each symmetrical kernel is shown, and all kernels are  
367 normalized to start at (0,1). All error bounds are 95% CIs. The horizontal dashed line in (C) is  
368 our estimate of the minimum threshold for a self-persistent habitat patch. See also Table S2 and  
369 Figure S1.

370

371

372 **Tables**

373

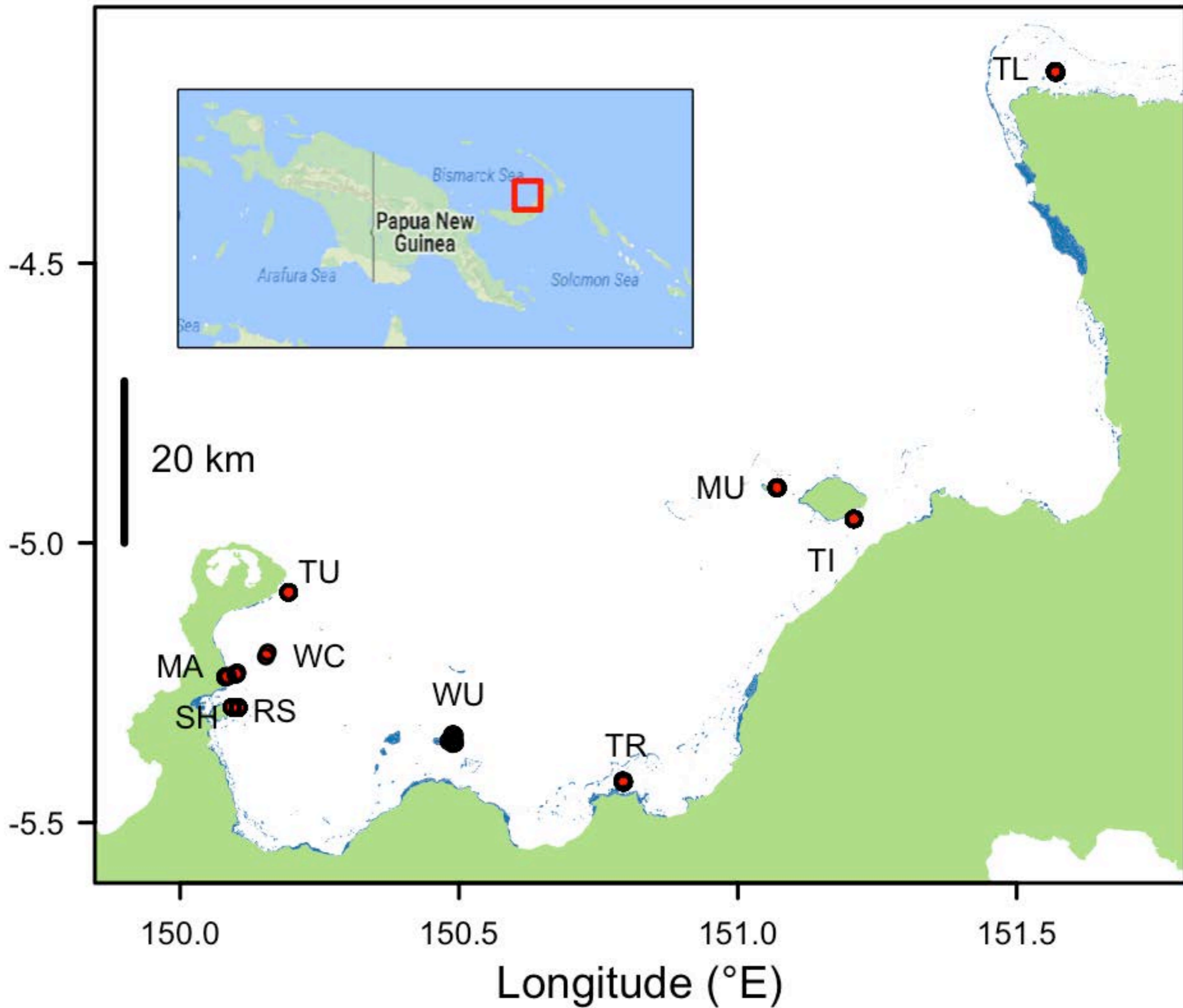
374 **Table 1.** Study sites and sample sizes for the isolation by distance (IBD) study in Kimbe Bay,  
 375 Papua New Guinea.

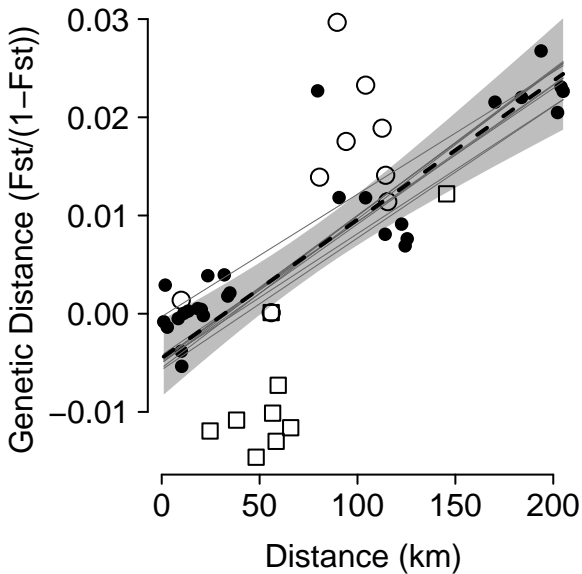
Site	Code	Total samples <sup>a</sup>	New recruits <sup>b</sup>
Tuare	TU	57	30
West Chaimain	WC	10	2
Malu	MA	29	9
Restorff	RS	52	18
Shuman	SH	14	6
Wulai	WU	51	25
Tarobi	TR	77	27
Muli	MU	57	18
Tiwongo	TI	65	23
Talele	TL	55	35
Total		467	193

376 <sup>a</sup> All samples (adults and new recruits) were used for isolation by distance analysis

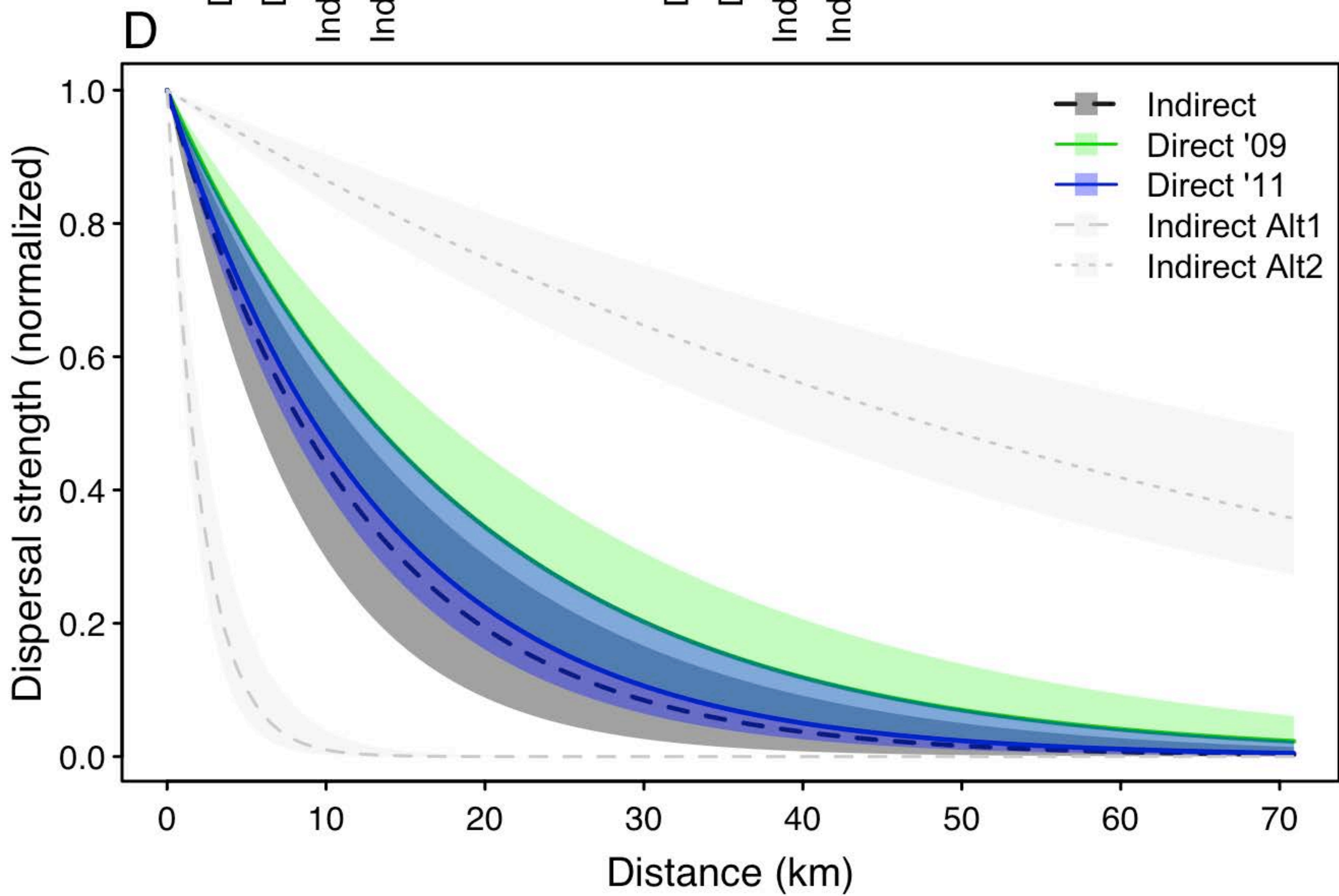
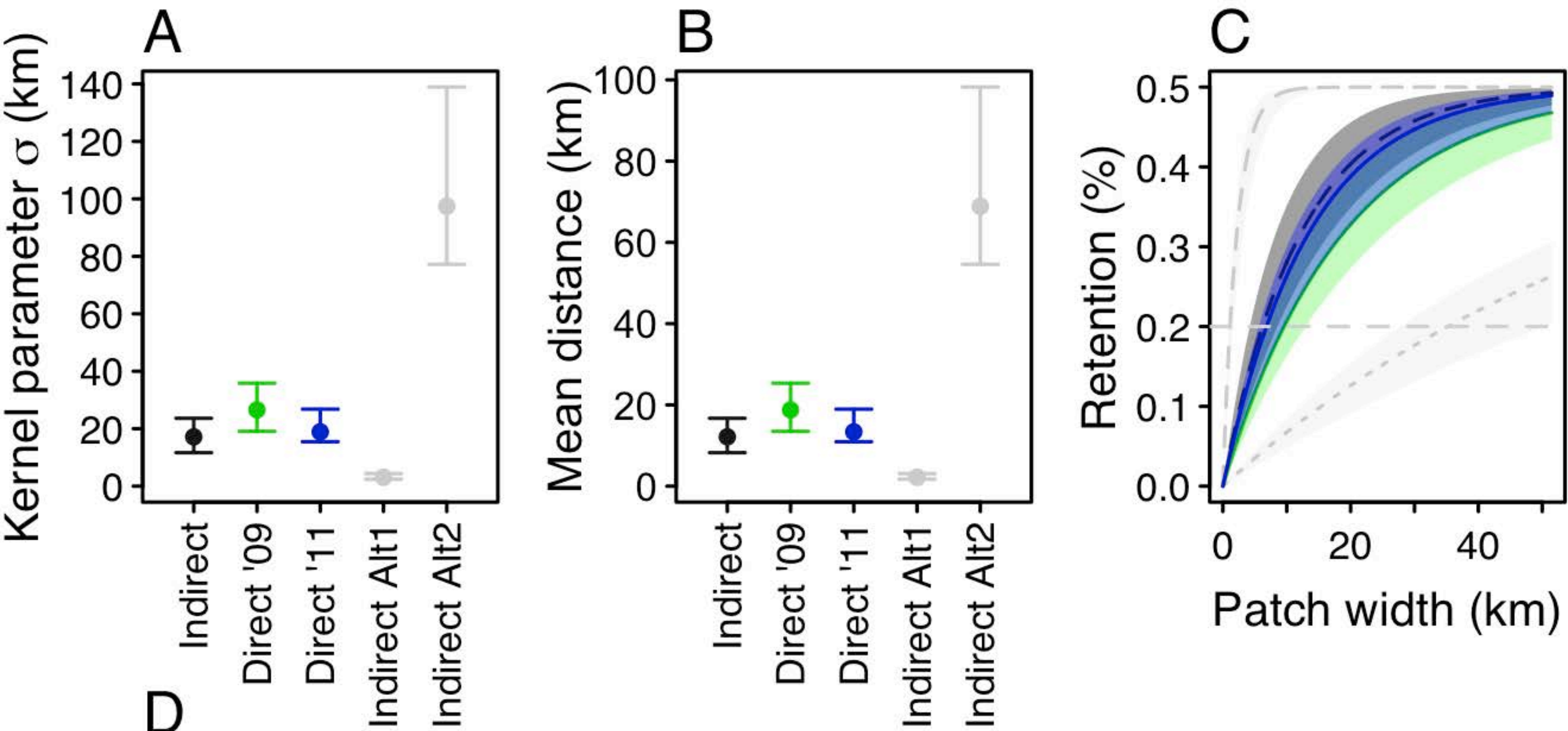
377 <sup>b</sup> The subset of samples that were new recruits were used for calculation of effective population  
 378 size ( $N_e$ )

Latitude ( $^{\circ}$ N)









## Supplemental Tables

**Table S1.** Related to Figure 2. Microsatellite locus statistics for samples used in the isolation by distance analysis, including number of alleles (Na), expected heterozygosity (He), and  $p$ -value for departure from Hardy-Weinberg proportions ( $p$ ). The average at the bottom is calculated without the excluded loci (perc14 and perc21). For more information about the loci and for statistics on the samples used in parentage, see Ref. [S1].

Name	Na	He	$p$
17	6	0.57	0.93
44	11	0.57	0.66
70	7	0.62	0.66
79	16	0.79	0.19
120	6	0.71	0.53
CF3	16	0.82	0.74
CF9	16	0.90	0.01
CF11	8	0.75	0.68
CF12	9	0.63	0.59
CF27	13	0.83	0.86
CF29	26	0.90	0.79
CF36	20	0.84	0.48
CF39	20	0.89	0.65
CF42	14	0.81	0.03
perc02	7	0.64	0.23
perc06	6	0.67	0.35
perc07	20	0.80	0.01
perc14*	31	0.91	<0.0001
perc16	5	0.51	0.006
perc21*	8	0.63	0.0001
perc38	9	0.60	0.25
perc41	4	0.54	0.14
perc42	7	0.59	0.61
Average	11.7	0.71	

\* Loci excluded from further calculations for lack of Hardy-Weinberg proportions at a Bonferroni-corrected  $\alpha$  of 0.002.



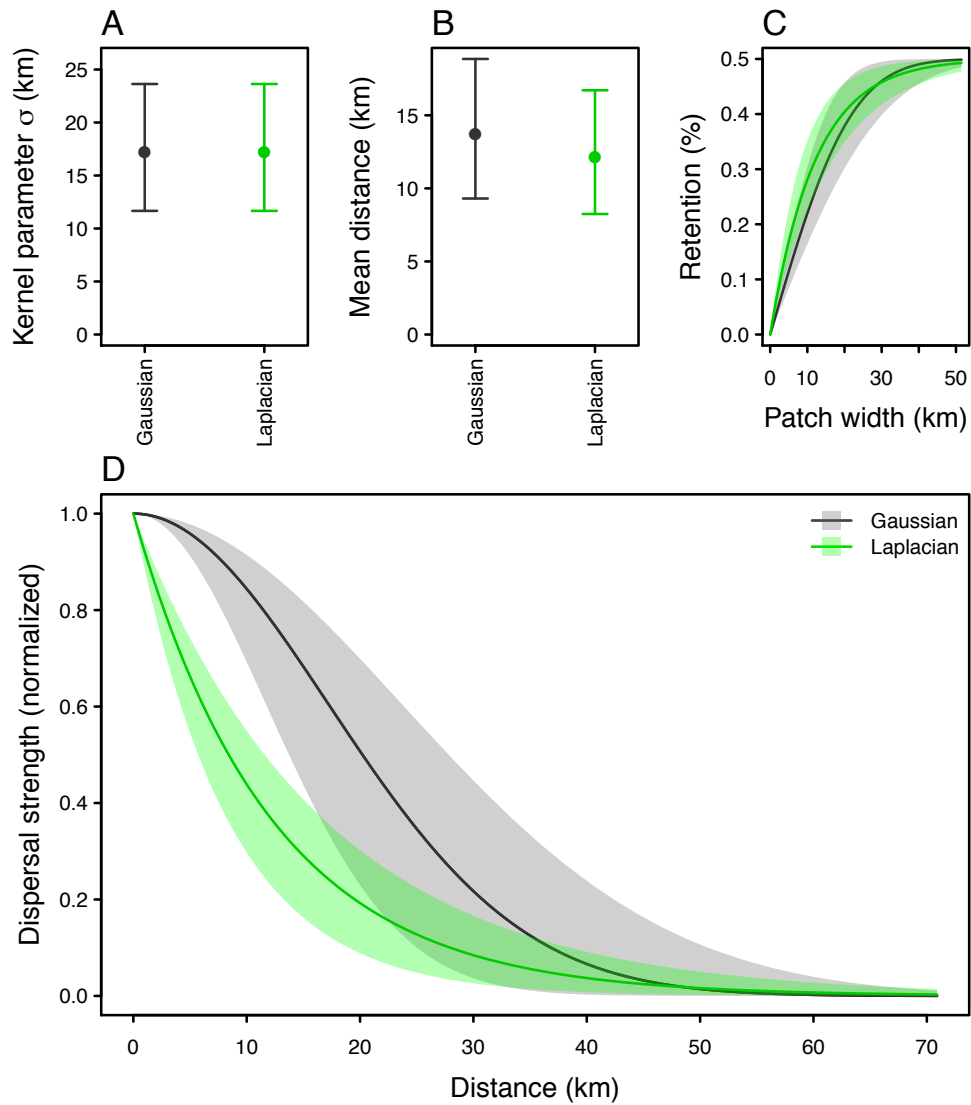
**Table S2.** Related to Figure 3. Probability distributions for propagating error through our calculations of dispersal kernel spread.

<b>Parameter</b>	<b>Error distribution</b>	<b>Equation reference</b>
$m$	Normal(mean=0.00014, sd=0.00002)	Eq. 1
$\widehat{N}_b$	$27*1425/\text{ChiSq}(\text{df}=27)$ *	Eq. 4
$\widehat{N}_b/\widehat{N}_e$	Normal(mean=1.199, sd=0.111)	Eqs. 4 and 5
$Nb_{\text{wright}}$	LogNormal(mean=8.954, sd=0.1113) †	Eq. 2

\* Following discussion of error structure in [S2]

† Mean and standard deviation of the distribution on the log scale

## Supplemental Figures



**Figure S1.** Related to Figure 3. Comparison of Gaussian and Laplacian kernels that have the same dispersal spread (A). The Laplacian kernel has slight lower mean dispersal distances (A), slightly more retention on small patches (C), and a more rapid decline in dispersal probability over short distances. Estimates of dispersal spread come from our isolation by distance method. Kernel fitting results from [S1] support a Laplacian kernel.

## Supplemental Experimental Procedures

### Study system, sampling, and genotyping

We studied aggregations of orange clownfish (*Amphiprion percula*) in Kimbe Bay, New Britain, Papua New Guinea (Fig. 1). These coral reef fish live in mutualistic association primarily with two species of sea anemone, *Heteractis magnifica* and *Stichodactyla gigantea*, and are found only in shallow waters. Female *A. percula* spawn benthic eggs that hatch after approximately 7 days, after which larvae spend about 11 days in the pelagic ocean before settling back to an anemone that will be home for the remainder of their adult life. *A. percula* are protandrous hermaphrodites, and on each anemone, the largest individual is a breeding female, the next largest is a breeding male, and remainder 0-4 individuals are non-breeders. This social structure creates permanent pair bonds that can last for years [S3].

For the isolation by distance analysis, we sampled 467 fish (including new recruits) in 2011 from ten sites selected to span the width of Kimbe Bay (Fig. 1, Table 1). Our goal was approximately 50 samples per site, a sample size that is considered relatively large for genetic differentiation calculations [S4]. We took fin clips from all fish, except for new recruits under 25 mm that were sampled whole. We stored samples in 90% ethanol, then extracted DNA and genotyped 23 microsatellites in all samples following published protocols [S5]. We had 3.9% missing data across all genotypes.

### Isolation by distance analysis

When the probability of dispersal declines with distance, theory predicts a positive correlation between genetic and geographic distances between genetic samples [S6]. This relationship is commonly called isolation by distance (IBD) and reflects a balance between genetic drift and dispersal among populations [S6]. The shape of the IBD relationship, however, depends on the dimensionality of the habitat. While the ocean has three dimensions, IBD relationships follow a 1D model in long and narrow habitats where distances between genetic samples are greater than the habitat width [S6]. Because clownfish larvae disperse through the water column and can traverse even long distances (120 km or longer, see [S1]), it is appropriate to view the entire 225 × 80 km Kimbe Bay as one, large habitat. In this study, we were focused on spatial scales up to 225 km, and the 1D formulation was therefore more appropriate. The 1D formulation for IBD theory predicts that the dispersal kernel spread ( $\sigma$ ) can be calculated as

$$\sigma = \sqrt{\frac{1}{4D_e m}} \quad \text{Eq. 1}$$

where  $D_e$  is effective density and  $m$  is the slope of the relationship between  $F_{ST}/(1-F_{ST})$  and geographic distance [S6]. Effective density is the effective population size ( $N_e$ ) per unit length of the population. Spread ( $\sigma$ ) is the standard deviation of parental position relative to offspring position, otherwise known as the standard deviation of the dispersal kernel [S7]. For example, if dispersal follows a Laplacian kernel, the probability of a larva settling at distance  $x$  away from its parent would be described by  $p(x) = \frac{1}{\sigma\sqrt{2}} e^{-\sqrt{2}x/\sigma}$ . The mean dispersal distance with a Laplacian kernel is  $\frac{\sigma}{\sqrt{2}}$  [S8]. Direct measurements of dispersal from parent-offspring assignments in *A. percula* suggest that a Laplacian kernel provides the best fit to the parentage assignments [S1]. Gaussian kernels have also been proposed of the form  $p(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(x^2)/2\sigma^2}$ , where the mean dispersal distance is  $\sigma\sqrt{2/\pi}$ .

IBD theory is built on a Wright-Fisher model of reproduction, assumes no selection, and assumes that the population is at drift-migration equilibrium. While true drift-migration equilibrium takes many generations to reach, the slope of IBD relationships ( $m$ ) reaches a stationary phase within a few generations for nearby populations, such as those separated by  $10\sigma$  to  $50\sigma$  or less [S9, 10].

We assessed departure from Hardy-Weinberg proportions and linkage among loci using Genepop [S11]. We excluded two loci (*perc14* and *perc21*) from further analysis because they failed to meet expectations for Hardy-Weinberg proportions ( $p < 0.003$ ). We then calculated  $F_{ST}$  in Arlequin 3.5.1.2 using the number of different alleles between multilocus genotypes [S12], which is equivalent to the Weir & Cockerham estimator [S13]. This estimator, like any statistical estimator, contains sampling variance, and negative  $F_{ST}$  values are therefore possible for populations that are weakly differentiated [S14]. These negative values contain information and changing them would introduce positive bias to our  $F_{ST}$  estimates [S14], so we do not replace negative  $F_{ST}$  values with zero.

To calculate distances in one dimension for IBD calculations, we first needed to define a primary axis in Kimbe Bay along which to measure distance. We used a Principal Components Analysis (PCA) of the  $x$  and  $y$  coordinates of the sites (UTM Zone 56S projection) as an objective method for identifying this primary axis, and then measured distance among sites along PC1. We measured the slope of the IBD pattern with a linear regression. In addition, we used a maximum likelihood estimator to fit a linear IBD model, as implemented in the program *Migraine* 0.4.1.0 [S15]. *Migraine* reports point estimates and 95% CIs for Wright's neighborhood size, where  $Nb_{Wright} = 4D_e\sigma^2$ , which we subsequently solved for  $\sigma$ :

$$\sigma = \sqrt{\frac{Nb_{Wright}}{4D_e}} \quad \text{Eq. 2}$$

A poor understanding of effective population size ( $N_e$ ) has been a long-standing challenge in population genetics and in the application of IBD theory [S16, 17]. However, there has been substantial progress in empirical methods for estimating  $N_e$ , particularly for species with overlapping generations [S18, 19]. We used the gametic disequilibrium method [S2] as implemented in *NeEstimator* [S20] to estimate the effective number of breeders ( $\hat{N}_b$ ) in Kimbe Bay. We applied the method to all 193 new recruits (those under 25 mm) in our isolation by distance samples that had been collected throughout the bay in 2011 (Table 1). We specified a monogamous mating model and a critical allele frequency of 0.02. We then used *Waples et al.*'s equations [S19] to correct the  $\hat{N}_b$  estimate for measurement bias and convert it to an estimate of  $\hat{N}_e$ :

$$(\widehat{N_b/N_e}) = 0.485 + 0.758 \times \log_{10}(AL/\alpha) \quad \text{Eq. 3}$$

$$\hat{N}_{b(Adj)} = \frac{\hat{N}_b}{1.26 + 0.323 \times (\widehat{N_b/N_e})} \quad \text{Eq. 4}$$

$$\hat{N}_e = \frac{\hat{N}_{b(Adj)}}{(\widehat{N_b/N_e})} \quad \text{Eq. 5}$$

where  $AL$  is the expected reproductive lifespan and  $\alpha$  is the minimum age of reproduction. For use in these equations, we calculated an expected reproductive lifespan of 13.1 years using standard equations for time until death in a stage-structured population [S21] and a published life table for *A. percula* [S22]. We used a minimum age of reproduction of 1.5 years, as would be expected for clownfish that mature under ideal conditions [S23]. We converted our estimate of  $\hat{N}_e$  to  $D_e$  by dividing by the length of the bay (225 km).

As a comparison to our genetic estimate of effective population size, we also calculated an ecological census size estimate for adult clownfish in Kimbe Bay. We overlaid our field observations of adult clownfish and our search areas on the 2012 version of a 16-class map of coral reef habitats produced from 30 m spatial resolution Landsat satellite images [S24]. We then calculated the average adult clownfish density per habitat class and multiplied these average densities by the total area of each habitat class in Kimbe Bay. The ecological census size is often larger than the genetic effective population size, particularly in marine species, because strong variance in reproductive success reduces the latter below the former [S17, 18, 25]. *Hare, et al.* [17] suggest that genetic effective population size in marine species may often be 1000 times smaller than census size. To contrast with our dispersal spread calculation from the *NeEstimator* estimate of  $N_e$ , we also report spread results erroneously calculated using census size or 0.1% of census size.

We propagated error in our estimates of  $m$  and  $D_e$  through the equations for  $\sigma$  by sampling 100,000 times from the error distributions for each parameter (Table S2). We used a normal distribution for  $m$ , a chi-squared distribution for  $\hat{N}_b$ , a normal distribution for the  $\widehat{N_b/N_e}$  ratio, and a log-normal distribution for  $Nb_{Wright}$ . To estimate the error distribution for  $\widehat{N_b/N_e}$ , we fit a linear regression for Eq. 2 using the data from [S18], then calculated a prediction and prediction confidence interval for  $\widehat{N_b/N_e}$  using our values of  $AL$  and  $\alpha$ . We drew two estimates of  $\widehat{N_b/N_e}$  for each estimate of  $\sigma$ , once for use in Eq. 3 and once for use in Eq. 4. Error distributions for the other parameters were fit to the standard error or 95% CI limits reported for each parameter.

### ***Direct measurements of dispersal kernels***

In a related study [S1], we sampled 1,447 juveniles and 2,546 potential parents from eight sites in Kimbe Bay in 2009, and another 1,547 juveniles and 2,913 adults from these sites in 2011. Sampling in each year was spread over four weeks and involved searching all suitable habitats. The total sample size was 18 times larger than that used for the isolation by distance study, reflecting the large sample sizes typically needed for finding parent-offspring matches in large populations. We used genetic parentage analysis to match offspring to parents across our full set of samples (8,453 individuals) and therefore identify individual dispersal events. The spatial patterns of parent-offspring assignments can then be used to compare alternative dispersal kernels that describe the relationship between dispersal probability and distance [S26, 27]. We fitted kernels after accounting for differences in population size and sampling effort among reefs, as well as the large number of unassigned juveniles at each sampled reef [S28]. Full details are explained in Almany, et al. [1].

### ***Comparison of kernel spread***

We compared the kernels by sampling from the error distributions for each kernel. We calculated percent differences as  $100(a - b)/a$ , where  $a$  is the direct kernel spread and  $b$  is the IBD kernel spread.

### ***Self-persistence calculations***

We used a previously published estimate of recruits/adult/month in *A. percula* [S29] and used Eq. 5.28 in Caswell [30] on an *A. percula* life table [S22] to calculate the probability of a new recruit surviving to reproductive age. We calculated six survival probabilities (one for each rank at which a new recruit could enter a group), then calculated an average survival weighted by the frequency of each group size [S22]. Following Botsford, et al. [8], we do our retention calculations for an individual on the edge rather than the center of a habitat patch.

### ***Data availability and scripts***

Data and scripts for analyses described in this paper are available from <https://dx.doi.org/10.6084/m9.figshare.4042881.v1>.

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