

Marine Dispersal Scales Are Congruent over Evolutionary and Ecological Time

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

3
4 Malin L. Pinsky^{a*}, Pablo Saenz-Agudelo^b, Océane Salles^c, Glenn R. Almany^d, Michael Bode^e,
5 Michael L. Berumen^f, Serge Andréfouët^g, Simon R. Thorrold^h, Geoffrey P. Jonesⁱ, Serge Planes^j
6

7 ^a Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College
8 Farm Rd., New Brunswick, NJ 08901, USA, malin.pinsky@rutgers.edu

9 ^b Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile,
10 pablo.saenzagudelo@gmail.com

11 ^c Laboratoire d'Excellence "CORAIL", USR 3278 CNRS-EPHE-UPVD CRIOBE, 58 Avenue
12 Paul Alduy, 66860 Perpignan, France, oceane.salles@gmail.com

13 ^d Laboratoire d'Excellence "CORAIL", USR 3278 CNRS-EPHE-UPVD CRIOBE, 58 Avenue
14 Paul Alduy, 66860 Perpignan, France (deceased)

15 ^e ARC Centre of Excellence for Environmental Decisions, School of Botany, The University of
16 Melbourne, Parkville, Melbourne, VIC 3010, Australia, bodem@unimelb.edu.au

17 ^f Red Sea Research Center, Division of Biological and Environmental Science and Engineering,
18 King Abdullah University of Science and Technology, Thuwal, 23955, Saudi Arabia,
19 michael.berumen@kaust.edu.sa

20 ^g UMR 250 ENTROPIE (Institut de Recherche pour le Développement, Université de la
21 Réunion, Centre National de la Recherche Scientifique), BP A5, Noumea, 98848, New
22 Caledonia, serge.andrefouet@ird.fr

23 ^h Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA,
24 sthorrold@whoi.edu

25 ⁱ ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD
26 4811, Australia, geoffrey.jones@jcu.edu.au

27 ^j Laboratoire d'Excellence "CORAIL", USR 3278 CNRS-EPHE-UPVD CRIOBE, 58 Avenue
28 Paul Alduy, 66860 Perpignan, France, planes@univ-perp.fr
29

30 *Corresponding author and lead contact

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

54
55

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 (± 1 SEM), or 188 ± 45 adults/km (± 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 (σ) 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 (σ) 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 (σ) 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 $10\text{-}50\sigma$, 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 (σ), (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 ^a	New recruits ^b
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 ^a All samples (adults and new recruits) were used for isolation by distance analysis

377 ^b The subset of samples that were new recruits were used for calculation of effective population
 378 size (N_e)