

Current Biology

Marine Dispersal Scales Are Congruent over Evolutionary and Ecological Time

Highlights

- Evolutionary estimates of dispersal matched direct observations in clownfish
- Dispersal kernels across short and long timescales were highly similar
- Our results suggest that evolutionary estimates of dispersal can be applied broadly

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In Brief

Population genetic patterns often suggest widespread dispersal in the ocean, despite direct observations of local larval retention. Here, Pinsky et al. reconcile the two approaches and demonstrate that both estimate the same dispersal kernel. This suggests that evolutionary approaches could be used to study dispersal across many more species.

Marine Dispersal Scales Are Congruent over Evolutionary and Ecological Time

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SUMMARY

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

RESULTS

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

Here, we reconcile evolutionary and ecological perspectives on dispersal in the orange clownfish (*Amphiprion percula*). This is a genus for which both long-distance gene flow over 1,000 km [13] and short-distance self-recruitment over 100 m has been reported [1, 14]. We compare dispersal measured from the direct detection of parent-offspring relationships [15] against an indirect approach based on isolation by distance

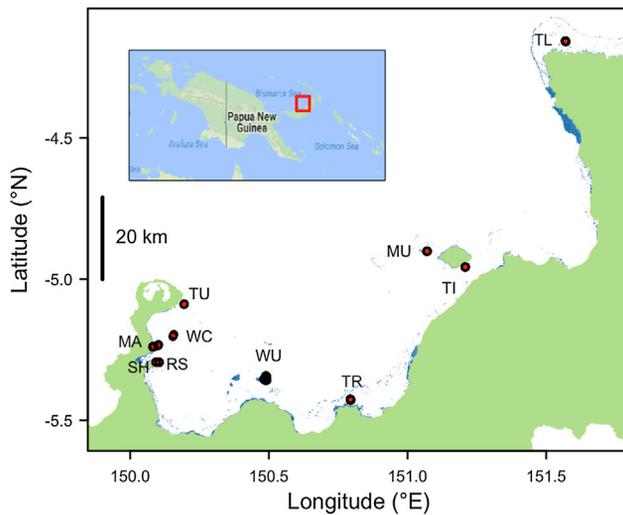


Figure 1. Sampling Locations in Kimbe Bay, West New Britain, Papua New Guinea

Red dots indicate samples used for population genetic analysis (see Table 1 for definition of two-letter population codes). Blue polygons indicate reefs; green polygons indicate land. Scale bar represents 20 km. Inset map data courtesy of Google Maps.

(IBD) genetic patterns [16]. Patterns of IBD are common in marine organisms, occurring in at least half of all species examined [17, 18].

IBD Patterns

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

Effective Density

Estimating dispersal distances from IBD patterns requires measurements of the strength of genetic drift. The effective population size for Kimbe Bay was 1,363 individuals (95% CI: 783–2,834 individuals) or 6.1 individuals/km (95% CI: 3.5–12.6 individuals/km) over the 225 km length of the bay, as estimated from gametic disequilibrium patterns in the cohort of new recruits (Table 1) and corrected for overlapping generations. As

Table 1. Study Sites and Sample Sizes for the IBD Study in Kimbe Bay, Papua New Guinea

Site	Code	Total Samples	New Recruits
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

Total samples (adults and new recruits) were used for IBD analysis. The subset of samples that were new recruits were used for calculation of effective population size (N_e).

expected, this is considerably lower than the number and density of adults estimated from visual surveys: $42,300 \pm 10,100$ individuals (± 1 SEM), or 188 ± 45 adults/km (± 1 SEM). These estimates put the N_e/N ratio at 3.4% (95% CI: 1.6%–8.5%).

Dispersal Kernel Measurements from IBD

Using IBD theory, we then used the slope of the IBD relationship and the effective density to estimate the spread (measured as the standard deviation) of the dispersal kernel while accounting for the uncertainty in each parameter (Table S2). The kernel is a probability distribution, and the height of the kernel provides the probability of larvae dispersing to each position (Figure 3D). The dispersal spread (σ) for *A. percula* in Kimbe Bay was 17.2 km (95% CI: 11.7–23.6 km). An alternative, maximum-likelihood method using Wright's neighborhood size instead of the IBD slope calculated a very similar dispersal spread of 17.9 km (95% CI: 12.2–24.1 km).

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

Comparison of Direct and Indirect Approaches

We then compared our evolutionary dispersal estimates to kernels that had been fit to directly detected larval dispersal events [15]. In 2009, 407 of 1,447 sampled recruits (28%) were assigned to one or both parents from a pool of 2,546 potential parents. In 2011, 437 of 1,547 recruits (28%) were assigned to parents from a pool of 2,913 adults. Both of the indirect dispersal spread values compared well to, but were slightly lower than, the direct ecological estimates of 26.5 km (95% CI: 19.1–35.8 km) in 2009 and 18.9 km (95% CI: 15.5–26.8 km) in 2011 (Figures 3A and 3D).

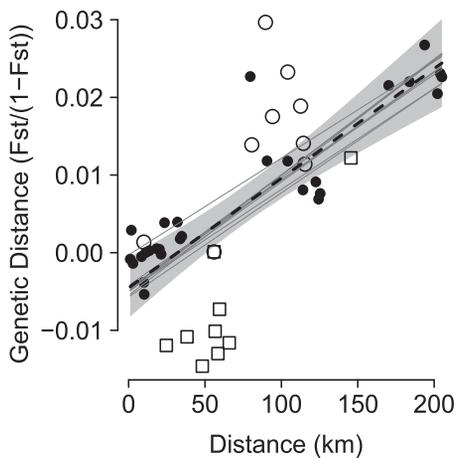


Figure 2. IBD Pattern among Orange Clownfish Populations

Points indicate pairwise comparisons among $N = 10$ populations. Comparisons involving the Muli population are plotted as open circles, those involving the Tarobi population as squares, and the rest as filled dots. The linear regression is shown as a thick dashed line with shaded 95% CIs ($r^2 = 0.54$, Mantel test $p = 0.0013$). Thin lines show regressions after jackknifing across populations. See also [Table S1](#).

Comparison of these kernels suggested that the 2009 kernel was 38% larger, with a 95% CI of 1% smaller to 61% larger, than the IBD kernel. The 2011 kernel was only 11% larger, with a 95% CI of 34% smaller to 44% larger. Compared to the range of potential scales, from hundreds of meters to hundreds of kilometers, these differences were slight.

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

DISCUSSION

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

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

If used more broadly, care must be taken to appropriately apply and interpret IBD approaches. Sampling for IBD patterns needs to be spread over scales of 10σ – 50σ , since these are the scales at which genetic patterns are dominated by recent drift and dispersal [19, 20]. When appropriate scales are unknown, sampling a range of distances can identify the scale of IBD [31]. Minimum age of reproduction and length of reproductive lifespan are also helpful to apply Waples et al.’s correction to effective population size for overlapping generations [30]. However, the correction was minor in clownfish (from $\hat{N}_b = 1,427$ to $\hat{N}_e = 1,363$) and will generally be minor in species with early maturity and long lifespans. Accurately estimating effective population size is important, and a $10\times$ error in effective population size translates to an $\sim 3\times$ error in the dispersal estimate (see [Supplemental Experimental Procedures](#)). In general, uncertainty about effective population size is more important than uncertainty in the IBD pattern [27]. Because IBD methods measure a long-term average, they will be most meaningful in systems without persistent changes in dispersal or abundance. (In contrast, variance around a stationary mean is less concerning.) Direct methods will continue to be important for research that requires finer temporal or spatial resolutions.

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

The degree to which marine larvae stay close to home or travel long distances has been a debate for decades. Our estimates of

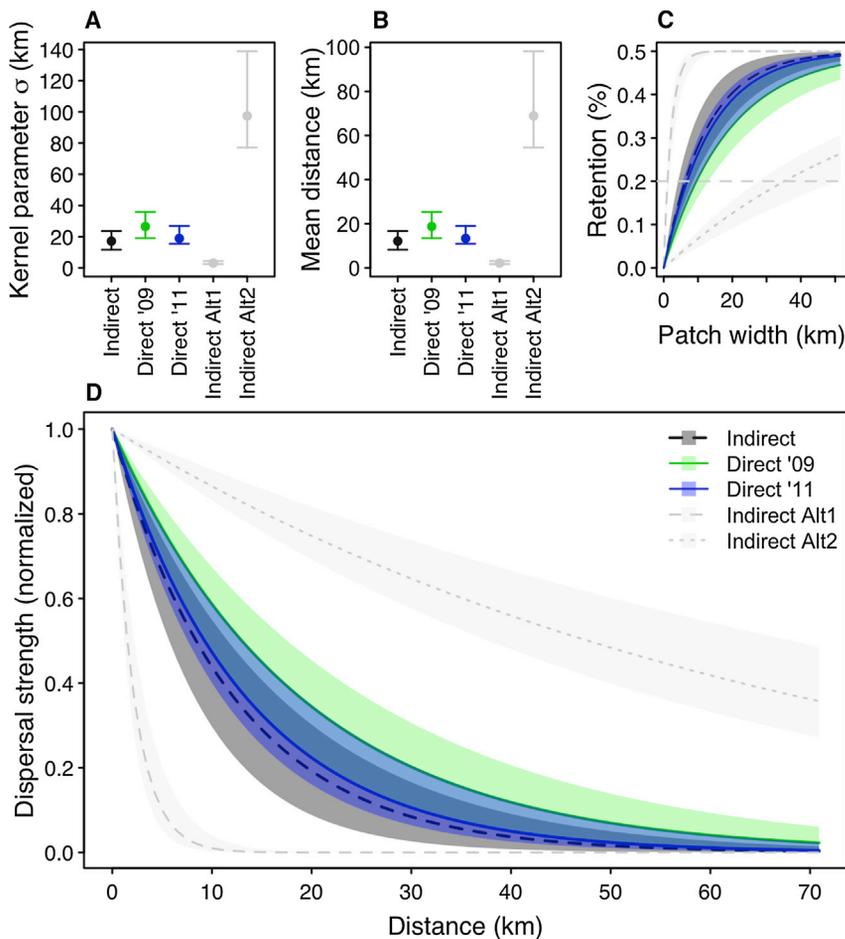


Figure 3. Congruence among Dispersal Kernels from Indirect Methods over Evolutionary Timescales and from Direct Methods over Ecological Timescales

Colors indicate indirect method (dark gray), direct method in 2009 (green), or direct method in 2011 (blue). For contrast, we also show indirect kernels calculated using erroneous estimates of effective population densities (light gray) using census densities (Indirect Alt1) and using 0.1% of census densities (Indirect Alt2). (A) does not assume a particular kernel shape, while calculations for (B)–(D) use a Laplacian kernel following [15]. Kernel shape in (B) and (C) was not estimated from IBD patterns. In (D), only one side of each symmetrical kernel is shown, and all kernels are normalized to start at (0,1). All error bounds are 95% CIs. The horizontal dashed line in (C) is our estimate of the minimum threshold for a self-persistent habitat patch. See also Table S2 and Figure S1.

(A) Estimates of the dispersal kernel spread (σ).
 (B) Estimates of the mean dispersal distance.
 (C) Fraction of larvae retained on a habitat patch of a given width under the conservative assumption that larvae are released from the patch edge.
 (D) Plot of the dispersal kernel shapes.

habitat patches 6 km or wider meet this criterion, suggesting that even small populations can be self-persistent despite extensive larval settlement beyond their bounds. This fact is a boon for marine reserves, which often aim to benefit both conservation within and fisheries beyond their boundaries.

dispersal spread in a clownfish suggest that typical dispersal distances are neither hundreds of meters nor hundreds of kilometers, both of which have been suggested [13, 36]. Evidence that the probability of recruitment declines quickly over the first kilometer in clownfish [14], in combination with our measurements of slower rates of decline over dozens of kilometers, suggests that different dispersal processes may operate at different spatial scales. This conclusion would be consistent with differences between the hydrodynamics immediately over and around reefs and the regional eddies, jets, and currents that act between reefs. There may be a hierarchy of processes, with one set of larvae settling on their natal reef after experiencing only near-shore hydrodynamics, and a second set of larvae that are swept off-shore and transported dozens of kilometers.

Our results also contribute to fundamental questions about metapopulation persistence [37]. For a population to persist, it needs to meet the replacement criterion, namely $F \times S \times LR > 1$, where F is per-capita lifetime fecundity, S is survival of recruits to adulthood, and LR is the proportion of locally retained larvae [37]. We can combine existing measurements of clownfish fecundity, lifespan, and survival [37–40] for a rough estimate of $F \times S = 0.08(\text{recruits/adult} \cdot \text{month}) \times 150(\text{months/adult}) \times 0.4(\text{adults/recruit}) = 4.8(\text{adults/adult})$. Therefore, populations with $LR > 20\%$ should be persistent. With Laplacian dispersal kernels,

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

ACCESSION NUMBERS

Data and R scripts associated with this paper are available at <https://dx.doi.org/10.6084/m9.figshare.4042881.v1>.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure, two tables, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.10.053>.

AUTHOR CONTRIBUTIONS

M.L.P. conceived the study. G.R.A., P.S.-A., M.L.B., S.R.T., G.P.J., S.P., and M.L.P. conducted fieldwork. P.S.-A., O.S., and M.L.B. led the lab work. S.A.

contributed environmental data. M.L.P. and M.B. conducted analyses. M.L.P. wrote the manuscript. All authors contributed to manuscript revisions.

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