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## Parentage analyses identify local dispersal events and sibling aggregations in a natural population of *Millepora* hydrocorals, a free-spawning marine invertebrate

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*Millepora*

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## Abstract

Dispersal is a critical process for the persistence and productivity of marine populations. For many reef species, there is increasing evidence that local demography and self-recruitment have major consequences on their genetic diversity and adaptation to environmental change. Yet empirical data of dispersal patterns in reef-building species remain scarce. Here, we document the first genetic estimates of self-recruitment and dispersal distances in a free-spawning marine invertebrate, the hydrocoral *Millepora* cf. *platyphylla*. Using twelve microsatellite markers, we gathered genotypic information from 3,160 georeferenced colonies collected over 9,000 m<sup>2</sup> of a single reef in three adjacent habitats in Moorea, French Polynesia; the mid slope, upper slope, and back reef. Although the adult population was predominantly clonal (85% were clones), our parentage analysis revealed a moderate self-recruitment rate with a minimum of 8% of sexual propagules produced locally. Assigned offspring often settled at less than 10 meters from their parents and dispersal events decrease with increasing geographic distance. There were no discrepancies between the dispersal distances of offspring assigned to parents belonging to clonal *versus* non-clonal genotypes. Inter-habitat dispersal events via cross-reef transport were also detected for sexual and asexual propagules. Sibship analysis showed that full siblings recruit nearby on the reef (more than 40% settled at < 30 m), resulting in sibling aggregations. Our findings highlight the importance of self-recruitment together with clonality in stabilizing population dynamics, which may ultimately enhance local sustainability and resilience to disturbance.

## Introduction

Understanding patterns of dispersal is a major goal in ecology and conservation biology (Botsford et al., 2009; Cowen et al., 2007; Warner & Cowen, 2002). These patterns shape species' distribution and abundance (Strathmann et al., 2002) and have major consequences for the persistence and adaptation of populations (Garant et al., 2007; Gilmour et al., 2013; Underwood et al., 2009). The dynamics of these populations can potentially be influenced by short-distance dispersal within populations (defined here at < 1 km and referred to as self-recruitment) and by the degree to which these populations are linked by long-distance dispersal events (defined here at > 1 km and referred to as connectivity) (Almany et al., 2017; Buston et al., 2012). Elucidating the respective contribution from self-recruitment *versus* connectivity has generated an impressive body of theoretical and empirical research in the past decades and has been stressed in conservation policies (Burgess et al., 2014; Pinsky et al., 2012). Yet the robust characterization of empirical estimates of dispersal remain a persistent challenge in ecology (Kopps et al., 2015), and particularly in populations of marine animals.

For most marine species whose adults are sessile or relatively sedentary, the early life history includes a propagule stage that represents the first step for successful recruitment. Propagule dispersal depends on many biological and physical processes, including the survival and development rates of propagules (Doropoulos et al., 2016; Figueiredo et al., 2013; Johnson et al., 2014), larval behavior (Gerlach et al., 2009; Paris et al., 2007), and hydrodynamic regimes and seascapes (Cowen et al., 2006; Cowen & Sponaugle, 2009; White et al., 2010). Parentage analysis can be used to assess *in situ* dispersal patterns in marine species in which characteristics of reproduction and early life stages make direct observation of dispersal events impossible or at least impractical (Jones et al., 2010). As such, genetic parentage data are an increasingly common source of empirical dispersal information, especially for reef fishes (Abesamis et al., 2017; Almany et al., 2017; Planes et al., 2009; Salles et al., 2016). For instance, parentage analysis has uncovered high levels of recruitment back to the parental source for some reef fish species (e.g., 30–60% of self-recruitment, Almany et al., 2007; Jones et al., 2005; Salles et al., 2016), while others have limited input of locally produced offspring (< 5%, D'aloia et al., 2013). These studies reinforce the idea that reef populations might be

less connected than previously thought. Improving our understanding of population processes in reef organisms, particularly those that contribute to the reef matrix, is therefore essential to furthering conservation and management of these ecosystems and the services (including fisheries, coastal protection, medicines, and tourism activities) they provide to millions of people (Cinner, 2014; Moberg & Folke, 1999).

In scleractinian corals, the extent of dispersal is largely governed by their reproductive biology and early life history ecology. Our ability to make inferences on what specific biological processes are driving dispersal and subsequent recruitment patterns in reef corals is limited due to their diverse dispersal strategies; gamete broadcasting, larval brooding, and asexual reproduction pathways, which includes fragmentation, budding, polyp bail-out, asexually produced planula, and embryo breakage (Harrison, 2011; Heyward & Negri, 2012). Nevertheless, high levels of self-recruitment and limited dispersal in corals at some reefs has been suggested in field surveys and associated population genetic studies (Baums et al., 2005; Concepcion et al., 2014; Gilmour et al., 2009; Shinzato et al., 2015; Torda et al., 2013). The application of genetic parentage analysis in reef corals has provided the first estimates of restricted sperm dispersal and limited siring distances in brooding species (corals that brood their offspring, Lasker et al., 2008; Warner et al., 2016; Yeoh & Dai, 2010). Broadcast spawning of gametes (external fertilization and planktonic larval development) is the most common sexual reproductive strategy in reef corals (Baird et al., 2009), among other free-spawning colonial marine organisms. Yet empirical data on the dispersal patterns of their early life stages are still missing. Such information is essential to disentangle whether or not this reproductive strategy increases larval dispersal ability via potentially long-distance dispersal events as commonly thought.

*Millepora* hydrocorals, also called fire corals, are an important component of reef communities where they, similar to scleractinian corals, contribute to the accretion of reefs (Lewis, 2006; Nagelkerken & Nagelkerken, 2004). *Millepora* species inhabit a wide range of habitats (Dubé et al., 2017a; Lewis, 2006) and often grow into large colonies that pre-empt space and compete with scleractinian corals (Dubé et al., 2016). Despite their importance in reef community dynamics, fire corals have been relatively

understudied and not much is known with respect to their reproduction and dispersal patterns. *Millepora* species are broadcast spawners that alternatively reproduce by shifting from sexual reproduction, by producing medusoids ('regressed' short-lived medusa) and planula larvae, to asexual pathway of fragmentation (Bourmaud et al., 2013; Dubé et al., 2019; Lewis, 2006). The use of sexual/asexual modes of reproduction has been recorded in *Millepora* cf. *platyphylla* (see Arrigoni et al., 2018; Boissin et al., 2020 for taxonomic description) at Moorea (Society Archipelago, French Polynesia), where habitat specific environmental conditions are thought to determine the levels of clonality (58–88% were clones, Dubé et al., 2017b). The spatial distribution of clone mates on a barrier reef (as in Moorea) has demonstrated that the dispersal of asexual fragments in fire corals was heavily influenced by a cross-reef gradient of wave energy from offshore reefs towards lagoonal habitats (Dubé et al., 2017b). However, it remains unknown whether the dispersal of their sexually produced propagules is driven by cross-reef transport. Although such information is crucial for understanding the replenishment and recovery of marine populations, there is no genetic study that has identified patterns of sexual dispersal and recruitment in these important reef-building species or in any other free-spawning marine invertebrates.

Here, we conducted an extensive field survey of 3,160 georeferenced colonies of *M. cf. platyphylla* over 9,000 m<sup>2</sup> of a single reef, based on replicated transects across three adjacent habitats (mid slope, upper slope, and back reef) at Moorea in French Polynesia, an insular and oceanic, and therefore relatively isolated, coral reef system. Using parentage analysis for the first time in *Millepora* hydrocorals, or in any non-brooding corals, i) we established the relative contribution of short- versus long-distance dispersal in local population replenishment (self-recruitment versus connectivity), ii) investigated dispersal patterns of sexual propagules within and across reef habitats (intra- versus inter-habitat dispersal), iii) determined how far siblings settle from each other and from their parents, and iv) assessed how fragmentation influences local recruitment in a partially clonal reef-building coral. Considering the particular larval development mode of *Millepora* hydrocorals, i.e. between the extremes of philopatry in brooders and potentially long-lived planktonic dispersal phases associated with broadcast spawners, we expect a high contribution from self-recruitment (< 1 km, the range of our studied area) with a

limited dispersal ability of early life stages, i.e. the short-lived medusoids and negatively buoyant eggs, sperm, and ciliate planula larvae.

## **Materials and Methods**

### **Study species**

*Millepora* cf. *platyphylla* is a gonochoric broadcast spawner that reproduces sexually by producing medusoids ('regressed' short-lived medusa) and planula larvae (Bourmaud et al., 2013; Dubé et al., 2019; Lewis, 2006). Medusoids are developed at the surface of the polyp coenosteum in cavities called ampullae and undergo sexual reproduction (Lewis, 1991). After the disintegration of the dense trabeculae network covering the ampullae, male and female medusoids detach themselves from the gravid colonies by active bell pulsations in a few minutes. Their swimming activity leads to the release of the ripe gametes in the water column, resulting in the spawning of gametes being almost synchronous with the release of medusoids (more or less one hour post-spawning) (Soong & Cho, 1998). Male and female medusoids are released synchronously and the spawning of the oocytes (2 to 5 per medusoid) and spermatozooids is also simultaneous. While the medusoids are positively buoyant and able to swim, eggs and spermatozooids are negatively buoyant (Bourmaud et al., 2013). Fertilization occurs rapidly and embryogenesis and planula larvae formation occur in less than 12 hours in aquarium (Bourmaud et al., 2013). The zooxanthellate planula larvae sink and move epibenthically (crawling not swimming) on the reef substratum before metamorphosing into a new calcifying polyp in one day to several weeks after spawning (Bourmaud et al., 2013). Fire corals also rely heavily on asexual reproduction through fragmentation for local replenishment (Dubé et al., 2017b), while the production of asexual larvae has never been documented so far within the *Millepora* genus.

### **Population sampling and microsatellite genotyping**

Between May and September 2013, a series of surveys were conducted on the north shore of Moorea, French Polynesia, across three adjacent reef habitats located in front of Papetoai village (17°29.900'S; 149°52.492'O): two on the fore reef, the mid slope (13 m depth) and upper slope (6 m depth), and one on the back reef (< 1 m depth) (Fig. 1).

Within each habitat, three 300 m long by 10 m wide belt transects were laid over the reef parallel to shore for a total of 9,000 m<sup>2</sup> of reef area surveyed. Each transect within each habitat were separated by 30 m. The mid slope and upper slope habitats were separated by 40 m, while the back reef habitat was located at 160 m and 210 m from the upper and mid slope, respectively (covering 220,800 m<sup>2</sup> of reef). All colonies of *M. cf. platyphylla* that were at least 50% within the transect borders were georeferenced by determining their position along the transect-line (0 to 300 m) and straight-line distance from both sides of the transect (0 to 10 m). From these measures, each colony was mapped with x and y coordinates. A map of the locations of each colony was produced using R version 3.0 (R Development Core Team, 2019). The colony size (projected surface) of each colony was estimated (in cm<sup>2</sup>) from 2D photographs using ImageJ 1.4f (Abràmoff et al., 2004). To determine the sex in *Millepora* it requires the presence of medusoids at the surface of the colony as well as their release in the water column to observe the reproductive gametes (oocytes and sperm sacs). Such observations have only been made from specimens in aquaria so far and appear to be not possible in the field (Bourmaud et al., 2013; Lewis, 1991; Soong & Cho, 1998; Weerd, 1984). Consequently, the sex of the colonies was not determined for this study. Small fragments of tissue-covered skeleton (< 2 cm<sup>3</sup>) were sampled during field surveys and preserved in 80% ethanol and stored at –20°C until DNA extraction.

All samples were incubated at 55 °C for 1 hour in 450 µL of digest buffer with proteinase K (QIAGEN, Hilden, Germany) and DNA was extracted using a QIAextractor automated genomic DNA extraction instrument, according to manufacturer's instructions. Each colony was amplified at twelve polymorphic microsatellite loci in four multiplex polymerase chain reactions (PCRs) using the Qiagen Multiplex PCR Kit (Table S1). Further details on these loci and the genotyping procedure are described in Dubé et al. (2017c). Samples were sent to GenoScreen platform (Lille, France) for fragment analysis on an Applied Biosystems 3730 Sequencer with the GeneScan 500 LIZ size standard. All alleles were scored and checked manually using GENEMAPPER version 4.0 (Applied Biosystems, Foster City, CA).

### **Multilocus genotypes and summary statistics**



Multilocus genotypes (MLGs) were identified using GENCLONE version 2.0 (Arnaud-Haond & Belkir, 2007). The genotyping error was estimated by re-sequencing and re-scoring a random subset of samples to calculate locus specific error rates ( $N = 145$ , see grey shaded IDs in Supplementary Data 1). To assess the discriminative power of the microsatellite markers, we also estimated the genotype probability (GP) for each locus and a combination of all loci in GENALEX version 6.5 (Peakall & Smouse, 2006). Colonies (ramets) with the same alleles at all loci were assigned to the same MLG (genet) and considered to be a product of asexual reproduction when  $GP < 0.001$ . To evaluate the probability that two identical MLGs arise from distinct random reproductive events, the probability of identity ( $P_{ID}$ ) was estimated (Waits et al., 2001). Once MLGs were assigned, the proportion of clones was estimated, as well as the standard genotypic diversity index, the clonal richness:  $R = (G - 1)/(N - 1)$ , where  $G$  is the number of MLGs and  $N$  the number of genotyped samples (Arnaud-Haond & Belkir, 2007). This index ranges from zero (all samples belong to the same lineage; asexually produced) to one (each sample belongs to a unique lineage; sexually produced). The probability of exclusion ( $P_{EX}$ ) was also computed in GENALEX and indicates the efficiency of a panel of microsatellite markers to exclude unrelated individuals when both parents are unknown (Jamieson & Taylor, 1997). Population genetic analyses were performed after the removal of all clonal replicates (genet level). Indices of genetic diversity, including the total number of alleles per locus ( $N_A$ ), observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosity (Weir & Cockerham, 1984) were estimated in GENALEX. Inbreeding coefficient  $F_{IS}$  (by locus and habitat) and linkage disequilibrium were estimated using GENETIX version 4.02 (Belkir et al., 1996), applying a permutation procedure (1,000 permutations) to assess statistical significance. In order to identify any potential genetic structure within the samples, a Bayesian clustering analysis was performed using STRUCTURE v2.3.4 (Pritchard et al., 2000). For this analysis, samples were selected randomly at the lowest number of colonies collected over the three surveyed habitats (back reef:  $n = 324$ ). STRUCTURE was run for each  $K$  from 1 to 10 using an admixture model and no prior on sample locations, where  $K$  represent the number of genetic populations. Runs were performed with the default setting, a burn-in period of 500,000, 500,000 MCMC repeats and 10 independent iterations per  $K$ . For this analysis, mean membership coefficients ( $q$ ) are calculated for each individual, corresponding to the likelihood that an individual

belongs to each of the inferred genetic clusters. The results were uploaded to STRUCTURE HARVESTER (Earl, 2012) and the most likely number of genetic clusters was determined using the ad hoc statistic  $\Delta K$  based on the posterior probability of the data (Evanno et al., 2005). The most likely  $K$  was retained for a second run in STRUCTURE with a burn-in period of 500,000, 500,000 MCMC repeats and 10 independent iterations. The results were once again uploaded to STRUCTURE HARVESTER and the resulting merged dataset was analyzed to estimate cluster assignment. GENETIX was also used to estimate genetic distance of *M. cf. platyphylla* samples collected in the three surveyed habitats using the unbiased Nei  $\theta$  estimator of  $F_{ST}$  (Nei, 1973) based on a permutation procedure (1,000 permutations). Pairwise relatedness coefficient (as an estimate of population inbreeding; Lynch & Ritland, 1999) was computed in GENALEX.

### **Kinship analyses**

Two kinship analyses were performed: parentage and sibship. Both analyses were based on individual MLGs after the removal of all clonal replicates; only the biggest clone of each MLG was retained in the dataset to infer parentage and sibling relationships. Only mature colonies (> 20 cm<sup>2</sup>) were considered as potential parents. Colonies smaller than 20 cm<sup>2</sup> were considered as juveniles (i.e. non-reproductive colonies, a threshold currently used for scleractinian species, see Penin et al., 2010; Sandin et al., 2008) and assumed to be the pool of potential offspring. Parent–offspring matches were established using the software CERVUS version 3.07 (Kalinowski et al., 2007; Marshall et al., 1998) with all parental genotypes entered into the analysis as candidate fathers because the sex of colonies could not be determined. The parameters of the simulated genotypes were the following: offspring 100,000; candidate fathers 300; proportion sampled 0.20 (based on the ratio of the area surveyed/area covered); proportion loci typed 0.9934 (based on our dataset); and proportion loci mistyped 0.03 (based on the mean genotyping error for all loci combined). A confidence level of the LOD score > 95% was considered to establish parentage relationships. Finally, two additional constraints were added to strengthen the results by allowing no loci mismatches in an inferred parent-offspring relationship that were identified in three independent simulation-runs. In order to test for long-distance dispersal, an additional parentage analysis was run using CERVUS with the same

parameters to establish parent-offspring relationships between juveniles collected in front of Papetoai and mature colonies from two other reef habitats located between 1.5 and 10 km away from our surveyed transects (Fig. S1 and Supplementary Data 1). COLONY version 2.0 (Jones & Wang, 2010) was used to identify full siblings in the juvenile samples only. COLONY was launched with the following parameters for each of the three medium length run: both sexes are polygamous and the organism is dioecious, with inbreeding, full-likelihood method, and a medium likelihood precision. Each run was launched with one CPU and included our estimated marker error rates, allele frequencies for the studied population computed with GENALEX, 20% sampled candidate fathers, and unknown maternal sibs. Only inferred assignments with a probability of 0.75 or greater were considered for the results. The program ML-RELATE (Kalinowski et al., 2006) was also used to determine relatedness values for each relationship identified with CERVUS and COLONY in order to validate parentage and sibling assignments. Pairwise geographic distances for strict parentage relationships (parent-offspring with LOD > 95%) and full siblings were estimated in R based on their associated x and y coordinates using the formula:  $d \leftarrow \text{round}(\sqrt{(a\$x-b\$x)^2+(a\$y-b\$y)^2}, 2)$ , where a and b are the colonies identified via parentage and sibship analyses. Dispersal distance estimates were also calculated between an offspring and all its potential clonal parents, i.e. for all combinations of clones belonging to the parent genotype and the assigned offspring. The closest dispersal event identified from a clonal parent-offspring pair was also retained to produce the bar plot showing the percentages of dispersal events found in each of the distance classes within the dispersal range of *M. cf. platyphylla* (Fig. 3). Such an estimate was used to avoid redundancy of dispersal estimates within the same distance class for an assigned offspring and its clonal parents, as most clonal replicates were close to one another. A spatial autocorrelation analysis was performed using the software SPAGeDi (Hardy & Vekemans, 2002), at both genet and ramet level, in order to test the null hypothesis that fire coral colonies are randomly distributed (by comparing simulated and empirical data).

### **Statistical analyses**

Two-tailed binomial tests (proportion test) were used to assess differences in proportion of juveniles, as well as variations in observed dispersal events, between the three

surveyed habitats. Pearson's correlation coefficient was used to determine whether the proportion of dispersal events (parent-offspring, full-sib pairs) decreases with increasing geographic distance, while differences for proportions between geographic distances were tested using two-tailed proportion tests. The shortest distance between an offspring and all its assigned candidate parents was used to perform statistical analyses. Pearson's correlation coefficient was also used to determine whether the number of offspring produced by each of the identified parents increases with their number of ramets (parents with or without clones of the same genotype) and colony size. Furthermore, differences in dispersal distances between offspring assigned to parents belonging to a clonal genotype (parents with clones) *versus* non-clonal genotype (parents without clone) were assessed using a two-tailed binomial test (Student's t-test). All statistical analyses were performed in the R programming environment.

## Results

### Population, clonal, and genetic structure

The population density was approximately one colony per 10 m<sup>2</sup> and the mean pairwise geographic distance between all colonies within the entire study area was 347 m ( $\pm$  228 SE; range: 0.01–979 m; median = 310 m). The size-frequency distribution of the population was skewed towards small colonies ( $g_1 = 0.395$ ;  $P_{\text{norm}} < 0.001$ ) with 64% of all colonies below 128 cm<sup>2</sup> (Fig. S2). Of all surveyed colonies, 1,059 were considered as juveniles ( $< 20$  cm<sup>2</sup>) and 2,101 as adults (Fig. 2 and Table 1). Fifty-six percent of all sampled colonies were observed in the upper slope, while the proportion of juveniles was much higher in the mid slope (48% of potential offspring within this habitat) compared to what was found in the other surveyed habitats (29% in the upper slope and 12% in the back reef) (Proportion test,  $P < 0.001$ , Table 1).

In total, 981 multilocus genotypes (MLGs, also called genets) were detected in the entire population and 281 of them belonged to clonal lineages (many colonies of the same genotype) with GP values ranging from 3.1E-16 to 1.0E-06 for all loci combined (Table 1 and Supplementary Data 1). Overall, 85% of adults were clones indicating that asexual reproduction prevails for population renewal ( $R = 0.31$ ). Sixty-five percent of juveniles (684 of 1,059) had at least one clonal replicate. Of these clonal juveniles, 678 were

genetically identical to one of the sampled adults. Given the low  $P_{ID}$  value estimated (4.5E-08), these 678 juveniles were assumed to be the result of asexual reproduction through fragmentation and were thus removed from the pool of potential offspring. Only 3 pairs of juveniles, located in close proximity with one another, were clones of the same genet (UPT1-R152 and UPT1-R153: 0.10 m; MDT2-L54 and MDT2-L55: 0.05 m; MTD2-R36 and MDT2-R37: 0.02 m, see Supplementary Data 1). Only one individual for each of these clonal juvenile pairs was retained for further analyses (reducing the pool of offspring to 378 individuals). After removing all but one ramet of each genet from the dataset, no genetic structure could be detected across the surveyed reef habitats, indicating a single population of fire corals at Papetoai (Fig. S3 and Table S2). Mean observed and expected heterozygosity were of 0.483 and 0.529, respectively, with 7.50 alleles per locus on average, and the combined probability of exclusion ( $P_{EX}$ ) for the microsatellite marker panel was 0.94 (Table S1), revealing some reliability for parentage assignments, as  $P_{EX}$  values  $> 0.99$  are common in other parentage studies (Almany et al., 2017; Robichaud et al., 2006; Sorin, 2004; Yeoh & Dai, 2010).

### Parentage assignment and recruitment

Following the removal of clonal replicates, 981 colonies with a unique MLG (genet level) remained to further assess parentage and sibship relationships among *M. cf. platyphylla* colonies with a candidate pool of 603 parents and 378 offspring (Table 1). Parentage analysis using CERVUS assigned 8% of the putative offspring (30 of 378) to parents that were sampled within the study area, and this with a high level of confidence ( $> 95\%$ ), thus corresponding to the minimum of self-recruitment in the population (Fig. 2 and Table 2). By restricting our dispersal analyses with the  $> 95\%$  of confidence threshold, we thus favor type II errors and are confident with the dispersal estimates calculated for the 8% of offspring assigned to local parents. No parent-offspring pair was identified between Papetoai and the other reef locations. All 30 identified parent-offspring pairs were validated using ML-RELATE. Sixty-seven percent of these assigned offspring (20 of 30) were found within the mid slope, where the highest proportion of juveniles was also recorded, and about 55% (17 of 30) were assigned to parents located in a different habitat than the one in which they were found (Table 2). This later result indicates that inter-habitat dispersal events occurred in *M. cf. platyphylla* population. Among the 603

parents sampled in the entire study area (after the removal of clones), only 26 of them contributed to self-recruitment (Fig. S4). Fourteen parents were genetically unique, while the other 12 belonged to clonal lineages with an average number of 7 ramets per genet (range: 2–20), totaling 98 potential parents. Of those, 18 were considered as juveniles based on their sizes  $< 20 \text{ cm}^2$  and were consequently removed from the dataset for downstream analyses. Clonal replicates of each clonal parent were closely related in space with a mean distance ranging from 0.18 to 129 m ( $\pm 102 \text{ m}$ ; SE) depending on the genet (median = 4 m, Supplementary Data 2).

Of the 30 identified parent-offspring pairs, only one offspring was assigned to a pair of parents that were separated by 2.44 m, while the offspring was at 1.97 m and 3.58 m from each parent providing the first evaluation of fertilization and dispersal distance. While most local parents were associated to only one offspring each (81%), five of them have been identified as the parent of two offspring within the study area. No significant difference was found in the number of offspring produced by parents as a function of their number of clonal replicates or their colony size (Fig. S5; Kruskal-Wallis tests:  $X^2 = 0.234$ ,  $P = 0.628$  and  $X^2 = 0.946$ ,  $P = 0.331$ , respectively). Furthermore, the mean pairwise genetic relatedness between parents contributing to self-recruitment (mean  $r = -0.020 \pm 0.004 \text{ SE}$ ) was less than the average among all the potential parents surveyed in the study area (mean  $r = -0.002 \pm 0.151 \text{ SE}$ ), indicating that inbreeding was limited.

### **Dispersal distances and sibling distribution patterns**

Observed dispersal distances between an offspring and all its candidate parent ranged from 0.05 to 884 m (ramet level, Table 3 and Supplementary Data 3). When including all clonal replicates of parents that contribute to self-recruitment, maximal differences in dispersal events among clones ranged from 0.12 to 101 m depending on the genet (median = 2.44 m, Supplementary Data 3). Sixty-five percent of assigned offspring settled within 300 m of the parental sources (at both genet and ramet levels, Fig. 3A and 3B, respectively) with a significant gradual decrease in the proportions of offspring that settled at larger distances ( $r = -0.744$ ,  $P < 0.05$ ). At smaller spatial scales (100 m), our results revealed a higher proportion of offspring (57%) settling within the first 10 m from

their closest parents (Proportion test,  $P < 0.001$ ), while the remaining 43% were distributed equally in three distance classes (60–70 m, 80–90 m, and 90–100 m). Consistently, spatial autocorrelation analysis using the complete dataset of *M. cf. platyphylla* genotypes (including clones;  $n = 3,160$ ) revealed significant positive spatial autocorrelation up to distances of 194 m at the scale of the entire study area and up to 28 m at smaller spatial scales (i.e. 100 m; Fig. 4A, 4B). After the removal of clones, we observed a significant positive spatial autocorrelation up to 304 m with coefficient values lower to those estimated with the entire dataset (Fig. 4C, 4D). These results suggest that the cause of the correlation between genetic and geographic distances over small distance classes is more influenced by asexual reproduction, likely via fragmentation, in *M. cf. platyphylla* population. Nevertheless, consistencies between simulated and direct estimates of dispersal events obtained using spatial autocorrelation and parentage analysis, respectively, suggest a significant impact of sexual reproduction on the local distribution of *M. cf. platyphylla* (mean dispersal distances when only the closest parent is retained: 294 m and 36 m, at large and small scales, respectively). Furthermore, parent-offspring distances revealed no significant differences in the dispersal abilities of non-clonal parents versus clonal parents (Student's test,  $t = -0.530$ ,  $P = 0.605$ ).

Over the 378 offspring surveyed, 71 (19%) were involved in full sibling relationships (totaling 41 full-sib pairs, Supplementary Data 4). Of those, none were assigned to local parent pairs, all were from parents that were outside our field surveys. Full siblings occurred within an aggregated pattern of distribution with nearly 50% settling within the first 100 m of their siblings (Proportion test,  $P < 0.001$ , Fig. 5A). At a smaller scale (100 m), more than 40% settled at  $< 30$  m (Proportion test,  $P < 0.001$ , Fig. 5B).

## Discussion

By conducting genetic parentage analyses in a natural population of the fire coral *Millepora cf. platyphylla*, this study is one of the first to provide empirical estimates of dispersal in a free-spawning marine invertebrate. This study points to self-recruitment together with clonality as potential drivers for the renewal of the population of *M. cf. platyphylla* at Moorea. Although the adult population is predominantly sustained through asexual reproduction (85% are clones), our parentage analysis identified a moderate

contribution from self-recruitment with a minimum of 8% of offspring produced locally and a limited dispersal ability of early life stages. These results support earlier observations indicating that self-recruitment at the reef scale (or finer) is critical for population replenishment in corals (Figueiredo et al., 2013; Gilmour et al., 2009; Underwood et al., 2018).

### **Moderate self-recruitment and limited dispersal ability**

This study unveils a minimum of self-recruitment rate of 8% in *M. cf. platyphylla* population. Because only 20% of the area covered was sampled to assess for parentage relationships, our sampling design might exclude potential parents occurring between our transects and surveyed habitats, which could potentially increase true values of self-recruitment in the studied population. In consideration of this, a relatively high investment in self-recruitment might well be an efficient process to sustain local populations in an isolated reef system such as Moorea (as described in Gilmour et al., 2009; Shinzato et al., 2015; Tsounis & Edmunds, 2016; Underwood et al. 2018; Zeng et al., 2017). For *M. cf. platyphylla*, we were expecting a moderate contribution from self-recruitment because of its intermediate larval development mode, i.e. between the extremes of philopatry often observed in brooders and potentially long-lived planktonic dispersal phases associated with broadcast spawners. The planula larvae of *Millepora* are zooxanthellate (vertically transmitted) and full of lipid droplets. As a consequence, *Millepora* larvae have the potential to live for several weeks before settlement (> 1 month in controlled conditions for *M. exaesa* at Reunion Island; Bourmaud et al., 2013). Consequently, the identified moderate rate of local recruitment does not exclude sporadic success of long-distance dispersal events, significant in dispersing genetic variants. A high potential for metapopulation connectivity has been revealed among islands of the Society Archipelago in French Polynesia for some scleractinian species (Moorea, Raiatea, Taha'a and Tahiti; Adjeroud et al., 2014). Preliminary results from samples of *M. cf. platyphylla* collected in several islands from French Polynesia revealed significant genetic differentiation among archipelagos (Marquesas, Austral, Gambier, Society and Tuamotu, Boissin et al., unpublished). Consistently, no offspring were assigned to adult colonies collected in other reef locations located at 1.5 to 10 km away from our studied area, and the spatial autocorrelation analysis also showed a negative relationship at distances > 200 m (i.e.



over-dispersion). Consequently, we suspect that unassigned offspring may be produced locally by colonies occurring between or nearby our transects, or even in our transects, but unassigned due to the lack of power of our microsatellite panel ( $P_{EX}$  of 0.94). Low connectivity was also observed in other hydrozoan species producing medusoids and had similar population genetic structure than species without medusoid (Boissin et al., 2018). This finding suggests that life cycles including this type of sexual propagules are comparable to brooders strategies in term of dispersal ability. Of note is that several other parentage studies in marine animals relied on a small number of microsatellite markers (Beldade et al., 2016; Bernardi et al., 2012; Li & Yu, 2009; Selwyn et al., 2016), suggesting that their kinship assignment rate might have a similar bias than what we found in this study, i.e. that the panel is conservatively underestimating the number of self-recruits (as shown by the almost linear increase in assignments as loci were added, Fig. S6).

Our results demonstrated that new recruits often settle within only few meters from their parents (< 10 m), highlighting non-random dispersal events in the studied population. While very few studies have investigated the reproductive biology and early life stages of *Millepora* hydrocorals (reviewed in Lewis, 2006; Dubé et al., 2019), our study revealed a limited dispersal ability of their sexual propagules (medusoids, gametes, and planula larvae). Although medusoids can swim by pulsation of their bell, hydrocoral eggs and spermatozoids are negatively buoyant and slowly sink after being released (Soong & Cho, 1998). The larvae is also negatively buoyant and crawl until it finds a sustainable substrate to fix and metamorphose (Bourmaud et al., 2013). Such early life history traits are most likely rising opportunities for self-recruitment in populations of fire corals when sexual propagules are produced together with conditions that favor retention processes, settlement, and post-settlement success. Still, before the larvae sink and crawl, there is exposure to the currents in the water column during its early life history (medusoid and gamete release, fertilization, and larval development). In addition, recruits with parents inhabiting distinct reef habitats that were separated by 40 to 210 m were recorded in large proportions (~55%, 17 out of 30). Such dispersal events must rely on the passive dispersal of their sexual propagules through water circulation patterns. This possibility can easily be accomplished through wave-driven and cross-reef transports that

characterize flow regimes on reefs located on the north shore of Moorea (Hench et al., 2008; Monismith et al., 2013).

### **Dispersal of early life stages with reef currents**

In Moorea, alongshore and cross-reef transports are known to affect recruitment of larvae and population connectivity among habitats within a single reef, both in corals (Edmunds et al., 2010; Leichter et al., 2013, Tsounis & Edmunds, 2016) and fishes (Belgrade et al., 2012; Bernardi et al., 2012). Here, the high dispersal among habitats indicates that cross-reef transport, from the fore reef towards the lagoon, is the major process driving the dispersal of offspring in *M. cf. platyphylla*. This dispersal pattern of sexual propagules is in accordance with the one reported for those that were produced asexually in the same fire coral population (Dubé et al., 2017b). In fact, asexual fragments were distributed perpendicularly to the reef crest, perfectly aligned with wave energy dispersal (see Fig. S4 for dispersal pattern of clones). A high proportion of juveniles was also reported on the mid slope, an exposed reef where wave energy is reduced (Hearn, 1999). As previously described in some Caribbean reefs (Paris & Cohen, 2004), water displacement decreases with increasing depth suggesting that larval behavior, such as swimming or crawling, may enhance local recruitment in deeper waters within the fore reef. Overall, our results indicate that the distribution of fire corals in Moorea is strongly influenced by the dispersal of sexual propagules with cross-reef transport, a process likely accentuated in deeper waters.

### **Influence of gamete dispersal and fertilization on sibling aggregations**

Sibship analyses revealed that siblings recruit close to one another on the reef (more than 40% settled at < 30 m), resulting in sibling aggregations. It is commonly assumed that medusoids, the early life stage during which a fire coral releases its gametes, facilitate fertilization rates through synchronous spawning (Lewis, 2006). This reproductive strategy enables gametes to aggregate at the water surface once they are released (Bourmaud et al., 2013; Soong & Cho, 1998), and most likely contributes to the sibling aggregation pattern observed in *Millepora* population. In many broadcast spawning species, the success of fertilization is proximity dependent (Carlson, 1999; Doropoulos et al., 2018; Teo & Todd, 2018) with sperm dispersal identified as the limiting

factor in numerous reef invertebrates, even at the scale of few meters (Coma & Lasker, 1997; Lasker et al., 2008; Pennington, 1985; Warner et al., 2016). In this study, we identified one pair of parents that were assigned to an offspring, with only 2.44 m separating the two parents. This result suggests that the almost synchronous release of medusoids and ripe gametes allows for a quick fertilization between proximate gravid colonies. This result is concordant with a recent study, where simulated intercolonial distances showed that fertilization events rarely occur between coral colonies separated by more than 30 to 40 m (Teo & Todd, 2018). The authors argued that such a limited distance for successful mating from different coral colonies is mostly due to sperm dilution and insufficient mixing between gametes. While the reproductive season of fire corals is still unknown at Moorea, reproduction can potentially occur during the summer when the water is calmer (as described in Reunion Island, Red Sea, and Taiwan; Bourmaud et al., 2013, Soong & Cho, 1998; Shlesinger & Loya, 2019), thus favoring both local dispersal and sibling aggregations.

### **Impact of clonal reproduction on self-recruitment and dispersal**

Even though adults were mostly clones, we found that genetically unique parents (only one ramet reproduces) contributed equally to self-recruitment than those of clonal genotypes (many ramets reproduce). Previous studies have shown that colonies that have suffered from stress due to fragmentation may further invest in growth rather than reproduction (Okubo et al., 2005; 2007). Since half of the clonal parents were smaller than 130 cm<sup>2</sup>, it is reasonable to assume that these fragments may preserve their energy to reach a larger size and increase their survival, or invest in a different reproductive strategy (e.g. reproduce less frequently or limited number of medusoids). Nevertheless, one could wonder if the dispersion of clones increases the area over which sexual propagules are dispersed. For instance, the maximal distance between clone mates in *M. cf. platyphylla* has been estimated to 450 m in a patch reef habitat located on the north shore of Moorea (Dubé et al., 2017b), which can ultimately increase the 'effective dispersal' for a single genotype. Our estimates for the dispersal distances were not higher for clonal parents suggesting that clonal lineages have no better ability for the dispersal of their offspring. It has to be noted that asexual fragments were in close

proximity to one another, which may further explain the similar dispersal extent of offspring among clonal and non-clonal parents.

Furthermore, most of the sampled juveniles were genetically identical to some parents. This result confirms that clonal aggregation of large colonies (i.e. when clones are distributed in patches) can increase local replenishment by supplying new recruits through their fragmentation (Highsmith, 1982). Despite the fact that large fragments are assumed to have a higher chance of survival (Lirman, 2000; Okubo et al., 2007), the large proportion of small fragments (< 20 cm<sup>2</sup>) observed in this study suggests that they can survive and effectively contribute to local sustainability. Still, these aggregations of clones combined with sibling aggregations and limited dispersal can increase inbreeding in the population due to cross fertilization of genetically related neighbors. Despite all of these reproductive features, comparisons of genetic relatedness (all sampled parents *versus* those contributing to self-recruitment) revealed that mating between closely related adults is less likely to occur. This result suggests that the dispersal of sexual propagules, although limited, is enough to restrict population inbreeding. Furthermore, we identified local parents that relied on multiple breeding by reproducing with at least two other adult colonies within or outside the study area. As in other broadcast spawning marine invertebrates (Johnson & Yund, 2007), multiple mating may limit inbreeding in the population (Foerster et al., 2003) and increase the performance and survival of offspring by increasing the genetic diversity in the brood (McLeod & Marshall, 2009; Underwood et al., 2018). Dispersal limitations of both asexual and sexual propagules may represent an efficient reproductive strategy to sustain local population abundance and genetic diversity, especially at the margins of *M. cf. platyphylla* range, such as Moorea (Randall & Cheng, 1984).

## **Conclusion**

Our study provides a robust example of direct dispersal estimates for a free-spawning marine invertebrate, and as such constitute a long-overdue counterpoint to the growing number of examples from reef fishes (Abesamis et al., 2017; Almany et al., 2007; Jones et al., 2005; Planes et al. 2009; Salles et al. 2016). Overall, our parentage analysis demonstrates that *M. cf. platyphylla* is capable of producing sexual propagules to support self-seeding in Moorea's populations, although they are predominantly sustained through

asexual reproduction. The standing stock of genetic diversity in the population of fire corals at Moorea may also be eroded by its high level of clonality, hindering the potential for adaptation in the absence of input of exogenous genes (Uecker, 2017). Nevertheless, such an asexual/sexual recruitment dynamics enables local sustainability and great opportunities to recover from major disturbances, which can occur frequently in coral reef ecosystems such as Moorea Island (Adjeroud et al., 2018). This study confirms theoretical considerations claiming that local dispersal is a key factor in stabilizing population dynamics of reef organisms, such as fishes and reef-building corals (Hastings & Botsford, 2006; Richmond et al., 2018). Our study showed that the early life history of fire corals promotes the dispersal of sexual propagules locally as well as sibling aggregations (short-lived dispersive phases via medusoid and gamete release, rapid embryogenesis, fertilization, and larval development). However, the dispersal distances seem extremely limited for a broadcasting species, thus highlighting the intermediate reproductive strategy of fire corals; dispersive planktonic phases associated with broadcast spawners and gregarious behavior of early life stages approaching brooder strategies. As such, further investigations are thus needed to develop an understanding of the life cycle of fire corals, and other free-spawning marine invertebrates, and to determine early life history traits that are involved in the proliferation of locally produced larvae.

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## **Data accessibility**

Microsatellite loci for *M. cf. platyphylla* are available in GenBank (KK670763–KX670777). All 3,160 georeferenced colonies and their associated multilocus genotypes, spatial

coordinates, and size are available in Dryad (<https://doi.org/10.5061/dryad.931zcrjfv>) and Supplementary materials.

## Author contributions

C.E.D. and S.P. designed research. C.E.D. and A.M. conducted field surveys and collected data. C.E.D. generated and analyzed the data, and drafted the manuscript. E.B., A.M., and S.P. contributed to data analyses. C.E.D. and E.B. wrote the manuscript with inputs from S.P. All authors contributed to the drafts and gave final approval for publication.

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**Tables**

**Table 1.** Details of *Millepora cf. platyphylla* population structure based on colony size (ramet and genet level) and clonal structure across the three surveyed habitats at Moorea.

Habitats	Population Structure							Clonal Structure			
	Ramet level				Genet level			# MLGs	# clonal MLGs	% clonal colonies	R
	# colonies	# adults	# juveniles	% juveniles	# colonies	# adults	# juveniles				
Mid Slope	1075	563	512	47.63	493	216	277	493	87	62.23	0.46
Upper Slope	1761	1253	508	28.85	358	268	90	358	153	88.36	0.20
Back Reef	324	285	39	12.04	130	119	11	130	41	72.53	0.40
<b>Total surveyed</b>	<b>3160</b>	<b>2101</b>	<b>1059</b>	<b>33.51</b>	<b>981</b>	<b>603</b>	<b>378</b>	<b>981</b>	<b>281</b>	<b>68.96</b>	<b>0.31</b>



% juveniles: proportion of juveniles within each habitat; % clonal colonies: proportion of colonies that belong to a clonal MLG within each habitat; R: genotypic richness.

**Table 2.** Parentage assignment for strict (> 95%) level of confidence.

> 95% confidence				
Habitats	# assigned	% assigned	% intra- habitat dispersal	% inter-habitat dispersal
Mid Slope	20	7.22	35.00	65.00
Upper Slope	9	10.00	66.67	33.33
Back Reef	1	9.09	0.00	100
<b>All assignments</b>	<b>30</b>	<b>7.94</b>	<b>44.33</b>	<b>56.67</b>

% assigned: proportion of offspring assigned to a sampled parent within each habitat; % intra-habitat dispersal: proportion of assigned offspring to a parent located within the same habitat in which the offspring was found; % inter-habitat dispersal; proportion of assigned offspring to a parent located in a different habitat than the one in which the offspring was found.

**Table 3.** Summary results of parentage analysis in *Millepora* cf. *platyphylla* within the entire reef area (9,000 m<sup>2</sup>). Characteristics of parents contributing to self-recruitment and comparisons between clonal and unique genotype parents are given: number of potential parents surveyed in the study area; number of parents assigned to an offspring within the surveyed area with their mean colony size (cm<sup>2</sup>), standard error (SE) and median; total number of assigned offspring and mean number of assigned offspring to one single parent with standard error (SE), maximum and median. All values are presented at the ramet level (with clonal replicates). Estimates of offspring dispersal within the study area are shown: mean distance between parents and their assigned offspring with standard error (SE), minimum, maximum and median.

	Parent total	Parent clonal genotype	Parent unique genotype
# potential parents	603	279	324
# parents	26	12	14
Mean parent size (cm <sup>2</sup> )	1125.68 (± 3285.83)	1061.51 (± 3344.72)	1428.22 (± 3091.15)
Median	138.25	138.25	175.21
# assigned offspring	30	13	17
Mean # assigned offspring per parent	1.30 (± 0.46)	1.30 (± 0.46)	1.28 (± 0.47)
Median	1.00	1.00	1.00

Mean dispersal distance parent-offspring (m)	313.83 ( $\pm$ 273.52)	313.51 ( $\pm$ 272.53)	315.18 ( $\pm$ 285.60)
Min	0.05	0.05	1.97
Max	883.61	816.69	883.61
Median	203.96	174.65	220.33

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## Figure captions

**Figure 1.** Aerial views showing the study area in Moorea, French Polynesia, and the locations of the three belt transects (300 x 10 m) within the three surveyed habitats. The world map was obtained from Aix-Marseille University (<http://www.d-maps.com>) and images from Google Earth (Map data © 2015 Google, DigitalGlobe). The figure was created using Adobe Photoshop CS6 software.

**Figure 2.** Spatial distribution and size of the 3,160 colonies sampled across the three surveyed habitats within three belt transects (300 x 10 m). Adult colonies (potential parents, N = 2,101) are shown in grey and juvenile colonies (< 20 cm<sup>2</sup>, N = 1,059) in white. Offspring assigned to at least one parent sampled within the study area, as revealed by parentage analysis, are shown in red (N = 30) for strict (> 95%) level of confidence.

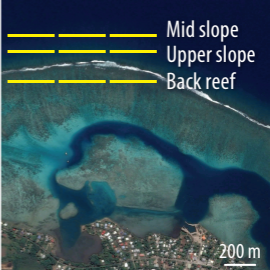
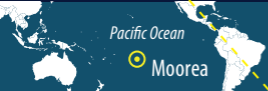
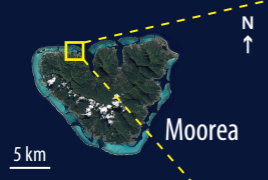
**Figure 3.** Dispersal distance distribution of parent-offspring pairs within the entire surveyed area. Minimal observed dispersal distribution based on the identified parent-offspring pair having the shortest distance (**A**) and full distribution of parent-offspring pairs (**B**), determined using parentage analysis, is given by the percentages of dispersal events (N = 30) distributed among nine distance classes, assigned at 100 m each over the entire dispersal range.

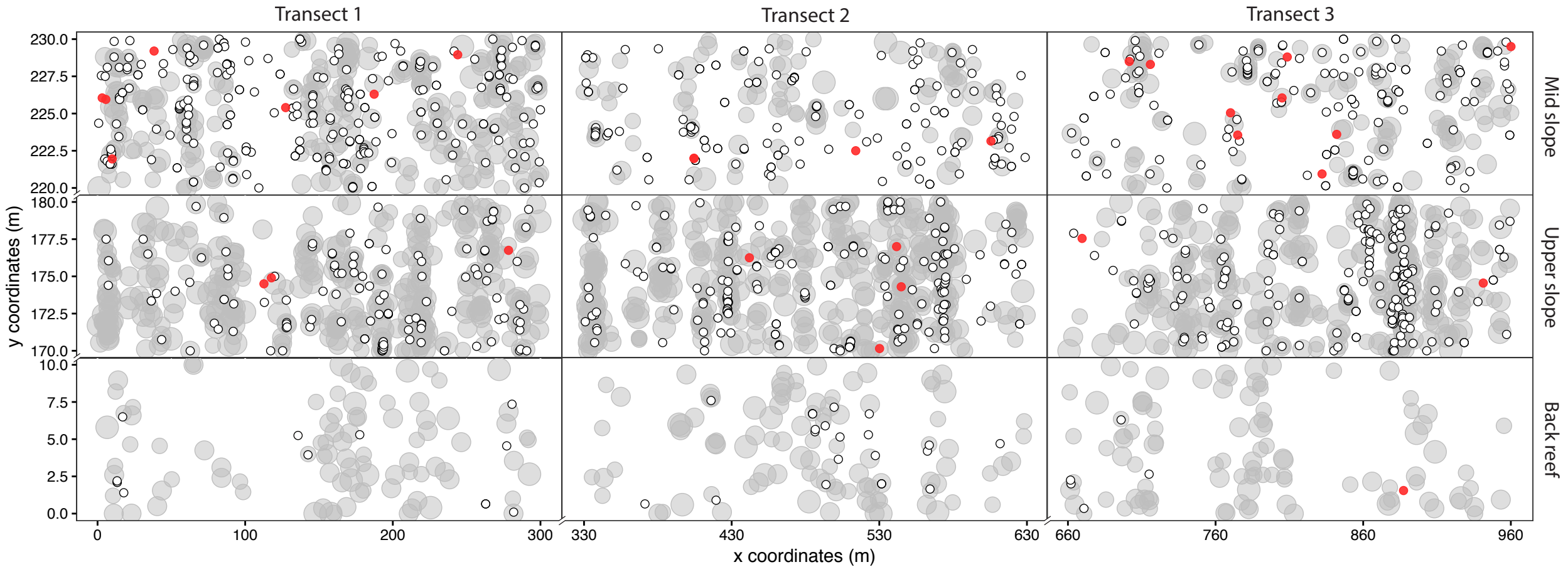
**Figure 4.** Spatial autocorrelation correlograms for *Millepora* cf. *platyphylla* at large and fine scales. Large scale spatial autocorrelation with clones included in the analysis (**A**) and clones removed (**B**). Fine scale spatial autocorrelation with clones included in the analysis (**C**) and clones removed (**D**). The endpoint of each distance class (in meters) is plotted on the x-axis and the spatial autocorrelation coefficient ( $r$ ) with 95% confidence error is plotted in blue on the y-axis. The top red dotted line is the upper 95% confidence limit and the bottom red dotted line is the lower 95% confidence limit of the null hypothesis (i.e. fire coral colonies are randomly distributed).

**Figure 5.** Distance between pairs of full siblings within the entire surveyed area. Observed distance between pairs of full siblings is given by the percentages of identified full sibling pairs (N = 41) distributed among six distance classes, assigned at 100 m each

over the entire dispersal range (**A**) and dispersal events ( $N = 19$ ) distributed among 10 distance classes, assigned at 10 m each over the first hundred meters of the dispersal range (**B**).

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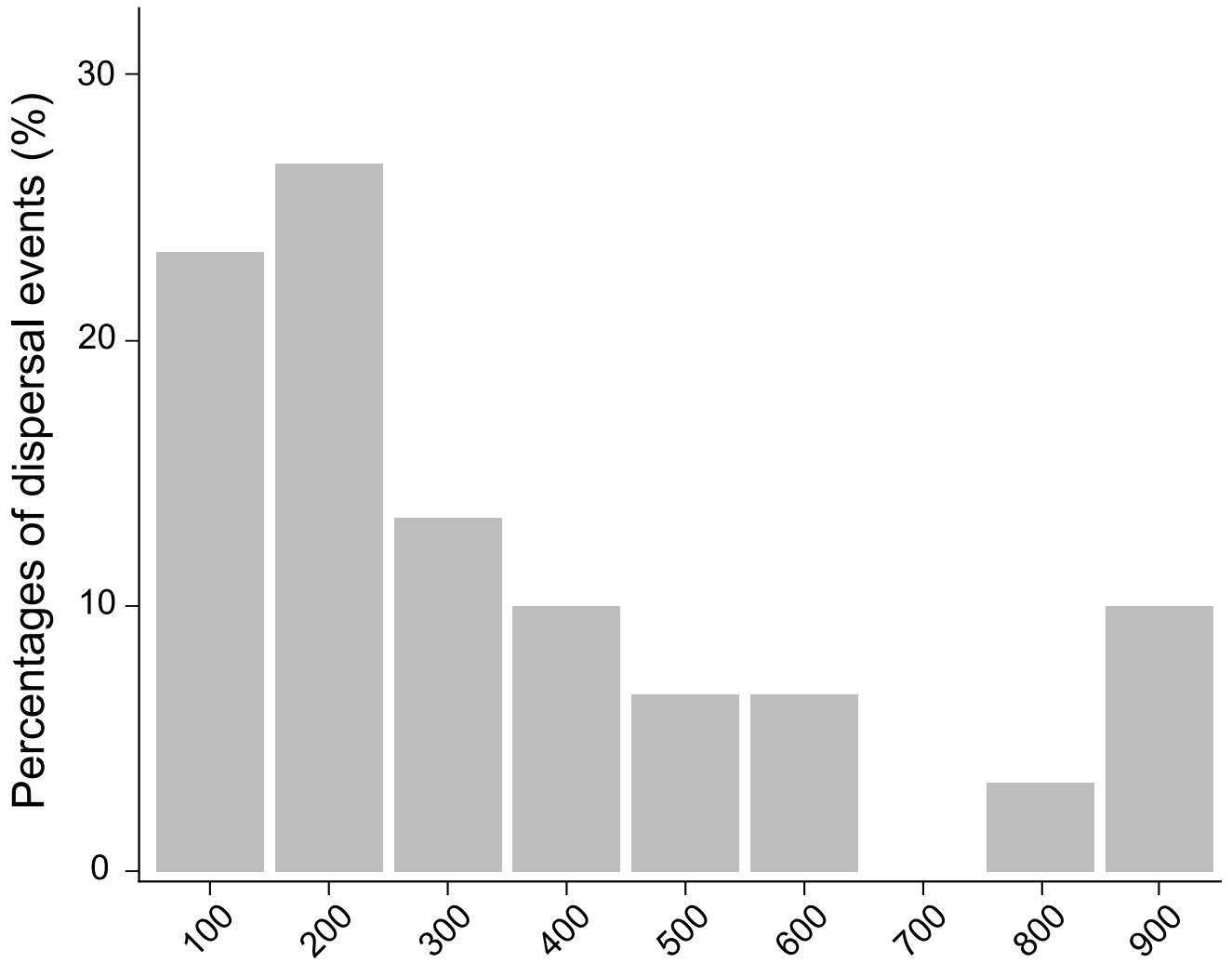
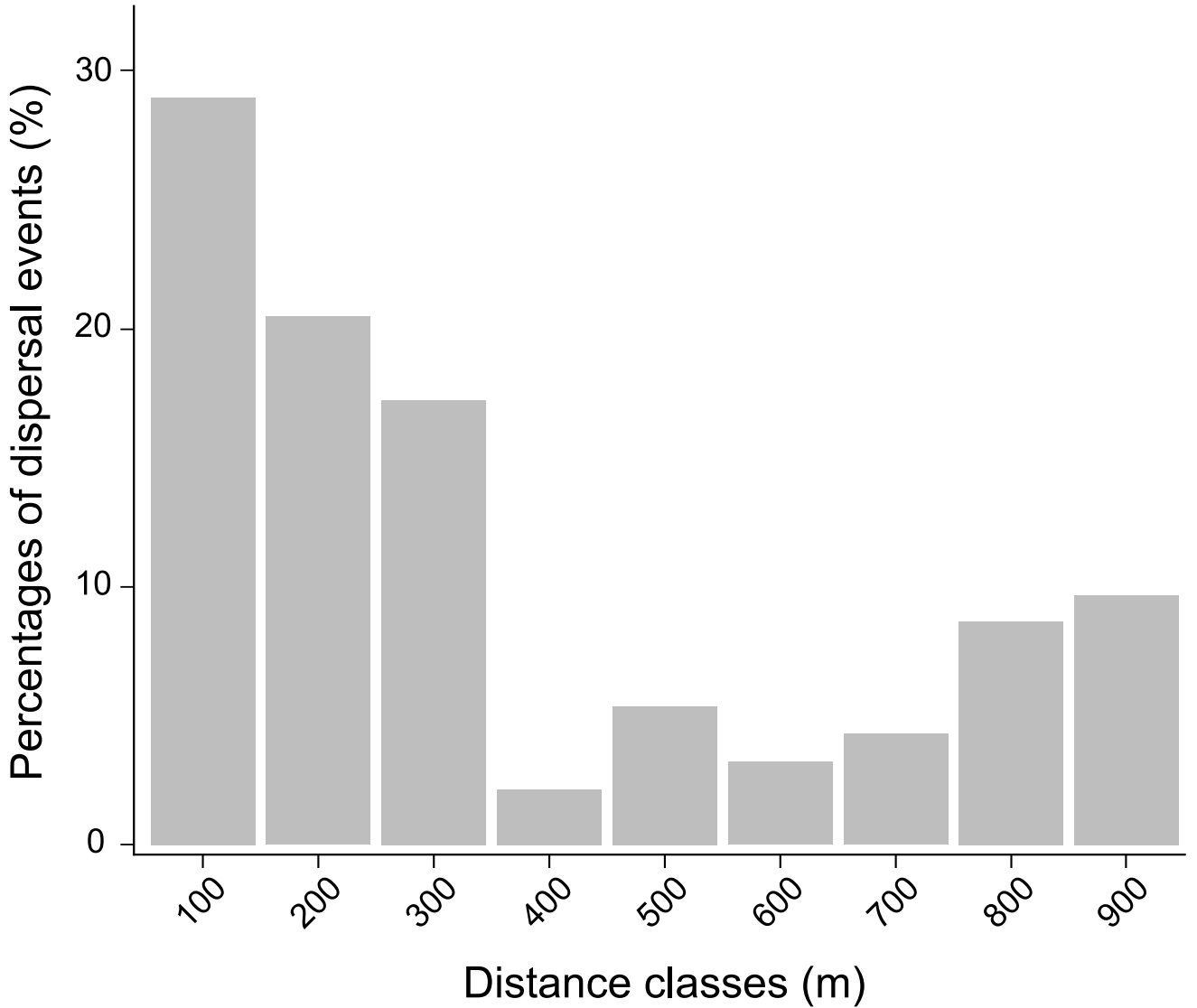


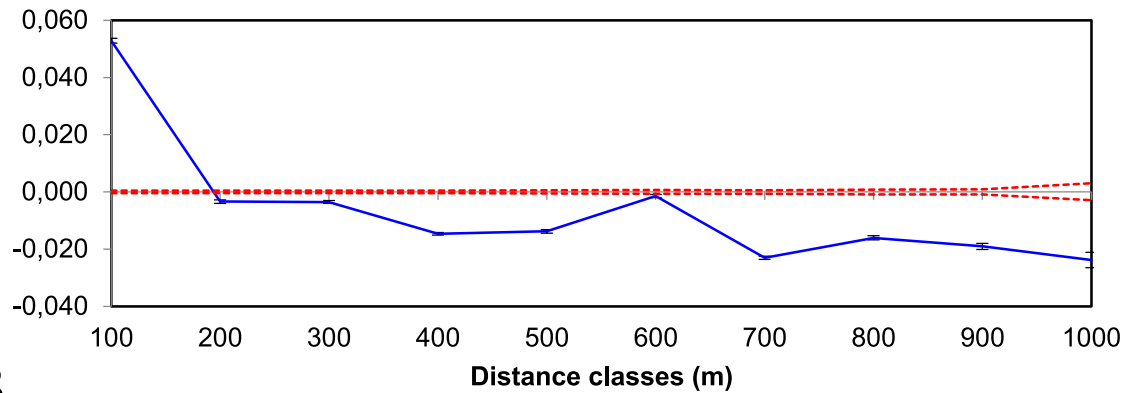
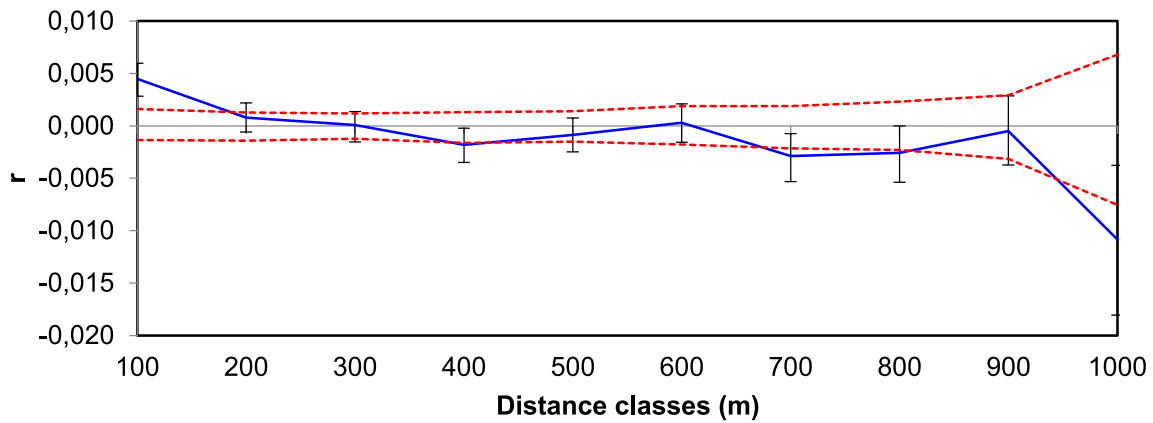
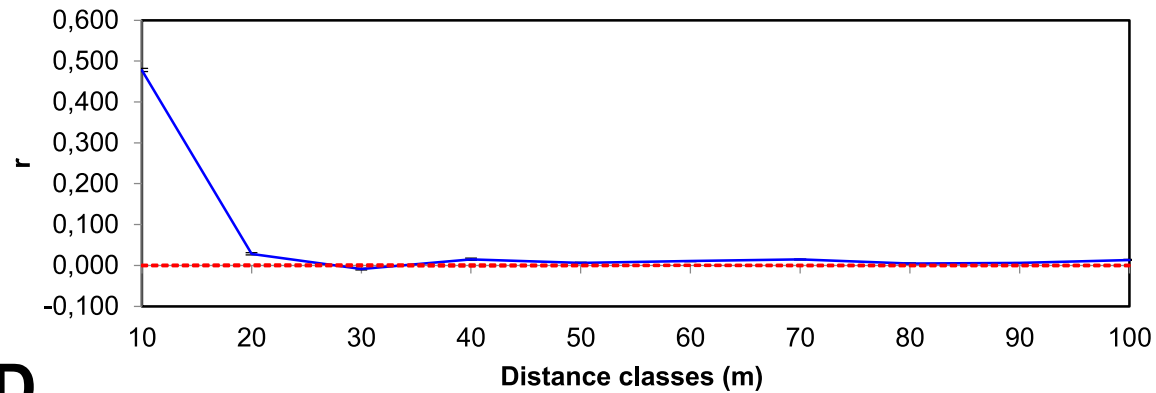
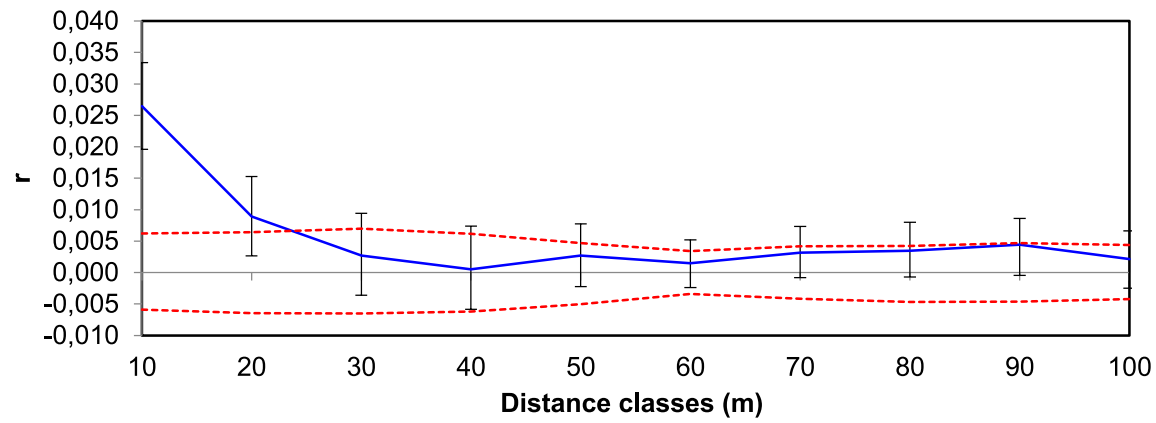


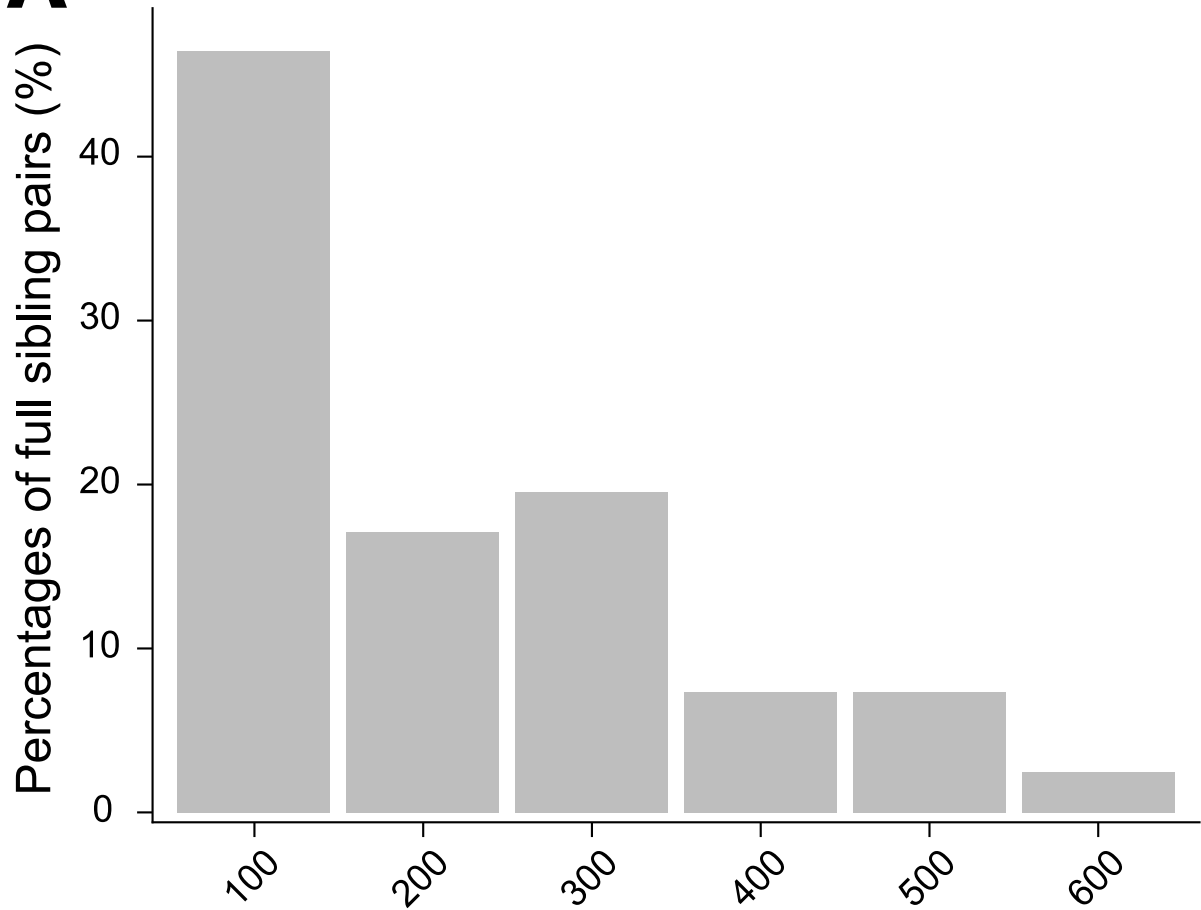
● Matures ○ Juveniles ● Assigned offspring (95%)

Size Area (cm<sup>2</sup>) ● > 0 - 20 ● > 20 - 128 ● >128 - 1000 ● >1000



**A****B**

**A****B****C****D**

**A****B**