PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Lord KS, Lesneski KC, Buston PM, Davies SW, D'Aloia CC, Finnerty JR. 2023 Rampant asexual reproduction and limited dispersal in a mangrove population of the coral *Porites divaricata*. *Proc. R. Soc. B* **290**: 20231070.
https://doi.org/10.1098/rspb.2023.1070

Received: 18 August 2022
Accepted: 8 June 2023

Subject Category:
Ecology

Subject Areas:
ecology, environmental science, genomics

Keywords:
coral, dispersal, reproduction, mangrove

Author for correspondence:
John R. Finnerty
e-mail: jrf3@bu.edu

†Present address: Department of Integrative Biology, University of Texas at Austin, Austin, TX 78712, USA.
‡Present address: Florida Keys National Marine Sanctuary, 95230 Overseas Highway, Key Largo, FL 33037, USA.

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6700115.

THE ROYAL SOCIETY PUBLISHING

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

Rampant asexual reproduction and limited dispersal in a mangrove population of the coral *Porites divaricata*

Karina Scavo Lord[1,†], Kathryn C. Lesneski[1,‡], Peter M. Buston[1], Sarah W. Davies[1], Cassidy C. D'Aloia[2] and John R. Finnerty[1]

[1]Boston University Department of Biology and Marine Program, 5 Cummington Mall, Boston, MA 02215, USA
[2]University of Toronto Mississauga Department of Biology, Mississauga, ON, Canada L5L 1C6

KSL, 0000-0002-6257-6270; KCL, 0000-0003-3378-9338; PMB, 0000-0001-5513-8259; SWD, 0000-0002-2113-9103; CCD'A, 0000-0002-0824-0151; JRF, 0000-0001-8576-6774

Corals are critical to marine biodiversity. Reproduction and dispersal are key to their resilience, but rarely quantified in nature. Exploiting a unique system—a fully censused, longitudinally characterized, semi-isolated population inhabiting mangroves—we used 2bRAD sequencing to demonstrate that rampant asexual reproduction most likely via parthenogenesis and limited dispersal enable the persistence of a natural population of thin-finger coral (*Porites divaricata*). Unlike previous studies on coral dispersal, knowledge of colony age and location enabled us to identify plausible parent–offspring relationships within multiple clonal lineages and develop tightly constrained estimates of larval dispersal; the best-fitting model indicates dispersal is largely limited to a few metres from parent colonies. Our results explain why this species is adept at colonizing mangroves but suggest limited genetic diversity in mangrove populations and limited connectivity between mangroves and nearby reefs. As *P. divaricata* is gonochoristic, and parthenogenesis would be restricted to females (whereas fragmentation, which is presumably common in reef and seagrass habitats, is not), mangrove populations likely exhibit skewed sex ratios. These findings suggest that coral reproductive diversity can lead to distinctly different demographic outcomes in different habitats. Thus, coral conservation will require the protection of the entire coral habitat mosaic, and not just reefs.

1. Background

A major challenge in marine ecology is measuring reproduction and dispersal. These demographic processes have fundamental ecological, evolutionary and conservation impacts on marine species. Ecologically, these processes affect population dynamics by influencing the exchange of individuals among populations. Evolutionarily, they affect population divergence by influencing gene flow among populations. Knowledge of the underlying ecology and evolution, in turn, is critical to conservation management of the seascape [1,2]. Recently, direct measures of reproduction and dispersal, made using genetic parentage analyses, have started to emerge in some marine taxa such as coral reef fishes [3,4]. However, such data remain scarce for reef-building corals, which are an object of intense conservation concern given the precipitous decline in coral reef cover over recent decades and the uncertain future of the world's coral reefs [5].

Coral demographic studies are complicated by the fact that the typical cnidarian can reproduce sexually and asexually, and may even have multiple distinct asexual reproductive strategies, such as budding, fragmentation or the production of asexual larvae [6,7]. Within a species, the relative contribution of alternative reproductive strategies is driven by variation in biotic or abiotic features of the environment [8–10]. While laboratory studies are useful for documenting how a species' reproductive toolbox can respond to variation in

© 2023 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

particular environmental parameters [11,12], genomic analyses of population structure are increasingly being used to identify the signature of alternative reproductive strategies in populations across a seascape [7,13]. However, many coral species can survive across of range of distinct habitats, from forereef, to backreef, to seagrass, and even mangrove forests, with each habitat representing a different ecological context potentially influencing reproduction and dispersal. Using genomic data alone, it is challenging to discriminate between alternative modes of asexual reproduction, e.g. production of ameiotic larvae versus polyp bail-out or fragmentation. However, it may be possible to speculate about the most likely reproductive mode(s) given the ecological context of the population.

A particularly important aspect of a coral's life cycle is larval dispersal, as it represents the primary mechanism of ecological and evolutionary connectivity between populations, and as such, it can be critical to population recovery and rescue [14]. Larval dispersal in brooders is assumed to be limited and local, while in broadcast spawners larval dispersal is thought to be expansive [15]. Larval dispersal distances might also be strongly impacted by oceanographic currents and local features of the seascape, as has been predicted by models [16]. To date, most evidence of coral larval dispersal distances is based on indirect measures provided by genomic data (e.g. F_{ST}, spatial autocorrelation in genetic structure within sites) [17]. However, direct measurements of larval dispersal are possible using parentage analysis [4,18], although, to date, this approach has only rarely been applied to scleractinian corals [6,19]. This scarcity is likely attributable to the combination of the low likelihood of identifying parent–offspring pairs over the large spatial scales that coral populations often span, as well as extensive asexual reproduction.

Here, we characterize reproduction and dispersal in a mangrove population of the Caribbean thin-finger coral, *Porites divaricata*. Importantly, the unique features of our experimental system—a fully censused, longitudinally characterized, semi-isolated population of corals inhabiting mangrove prop-roots [20,21]—have allowed us to directly measure larval dispersal. Using 2bRAD sequencing across 136 geotagged corals spanning a 3-year range of ages, we show that the extensive recruitment previously documented in this population—i.e. the appearance of small, generally unbranched coral colonies [21]—results almost exclusively from asexual reproduction, and the asexual propagules generally disperse very short distances from their parent colonies (within a few metres). Given the constraints imposed by the habitat, we discuss how the most plausible mode of asexual reproduction that could produce such recruits would be the asexual production of larvae, which has been documented in a closely related species [22]. Importantly, the only previously known mode of asexual reproduction in this species, fragmentation, is not viable in the mangrove habitat, as negatively buoyant branch fragments will sink into the mud below the mangrove prop-roots, thus revealing that key life-history traits of corals can vary dramatically across habitats.

2. Results and discussion

(a) Generation of molecular markers

Using the reduced-representation genomic sequencing approach known as 2bRAD [23], we genotyped 136 colonies from a population of *Porites divaricata* growing on mangrove prop-roots in a relatively isolated mangrove channel located at Calabash Caye, Belize (figure 1). On an annual basis, in November–December of 2015–2018, this population was fully censused, and longitudinal monitoring of recruitment, growth, health and mortality of individual coral colonies was conducted. This longitudinal monitoring revealed a stable population where the loss of adult colonies was more than offset by larval recruitment [21]. We determined the genotypes of corals from four different annual cohorts that ranged in age from 0 to 3+ years and ranged in ecological volume from 0.22 to 11 817 cm^3 (table 1).

(b) Evidence of rampant asexual reproduction

Regardless of whether we used Prevosti distance based upon the called single-nucleotide polymorphisms (SNPs) or Identity by State (IBS) based on genotype likelihoods calculated under a broad range of parameters (electronic supplementary material, table S1), the results are the same: this *P. divaricata* population reproduced predominantly asexually. Whether we mapped our reads to the assembled genome of *Porites lutea* or to a *de novo* assembly of RAD tags, and regardless of which ANGSD parameters we used to call SNPs, we identified 10 clonal lineages (labelled A–J in figure 2; electronic supplementary material, figures S1 and S2) with almost identical membership (electronic supplementary material, table S2). For example, if we base our analysis on the highest confidence 118 SNPs (i.e. the 'hard-called' SNPs identified after mapping the sequencing reads to the *P. lutea* genome), 126 of 136 colonies (92.6%) belong to clonal groups A–J, which each comprise 2 to 39 individuals (figure 2). Mean pairwise distances between individuals within these clonal groups were 0.11% ± 0.004 s.e., less than or equal to the distance observed between technical replicates [24,25]. By contrast, the mean pairwise distance between individuals from different groups was 21.1% ± 0.045 s.e. The average relatedness between individuals that were not part of the same clone was generally equivalent to that of first cousins ($r_{ab} = 0.174 \pm 0.04$ s.e.). The most closely related clones exhibited a relatedness equivalent to that of half-siblings ($r_{ab} = 0.31$, e.g. clones F and G, figure 2), while the most distant clone lines (e.g. cluster A relative to clusters B–J) exhibit a coefficient of relatedness $r_{ab} = 0.056$, similar to that exhibited by second cousins (figure 2).

Though a range of asexual reproductive strategies has been documented in corals, including colony fragmentation [26], polyp bail-out [11,27] and the asexual production of larvae [12,28,29], the unique ecological context of the mangrove population studied here implicates asexual production of planula larvae as the only plausible mode of clonal reproduction. Given that individuals are growing on prop-roots suspended over a mud/silt bottom, reproduction via colony fragmentation, which is thought to be a common mode of asexual reproduction in *P. divaricata* [30], would invariably result in mortality because colony fragments cannot re-adhere to the prop-roots, and those that fall to the bottom are quickly submerged in soft sediment, a phenomenon that we have repeatedly observed in the field (figure 1*d*). Similarly, isolated individual polyps produced by polyp bail-out, a mechanism of asexual reproduction that has never been reported in poritid corals, would be unable to colonize prop-roots and would fall to

royalsocietypublishing.org/journal/rspb *Proc. R. Soc. B* **290**: 20231070

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

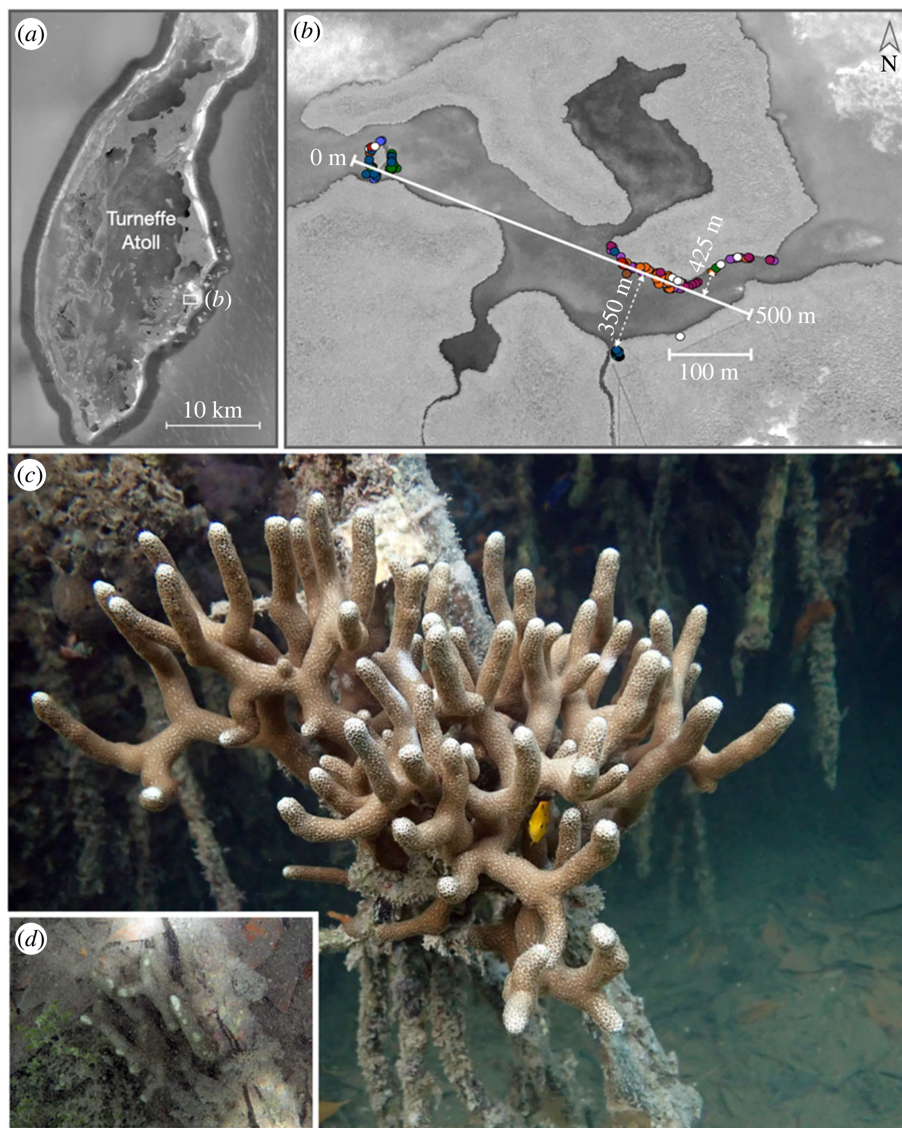

Figure 1. Map of study site and representative coral colonies. (*a*) Turneffe Atoll, Belize, and (*b*) the mangrove channel study site at Calabash Caye. Coloured circles indicate the locations of sampled *Porites divaricata* colonies, with different colours representing individuals belonging to distinct clonal groups. White circles represent individuals not assigned to clones. To simplify dispersal simulations, the locations of coral colonies were orthogonally projected onto the white line shown in the figure (see examples of colonies projected onto the line at 350 m and 425 m). (*c*) A representative coral colony growing on a mangrove root, with soft sediment containing decaying mangrove leaves visible in the background. (*d*) A dying coral colony that fell from a mangrove root is partially buried in the sediment.

Table 1. Coral colonies sampled by age and size. All collections occurred in 2018.

		age and size at time of sampling		
n	appeared in	age (years)	avg. ecological volume (cm^3)	avg. branch tips
55	2015 or prior	3+	1348.9 ± 356.5	16.1 ± 2.6
19	2016	2–3	803.0 ± 157.3	20.9 ± 5.1
30	2017	1–2	142.4 ± 50.3	5.2 ± 1.2
32	2018	0–1	10.7 ± 3.0	0.9 ± 0.3

the mud bottom because they are ‘slightly negatively buoyant’, with limited mobility [11,27]. By contrast, planulae are capable of directed swimming, searching behaviour and settlement, and asexual planulation has been reported in another *Porites* species [12]. Because *P. divaricata* is a gonochoric species that broods its larvae [30], we deduce that asexual larvae are produced through parthenogenesis and brooded by females.

(c) Evidence of limited dispersal

Previous studies have noted the dense clustering of individuals in this population and suggested that dispersal may be predominantly local [20,21]. Indeed, when we transposed the locations of corals living along the undulating banks of the channel to a common line (figure 2), most or all colonies within each clonal group are tightly clustered within a 50–100 m distance. However, a handful of individuals are hundreds of metres distant from their nearest clonemate (figure 2).

Unlike previous studies [20,21], here we have explicit knowledge of the underlying clonal relationships, allowing us to generate more tightly constrained estimates of dispersal. We first identified potential parent–offspring pairs within each clonal lineage (A–J) by assuming that new recruits identified

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

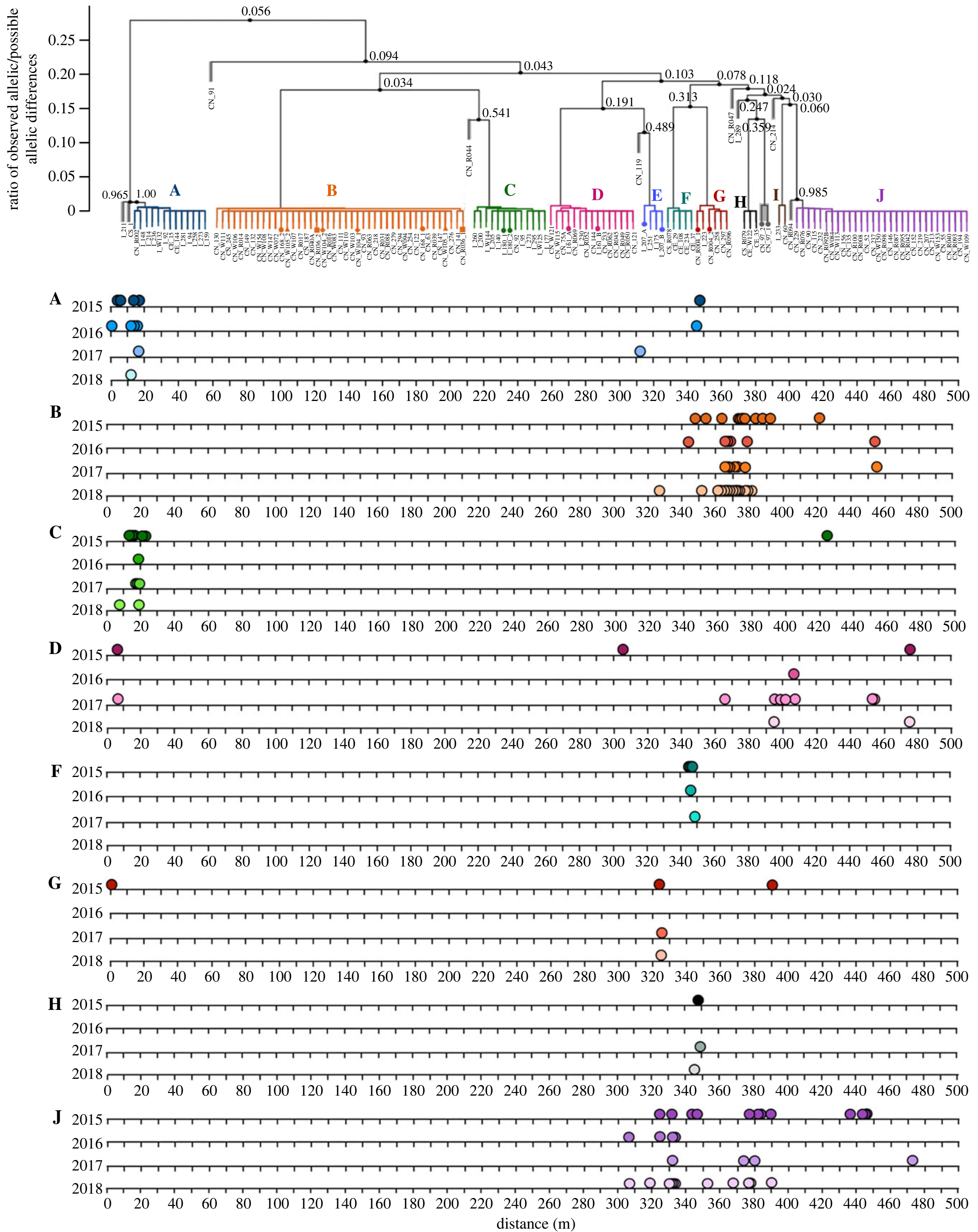

Figure 2. A distance tree showing the relationship between individual coral colonies based on pairwise Prevosti distances. Clonal groups are outlined in the same colour, and individuals with unique genotypes are shaded in grey. Technical replicates are indicated by the circles at the branch tips. The number of inferred sexual reproductive events is displayed by black circles on interior nodes of the dendrogram, with numbers at the nodes representing the relatedness value (r_{ab}) between the two lineages descended from the node. Below the dendrogram, the locations of each colony have been orthogonally projected onto a common line to visualize their relative positions in the study area. Colonies are divided into their respective clonal groups, designated by the same colours/letters as shown on the dendrogram. Within a clonal group, colonies are depicted in different shades and placed on distinct lines based upon the year that they were found in population surveys (2015–2018). Clonal groups E and I were excluded because all colonies in these groups were found in 2015.

in 2016–2018 could have derived from any clonemate from a prior year (2015–2017), irrespective of colony size. We then calculated the distance between all possible parent–offspring pairs based on their GPS locations. From these distances, we determined the minimum, maximum, mean and median distance that each offspring could have dispersed from potential

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

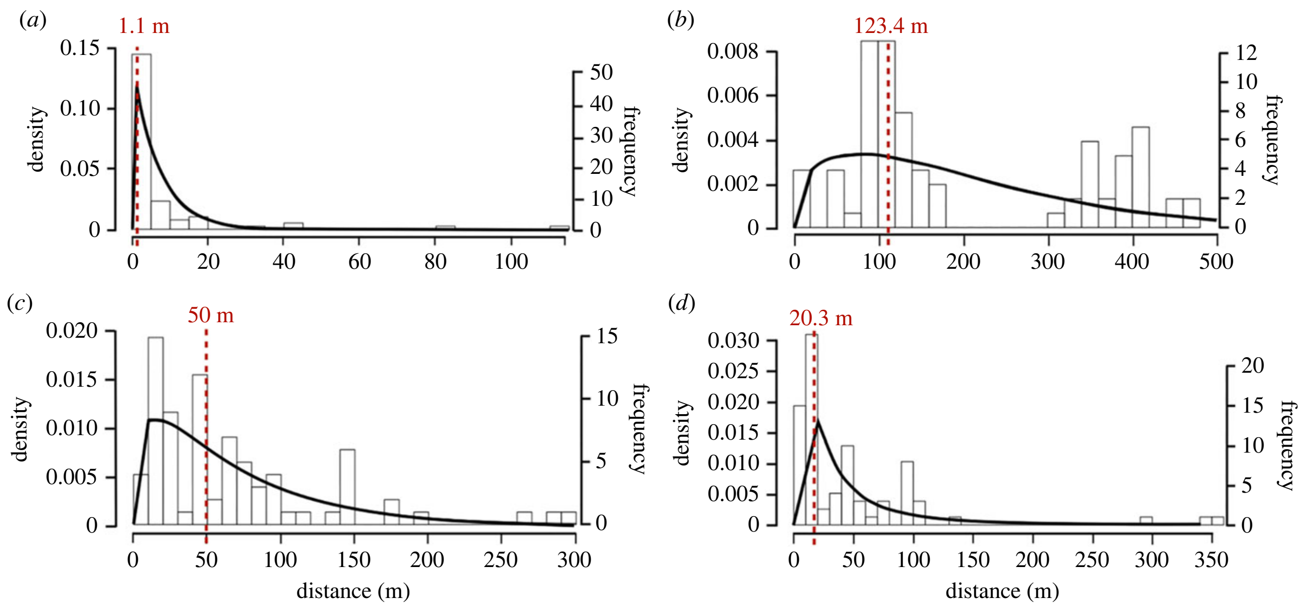

Figure 3. Dispersal curves showing the best-fit probability density function for each empirical distribution of dispersal distances, when distances between parents and offspring of the same clone were measured as (*a*) minimum distance (exponential); (*b*) maximum distance (Weibull); (*c*) mean distance (gamma); and (*d*) median distance (lognormal). The *y*-axes display the scales for density and frequency (left and right, respectively), while the *x*-axis represents the dispersal distance in metres (m). The dashed red vertical lines indicate the median dispersal distance under each distribution.

parents. We then generated minimum, maximum, mean and median dispersal distance distributions for the population and fitted probability density functions to these distributions (figure 3). Across all 28 combinations of dispersal distances and probability density functions explored, the best-fitting model was the exponential distribution fitted to the minimum dispersal distances (figure 3*a*; electronic supplementary material, table S3). Under this model, the median dispersal distance is 1.1 m and the 99th percentile for dispersal is 89.2 m.

In addition to the distances between potential parent–offspring pairs, another measurement we used to compare the performance of alternative dispersal models was the distance between members of the same clone-cohort, i.e. clonemates that appear in the same year. We simulated annual dispersal events of larvae within each clonal lineage under the probability density functions that represented the best fit to the minimum (exponential), maximum (Weibull), mean (lognormal) and median (gamma) distance distributions and compared the observed versus expected distribution of distances between members of the same clone-cohort generated under each simulation. For all five clone lines for which we could obtain distances between members of the same cohort, the expected distribution generated under the minimum dispersal model most closely resembled the observed distribution (figure 4; electronic supplementary material, table S4).

Prior studies have also provided evidence of highly localized dispersal of larvae in brooding corals. For example, spatial autocorrelation analysis of within-site structuring in another brooding coral, *Seriatopora hystrix*, revealed that colonies within 20 m of each other were most similar genetically, suggesting that recruits typically settle within 20 m of parents [17]. Of note, the minimum dispersal model (figure 3*a*) generates a more leptokurtic distribution than the other models, especially the maximum dispersal model (figure 3*b*). Leptokurtic dispersal distributions are common in nature [31–33], including marine taxa [3,4,34]. Dynamic models of coral dispersal that incorporated empirical measurements of larval period and settlement competence also produced leptokurtic distributions [35].

This study represents the first population genomic analysis of mangrove corals, and we find evidence that asexual reproduction predominates in the sampled population. This asexual reproduction, in conjunction with high survivorship and high growth rates of recruits, is critical to maintaining population viability [21]. Other coral populations have been found to reproduce predominantly asexually [13], particularly at the edge of their range or in ecologically marginal habitats [10]. Asexual reproduction allows for rapid population expansion and colonization of available substrate without requiring sexual partners, and it facilitates the spread of locally adapted genotypes in the absence of gene flow [7,13]. Despite these advantages, populations dominated by asexual reproduction may be more vulnerable to environmental change given their low genetic diversity, which may limit the rate of adaptive evolution, especially if these populations are relatively isolated [7,13].

Due to the unique ecological context of colonies in this mangrove habitat, we propose that asexual reproduction is most likely occurring through the production of parthenogenetic larvae, a reproductive mode that has not previously been documented in *P. divaricata* to our knowledge, although it has been reported in the closely related mounding coral, *P. astreoides* [12]. The production of asexual larvae could represent an adaptation to growing on a substrate suspended over a mud bottom. It is also possible that parthenogenesis is similarly common in populations of *P. divaricata* found in other settings, such as reefs. However, in habitats with suitable hard-bottomed substrate (e.g. reefs), fragmentation, which is the only previously documented mode of asexual reproduction in *P. divaricata*, may also be an important mode of asexual reproduction [30]. The ability to produce asexual larvae could facilitate colonization of mangroves by *P. divaricata*, making this species a case study for how possessing multiple mechanisms of asexual reproduction can facilitate niche expansion. Of note, if parthenogenetic larvae are produced solely by

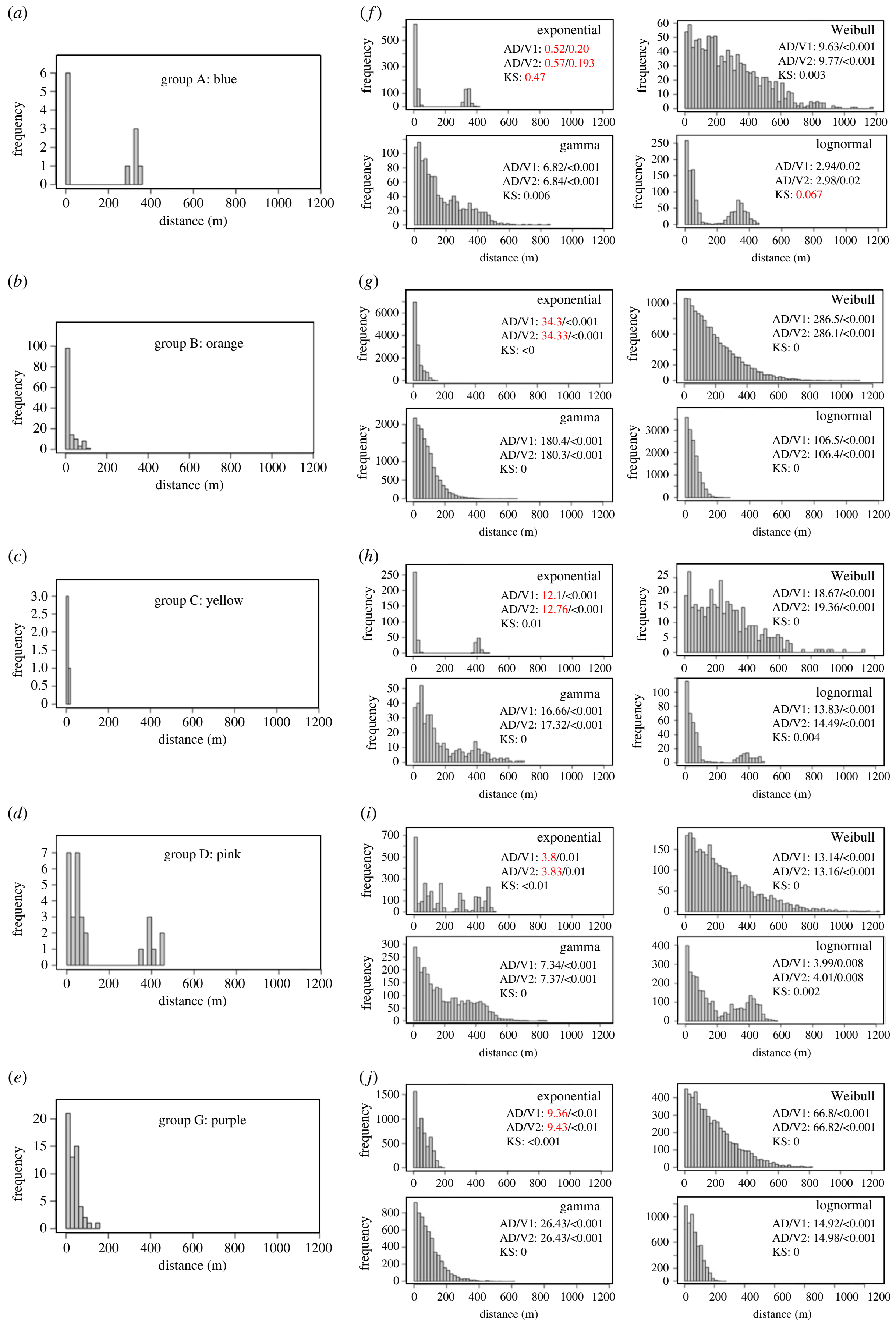

Figure 4. Empirical (*a–e*) and simulated (*f–j*) distributions of the distances between siblings of the same clone for clonal groups A, B, C, D and G. Results from *k* sample Anderson–Darling tests (AD) and Kolmogorov–Smirnov (KS) tests comparing observed and simulated distributions are shown. The test statistics and *p*-values for both versions (V1, V2) of the AD test are displayed (test statistic/ *p*-value). The lowest value of the AD statistic for each set of four simulations is displayed in bold red type, as are *p*-values of simulated distributions not significantly different from the observed distribution.

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

females, reliance on different modes of asexual reproduction in different habitats could lead to differing sex ratios in those habitats, e.g. female colonies may be more abundant in mangrove populations than in reef populations of *P. divaricata*.

The preponderance of asexual reproduction in this particular population of *P. divaricata* could have multiple explanations. First, it may be typical of *P. divaricata*. Unfortunately, there is limited basis for comparison, as there is only one prior study of reproduction in a natural population of *P. divaricata* [30]. McDermond [30] suggested that asexual reproduction by fragmentation was the primary mechanism for population maintenance and growth of *P. divaricata* at Rodriguez Key in Florida, a shallow carbonate bank described as marginal habitat [30]. The conditions at Rodriguez Key could make larval settlement difficult while promoting fragmentation. Asexual reproduction could also be advantageous in a marginal habitat because of low mate availability and because it would facilitate the spread of locally adapted genotypes. Mate availability could be limiting sexual reproduction in Calabash Channel, if, as we suspect, the population is largely female colonies produced by parthenogenesis. It is also possible that asexual reproduction is causing a mangrove-adapted genotype or genotypes to spread. Indeed, a proclivity to reproduce via parthenogenesis could be an adaptation to living in the mangroves.

The best-supported model of dispersal suggests that asexually generated *P. divaricata* larvae typically disperse only a few metres from their parent colony and rarely disperse distances greater than 100 m. Such limited dispersal is presumed to be characteristic of brooding corals based on observations of the settlement competency of larvae in the laboratory [36], as well as population genetic structure of brooding corals *in situ*, e.g. [17]. However, few studies have provided direct estimates of coral dispersal. In earlier work, parentage analyses provided evidence for limited sperm dispersal among brooding corals, including the octocoral *Pseudopterogorgia elisabethae* [37] and the stony coral *Seriatopera hystrix* [38]. Limited sperm dispersal was also found in the stony coral *Pocillopora damicornis*, which exhibits both brooding and broadcasting reproductive modes [28]. More recently, parentage analysis of larvae from the broadcast spawning fire coral *Millepora* cf. *platyphylla* also revealed limited dispersal with recruits often settling within 10 m of parent colonies, which is counter to the general expectation of increased dispersal in broadcast spawning species [6]. Unlike these previous studies, explicit knowledge of clone age and location enabled us to identify plausible parent–offspring relationships within multiple clonal lineages, providing an opportunity to compare field-based estimates of larval dispersal with alternative dispersal curves.

Occasional longer-distance dispersal may be occurring in the mangrove *P. divaricata* population studied here. Intermittent long-distance dispersal is thought to be possible in brooding corals because larvae are provisioned with photosynthetic symbionts. This energy source can extend the larval period and enable longer transit times [39], especially where facilitated by local oceanographic processes [36]. This research sets the foundation to investigate dispersal patterns of *P. divaricata* across a variable seascape. Such an analysis may reveal connectivity between habitat types, although we suspect it will continue to reveal predominantly local dispersal observed here given that research on marine fishes found that initial dispersal curves generated at small spatial scales [40,41] were generally corroborated by data collected over a larger scale [3,4].

The findings described here advance the field of coral reproductive and dispersal ecology by revealing a novel asexual strategy in *P. divaricata* that serves to ensure reproductive viability in a particular ecological context. In addition, we produce the first empirical larval dispersal curves for a scleractinian coral. These results represent the first data on reproduction and dispersal in a mangrove coral population. Recent studies suggest mangroves may be critical to the survival of many coral species by providing an ecological refuge during periods of extreme heat and ultraviolet radiation [42–44] and/or by promoting the evolution of resilient individuals [42,45]. Documenting the asexual production of larvae and their predominantly local dispersal helps to explain the 4-year stability of this population [21]. It also suggests that the movement of recruits between spatially isolated habitats, such as reef habitats and mangroves, might be more limited. Future work investigating dispersal patterns between this population and nearby *P. divaricata* populations in other habitat types can reveal potential patterns of gene flow as well as provide insight into the colonization history of this population. Additionally, future studies should investigate dispersal patterns in other mangrove-dwelling coral species with different life-history strategies and reproductive modes, while also sampling over larger spatial scales to estimate the potential for larvae to disperse between habitats. Further, methods developed here could be applied to other populations of reef-building corals, providing insights into modes of reproduction and how this might influence genetic diversity, which will facilitate optimization of coral reef restoration projects.

3. Materials and methods

(a) Study site

This study was conducted in a mangrove channel at Calabash Caye, located approximately 33 km off the coast of Belize within the Turneffe Atoll Marine Reserve (figure 1). 'Calabash Channel' is a tidal channel fringed by red mangroves (*Rhizophora mangle*). Previous research revealed a dense population of *Porites divaricata* growing on the submerged prop-roots lining the channel [20]. Longitudinal monitoring of this population has shown it to be stable and slightly increasing in size over the monitoring period, with colonies spanning a wide range of sizes and ages [21]. The roots occupied by corals are suspended over a mud/silt bottom in approximately 1–2 m of water (figure 1*c*). During exhaustive field surveys, dense concentrations of coral colonies were located and tagged along three discontinuous sections of the shoreline (figure 1*b*). Other stretches of shoreline were largely devoid of *P. divaricata* colonies, with few scattered colonies found on the roots, in comparison to the dense clustering of colonies along the sampled shorelines. No colonies were ever observed in the two mangrove ponds despite repeated surveys (figure 1*b*). The population is located approximately 1.5 km from the nearest known reef population of *P. divaricata*.

(b) Field tissue sampling

In 2018, tissue samples were collected from 141 spatially discrete *P. divaricata* colonies growing on mangrove roots in Calabash Channel (figure 1*b*). Samples were collected from individuals known to have recruited into the population in (i) 2018, (ii) 2017, (iii) 2016 or (iv) 2015 and prior (table 1). Colonies sampled included larger, branched individuals and smaller, unbranched individuals (recruits). The smallest colonies were not collected to avoid lethal sampling. For branched individuals, 1–2 branch

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

fragments (approx. 2–3 cm) were collected from each discrete colony, and for encrusting individuals, 1–2 small fragments were chiselled from the edge of the colony. All fragments were immediately placed in 100% EtOH, and upon return to Calabash Caye Field Station were frozen until DNA isolation.

(c) 2bRAD sequencing

Genomic DNA was isolated using the Qiagen DNeasy Blood and Tissue sample kit [46]. Anonymous genomic loci were obtained for each individual using the 2bRAD sequencing approach designed by Wang *et al.* 2012 [23]. During library preparation, technical replicates were performed by producing two libraries from each of nine samples. Libraries were sequenced on the Illumina HiSeq 2500 platform (single end 50 bp) at The Tufts University Core Facility.

Raw reads were deduplicated, separated into individual barcoded samples, trimmed of adapters and quality-filtered with *cutadapt* to remove both low-quality scores (less than 15) and short read lengths (less than 36 bp). The deduplicated, trimmed, filtered reads were deposited in the Short Read Archive at NCBI (https://www.ncbi.nlm.nih.gov/sra/PRJNA833675).

(d) Read mapping

The processed sequencing reads were mapped to the *Porites lutea* genome, the most closely related species to *P. divaricata* with a sequenced genome (downloaded at: http://plut.reefgenomics.org/download/) using the local alignment option of *bowtie2* and the following parameters: a seed length of 16, a minimum alignment score of $f(x) = 16 + 1 * x$, where x = read length, and a disposal of unaligned reads. This yielded an average mapping rate of 42%. Reads were also mapped to a *de novo* assembly produced from trimmed reads following the guidelines provided in the '2bRAD denovo' github repository (https://github.com/z0on/2bRAD_denovo). This yielded an average mapping rate of 86%.

(e) Identification of single-nucleotide polymorphisms and genotyping

Single-nucleotide polymorphisms were identified by ANGSD [47]. Using the reads mapped to the *P. lutea* genome as well as the reads mapped to the de novo assembly, we identified SNPs using four different sets of ANGSD parameters, for a total of eight different approaches (electronic supplementary material, table S1). First, following Manzello *et al*. [48], we used default parameters for ANGSD, which include a minimum read depth of 1. Second, following a recent study by Sturm *et al*. [49], which also used a minimum read depth of 1, we specified the following conditions: remove tri-allelic SNPs; base quality score greater than 25; minimum *p*-value for deviation from Hardy Weinberg equilibrium = 10^{-5}; minimum *p*-value for a variable locus = 10^{-5}; minimum *p*-value for strand bias = 10^{-5}. Third, following a study by Fifer *et al*. [50], we required a minimum of five sequencing reads to score the genotype of an individual at each SNP and specified a minimum *p*-value for heterozygosity bias of 10^{-5}. In our final set of ANGSD parameters, we required a minimum of eight sequencing reads to score the genotype of an individual at each SNP and set the minimum *p*-value for a variable locus to 10^{-6}. Additionally, if a sample did not reach these thresholds for a particular SNP, and if the SNP could not be genotyped in at least 80% of individual samples, the genotype was scored as missing. We conducted the same four analyses to identify SNPs and call genotypes on samples mapped to the de novo assembly (electronic supplementary material, table S1).

(f) Identification of clones

Two different methods were used to identify clones from the eight ANGSD outputs: IBS and genetic distance. IBS is the proportion of times that two reads at the same locus are identical between individuals [48]. The resulting IBS matrices containing pairwise IBS distances between individuals were imported into R, clustered using the *hclust()* function using the 'average' agglomeration method of the R package *stats* v.4.0.1. Distance trees were then generated to visually assess the placement of individuals (electronic supplementary material, figure S1). The greatest IBS distance between technical replicates was used as the threshold for clonality. IBS is popular in previous 2bRAD studies because it is robust to variation in sequencing coverage among individuals [48]. The rationale for using IBS to identify clones is that clones are more likely to exhibit 'identity by state' than non-clones across a collection of SNPs. However, IBS was not expressly intended for identifying clones, and it can be positively misleading at loci where the clonemates are heterozygous, because, at such sites, despite sharing the identical genotype, IBS will be only 50% between clonemates. IBS would also be 50% between non-clonemates at a locus that differs in genotype, if one individual is heterozygous and the other is homozygous. For that reason, we also employed genetic distance (Prevosti's distance) between individuals based upon their genotypes at SNPs, as in prior studies [51]. The R package *poppr* v.2.8.5 [24] was used to cluster genotypes and identify clones. Using the ANGSD *vcf* outputs with called genotypes, Prevosti's absolute genetic distance was calculated between all pairs of individuals using the *dist.diss()* function [52]. The function *mlg.filter()* identified the presence of clones in the population by using the highest fraction of allelic differences observed between technical replicates as the threshold of clonality. A list of the individuals in the population collapsed into clonal groups was provided by the function *mlg.id()*. Distance trees were also generated by clustering individuals using the 'average' agglomeration method of the *hclust()* function (electronic supplementary material, figure S2).

All four SNP calling methods identified the same 10 clonal lineages with nearly identical clonal membership when mapped to either the *P. lutea* genome or de novo assembly of RAD tags, and when using IBS or genetic distances (electronic supplementary material, table S2). All remaining analyses on the ANGSD output were performed using the highest confidence 118 SNPs (i.e. the 'hard-called' SNPs identified after mapping the sequencing reads to the *P. lutea* genome). To confirm that these SNPs were sufficient to discriminate individuals present in this analysis, we produced a genotype accumulation curve using the R function *genotype_curve()*. The curve achieved a plateau just before the maximum number of markers was reached, indicating that we identified an adequate number of markers (electronic supplementary material, figure S3). Prior to calculating pairwise genetic distances, we removed 5 of the 141 individuals that were scored as missing data at more than 50% of SNPs. Basic population genetic statistics including observed heterozygosity (H_o), expected heterozygosity (H_e) and inbreeding coefficient (F_{IS})) were calculated in the R packages *adegenet* v.2.1.10 [53] and *hierfstat* v.0.5-11 [54] and are reported in electronic supplementary material, table S5.

(g) Determination of relatedness

We calculated the pairwise relatedness coefficient (r_{ab}) between all individuals with *NgsRelate v.2* [55], using the estimated population allele frequencies and genotype likelihoods generated from the ANGSD output (using option *-doglf 3*) [56]. We estimated pairwise relatedness (r_{ab}) at each node in the distance tree by taking the average r_{ab} of all individuals descended from each node.

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

(h) Estimating dispersal distances

Within each clonal group, putative parents and offspring were identified based upon the year each colony first appeared during exhaustive surveys of the population conducted from 2015 to 2018 [21]. The geodesic distance—the shortest path between two points along earth's surface—between each possible parent–offspring pair was then computed using Vincenty's formulae [57] from the GPS coordinates obtained in the field [21]. The calculated distances did not account for differences in depth, e.g. two colonies with identical GPS coordinates but located at different depths would be scored as having distance equal to zero. The distribution of potential dispersal distances was estimated under four different assumptions: (i) minimum possible distance, (ii) maximum possible distance, (iii) median distance and (iv) mean distance between possible parent–offspring pairs. A density function was then fitted to each distribution based on Akaike's information criterion using the package *fitdistrplus* [58] (figure 3).

(i) Testing alternative dispersal models

To simplify the simulation of dispersal distances, a common line was used to represent the relative location of all colonies. The line was drawn through the points representing the GPS location of all colonies using least-squares regression. Each colony's location was then transposed onto this line at the point representing the shortest distance from the line to the colony. For each observed dispersal event that occurred within a clonal group in a given year (2015, 2016 and 2017), the four alternative probability density functions representing the four dispersal distance models (exponential/minimum distance, Weibull/maximum distance, gamma/mean distance and lognormal/median distance; figure 3) were used to generate expected dispersal events along the line as follows. First, a parent colony was chosen at random in each clonal group from all potential parents in a given year. For a given dispersal curve (figure 3), a random larval dispersal distance was drawn and randomly multiplied by 1 or −1 to determine the direction of dispersal. This distance represented displacement of the larva from its parent along the line, i.e. the location of the new recruit. This process was repeated for each clonal group using each dispersal curve until the number of simulated dispersal events equalled the number of observed recruits in a given year. Each year, the number of potential parents increased as colonies from the year prior were presumed to be potential parents of larvae (table 1). After all the locations of the new recruits were generated, the distances between clone mates were calculated. Clone mates are defined as colonies in the same clonal group that recruited to the population in the same year. This entire process was repeated one hundred times for each alternative dispersal curve. Finally, the expected distances between clone mates were compared to the observed (i.e. empirical) distances between clone mates using alternative goodness of fit tests including k sample Anderson–Darling and two-sample Kolmogorov–Smirnov tests. A k sample Anderson–Darling test was conducted using the *ad.test* function from the R package *ksamples v. 1.2-9* [59,60]. Two-sample Kolmogorov–Smirnov tests were also conducted using the *ks.boot* function in the R package *Matching v. 4.9.11* [61]. A bootstrap p-value was obtained from 10 000 bootstraps. These simulations were only conducted for clonal groups that contained at least two or more clonemates within a cohort: Group A, Group B, Group C, Group D and Group J.

Ethics. The research was conducted under Aquatic Scientific Research Permit #0041-18 (2018) issued by the Belize Fisheries Department.

Data accessibility. The deduplicated, trimmed, filtered DNA sequencing reads generated in this study were deposited in the Short Read Archive at NCBI (https://www.ncbi.nlm.nih.gov/sra/PRJNA833675).

The data are provided in the electronic supplementary material [62].

Authors' contributions. K.S.L.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, writing—original draft and writing—review and editing; K.C.L.: investigation and writing—review and editing; P.M.B.: formal analysis and writing—review and editing; S.W.D.: investigation and writing—review and editing; C.C.D.: formal analysis and writing—review and editing; J.R.F.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. The authors declare that they have no competing interests.

Funding. This research described here was supported by National Science Foundation grant nos. DGE-1247312 to K.S.L. and IOS-1354935 to J.R.F. Fieldwork in 2018 was supported by Boston University through a Graduate Research Abroad Fellowship to K.S.L.

Acknowledgements. The research was conducted under Aquatic Scientific Research Permit #0041-18 (2018) issued by the Belize Fisheries Department. We thank Felicia Cruz and Mauro Gongora at the Belize Fisheries Department for assistance in obtaining these research permits. We also thank Julia Hammer-Mendez, Jonathan Perry and Justin Scace, staff of the Boston University Marine Program, for their logistical and technical support in the Marine Semester. We are grateful for the expert technical assistance and natural history knowledge of boat captains, staff and researchers at Calabash Caye Field Station and the University of Belize (including Berris Torres, Derron Torres, Joshua Morey and Javon Castillo). We are also grateful to the Bertarelli Foundation and the Oak Foundation for their contributions to the research infrastructure at Calabash Caye Field Station, which facilitated the marine conservation-related research described here.

References

1. Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, Van Oppen MJH, Willis BL. 2009 Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* **28**, 307–325. (doi:10.1007/s00338-009-0469-9)
2. Botsford LW, White JW, Coffroth MA, Paris CB, Planes S, Shearer TL, Thorrold SR, Jones GP. 2009 Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* **28**, 327–337. (doi:10.1007/s00338-009-0466-z)
3. Almany GR *et al.* 2017 Larval fish dispersal in a coral-reef seascape. *Nat. Ecol. Evol.* **1**, 148. (doi:10.1038/s41559-017-0148)
4. D'Aloia CC, Bogdanowicz SM, Francis RK, Majoris JE, Harrison RG, Buston PM. 2015 Patterns, causes, and consequences of marine larval dispersal. *Proc. Natl Acad. Sci. USA* **112**, 13 940–13 945. (doi:10.1073/pnas.1513754112)
5. Hughes TP *et al.* 2018 Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83. (doi:10.1126/science.aan8048)
6. Dube CE, Boissin E, Merciere A, Planes S. 2020 Parentage analyses identify local dispersal events and sibling aggregations in a natural population of *Millepora* hydrocorals, a free-spawning marine invertebrate. *Mol. Ecol.* **29**, 1508–1522. (doi:10.1111/mec.15418)
7. Gelin P, Fauvelot C, Mehn V, Bureau S, Rouze H, Magalon H. 2017 Superclone expansion, long-distance clonal dispersal and local genetic structuring in the Coral *Pocillopora damicornis* Type beta in Reunion Island, South Western Indian

Ocean. *PLoS ONE* **12**, e0169692. (doi:10.1371/journal.pone.0169692)
8. Coffroth MA, Lasker HR. 1998 Population structure of a clonal gorgonian coral: the interplay between clonal reproduction and disturbance. *Evolution* **52**, 379–393. (doi:10.2307/2411075)
9. Munday PL, Buston PM, Warner RR. 2006 Diversity and flexibility of sex-change strategies in animals. *Trends Ecol. Evol.* **21**, 89–95. (doi:10.1016/j.tree.2005.10.020)
10. Miller KJ, Ayre DJ. 2004 The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. *Heredity* **92**, 557–568. (doi:10.1038/sj.hdy.6800459)
11. Sammarco PW. 1982 Polyp bail-out: an escape response to environmental stress and a new means of reproduction in corals. *Mar. Ecol. Prog. Ser.* **10**, 57–65. (doi:10.3354/meps010057)
12. Vollmer AA. 2018 *Rare parthenogenic reproduction in a common reef coral, Porites astreoides*. Fort Lauderdale, FL: Nova Southeastern University.
13. Baums IB, Devlin-Durante M, Laing BAA, Feingold J, Smith T, Bruckner A, Monteiro J. 2014 Marginal coral populations: the densest known aggregation of *Pocillopora* in the Galápagos Archipelago is of asexual origin. *Front. Mar. Sci.* **1**, 59. (doi:10.3389/fmars.2014.00059)
14. Cowen RK, Sponaugle S. 2009 Larval dispersal and marine population connectivity. *Ann. Rev. Mar. Sci.* **1**, 443–466. (doi:10.1146/annurev.marine.010908.163757)
15. Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP. 2009 Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecol. Appl.* **19**, 18–29. (doi:10.1890/07-1461.1)
16. Japaud A, Bouchon C, Magalon H, Fauvelot C. 2019 Geographic distances and ocean currents influence Caribbean *Acropora palmata* population connectivity in the Lesser Antilles. *Conserv. Genet.* **20**, 447–466. (doi:10.1007/s10592-019-01145-9)
17. Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP. 2007 Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Mol. Ecol.* **16**, 771–784. (doi:10.1111/j.1365-294X.2006.03187.x)
18. Jones GP, Planes S, Thorrold SR. 2005 Coral reef fish larvae settle close to home. *Curr. Biol.* **15**, 1314–1318. (doi:10.1016/j.cub.2005.06.061)
19. Annick C, Toonen R, Karl SA. 2020 Is post-bleaching recovery of *Acropora hyacinthus* on Palau via spread of local kin groups? *Coral Reefs* **39**, 687–699. (doi:10.1007/s00338-020-01961-3)
20. Bengtsson ZA *et al.* 2019 Corals of the genus *Porites* are a locally abundant component of the epibiont community on mangrove prop roots at Calabash Caye, Turneffe Atoll, Belize. *Carib. Natural.* **67**, 1–16. (doi:10.7287/peerj.preprints.1453v1)
21. Scavo Lord K *et al.* 2020 Multi-year viability of a reef coral population living on mangrove roots suggests an important role for mangroves in the broaderhabitat mosaic of corals. *Front. Mar. Sci.* **7**, 377. (doi:10.3389/fmars.2020.00377)
22. Vollmer AA. 2018 *Rare parthenogenic reproduction in a common reef coral, Porites astreoides*. The Florida Keys, FL: Nova Southeastern University.
23. Wang S, Meyer E, Mckay JK, Matz MV. 2012 2b-RAD: a simple and flexible method for genome-wide genotyping. *Nat. Methods* **9**, 808–810. (doi:10.1038/nmeth.2023)
24. Kamvar ZN, Tabima JF, Grünwald NJ. 2014 Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ* **2**, e281. (doi:10.7717/peerj.281)
25. Kamvar ZN, Brooks JC, Grunwald NJ. 2015 Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Front. Genet.* **6**, 208. (doi:10.3389/fgene.2015.00208)
26. Highsmith RC. 1982 Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* **7**, 207–226. (doi:10.3354/meps007207)
27. Wells CD, Tonra KJ. 2021 Polyp bailout and reattachment of the abundant Caribbean octocoral *Eunicea flexuosa*. *Coral Reefs* **40**, 27–30. (doi:10.1007/s00338-020-02043-0)
28. Yeoh SR, Dai CF. 2010 The production of sexual and asexual larvae within single broods of the scleractinian coral, *Pocillopora damicornis*. *Mar. Biol.* **157**, 351–359. (doi:10.1007/s00227-009-1322-y)
29. Ayre DJ, Resing JM. 1986 Sexual and asexual production of planulae in reef corals. *Mar. Biol.* **90**, 187–190. (doi:10.1007/BF00569126)
30. McDermond J. 2014 *Reproduction and population of Porites divaricata at Rodriguez Key*. The Florida Keys, USA: Nova Southeastern University.
31. Bullock JM, Mallada González L, Tamme R, Götzenberger L, White SM, Pärtel M, Hooftman DA. 2017 A synthesis of empirical plant dispersal kernels. *J. Ecol.* **105**, 6–19. (doi:10.1111/1365-2745.12666)
32. Jordano P, Garcia C, Godoy JA, Garcia-Castano JL. 2007 Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl Acad. Sci. USA* **104**, 3278–3282. (doi:10.1073/pnas.0606793104)
33. Chesson P, Lee CT. 2005 Families of discrete kernels for modeling dispersal. *Theor. Popul. Biol.* **67**, 241–256. (doi:10.1016/j.tpb.2004.12.002)
34. Williamson DH *et al.* 2016 Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park. *Mol. Ecol.* **25**, 6039–6054. (doi:10.1111/mec.13908)
35. Connolly SR, Baird AH. 2010 Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. *Ecology* **91**, 3572–3583. (doi:10.1890/10-0143.1)
36. Harrison PL, Wallace CC. 1990 Reproduction, dispersal and recruitment of scleractinian corals. *Ecosyst. World* **25**, 133–207.
37. Lasker HR, Gutiérrez-Rodríguez C, Bala K, Hannes A, Bilewitch JP. 2008 Male reproductive success during spawning events of the octocoral *Pseudopterogorgia elisabethae*. *Mar. Ecol. Prog. Ser.* **367**, 153–161. (doi:10.3354/meps07614)
38. Warner PA, Willis BL, Van Oppen MJ. 2016 Sperm dispersal distances estimated by parentage analysis in a brooding scleractinian coral. *Mol. Ecol.* **25**, 1398–1415. (doi:10.1111/mec.13553)
39. Richmond RH. 1987 Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Mar. Biol.* **93**, 527–533. (doi:10.1007/BF00392790)
40. D'Aloia CC, Bogdanowicz SM, Majoris JE, Harrison RG, Buston PM. 2013 Self-recruitment in a Caribbean reef fish: a method for approximating dispersal kernels accounting for seascape. *Mol. Ecol.* **22**, 2563–2572. (doi:10.1111/mec.12274)
41. Buston PM, Jones GP, Planes S, Thorrold SR. 2012 Probability of successful larval dispersal declines fivefold over 1 km in a coral reef fish. *Proc. R. Soc. B* **279**, 1883–1888. (doi:10.1098/rspb.2011.2041)
42. Yates KK, Rogers CS, Herlan JJ, Brooks GR, Smiley NA, Larson RA. 2014 Diverse coral communities in mangrove habitats suggest a novel refuge from climate change. *Biogeoscience* **11**, 4321–4337. (doi:10.5194/bg-11-4321-2014)
43. Rogers CS, Herlan JJ. 2012 *Life on the edge: corals in mangroves and climate change*. In *Proc. of the 12th Int. Coral Reef Symp., Cairns, Australia, 9–13 July 2012*. Townsville, QLD: James Cook University.
44. Stewart HA, Kline DI, Chapman LJ, Altieri AH. 2021 Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness. *Ecosphere* **12**, e03413. (doi:10.1002/ecs2.3413)
45. Camp EF, Suggett DJ, Gendron G, Jompa J, Manfrino C, Smith DJ. 2016 Mangrove and seagrass beds provide different biogeochemical services for corals threatened by climate change. *Front. Mar. Sci.* **3**, 52. (doi:10.3389/fmars.2016.00052)
46. Crabbe MJC. 2003 A novel method for the transport and analysis of genetic material from polyps and zooxanthellae of scleractinian corals. *J. Biochem. Biophys. Methods* **57**, 171–176. (doi:10.1016/S0165-022X(03)00051-4)
47. Korneliussen TS, Albrechtsen A, Nielsen R. 2014 ANGSD: analysis of next generation sequencing data. *BMC Bioinf.* **15**, 1–13. (doi:10.1186/s12859-014-0356-4)
48. Manzello DP, Matz MV, Enochs IC, Valentino L, Carlton RD, Kolodziej G, Serrano X, Towle EK, Jankulak M. 2019 Role of host genetics and heat-tolerant algal symbionts in sustaining populations of the endangered coral *Orbicella faveolata* in the Florida Keys with ocean warming. *Glob. Chang. Biol.* **25**, 1016–1031. (doi:10.1111/gcb.14545)
49. Sturm AB, Eckert RJ, Mendez JG, Gonzalez-Diaz P, Voss JD. 2020 Population genetic structure of the great star coral, *Montastraea cavernosa*, across the Cuban archipelago with comparisons between microsatellite and SNP markers. *Sci. Rep.* **10**, 15432. (doi:10.1038/s41598-020-72112-5)
50. Fifer JE, Yasuda N, Yamakita T, Bove CB, Davies SW. 2022 Genetic divergence and range expansion in a western North Pacific coral. *Sci. Total Environ.* **813**, 152423. (doi:10.1016/j.scitotenv.2021.152423)
51. Kitchen SA, Von Kuster G, Kuntz KLV, Reich HG, Miller W, Griffin S, Fogarty ND, Baums IB. 2020 STAGdb: a 30K SNP genotyping array and Science

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023

Gateway for *Acropora* corals and their dinoflagellate symbionts. *Sci. Rep.* **10**, 12488. (doi:10.1038/s41598-020-69101-z)

52. Prevosti A, Ocana J, Alonso G. 1975 Distances between populations of *Drosophila subobscura*, based on chromosome arrangement frequencies. *Theor. Appl. Genet.* **45**, 231–241. (doi:10.1007/BF00831894)
53. Jombart T. 2008 adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* **24**, 1403–1405. (doi:10.1093/bioinformatics/btn129)
54. Goudet J. 2005 Hierfstat, a package for R to compute and test hierarchical *F*-statistics. *Mol. Ecol. Notes* **5**, 184–186. (doi:10.1111/j.1471-8286.2004.00828.x)
55. Hanghoj K, Moltke I, Andersen PA, Manica A, Korneliussen TS. 2019 Fast and accurate relatedness estimation from high-throughput sequencing data in the presence of inbreeding. *Gigascience* **8**, giz034. (doi:10.1093/gigascience/giz034)
56. Hedrick PW, Lacy RC. 2015 Measuring relatedness between inbred individuals. *J. Hered.* **106**, 20–25. (doi:10.1093/jhered/esu072)
57. Vincenty T. 1975 Direct and inverse solutions of geodesics on the ellipsoid with application of nested equations. *Surv. Rev.* **23**, 88–93. (doi:10.1179/sre.1975.23.176.88)
58. Delignette-Muller ML, Dutang C. 2015 fitdistrplus: an R package for fitting distributions. *J. Stat. Softw.* **64**, 1–34. (doi:10.18637/jss.v064.i04)
59. Scholz FW, Zhu A, Scholz MF. 2019 *Suppdists, package 'kSamples'*. See https://www.rdocumentation.org/packages/kSamples/versions/1.2-9.
60. Scholz FW, Stephens MA. 1987 K-sample Anderson–Darling tests. *J. Amer. Stat. Assoc.* **82**, 918–924. (doi:10.2307/2288805)
61. Sekhon JS. 2008 Multivariate and propensity score matching software with automated balance optimization: the matching package for R. *J. Stat. Softw.* **42**, 1–52. (doi:10.18637/jss.v042.i07)
62. Lord KS, Lesneski KC, Buston PM, Davies SW, D'Aloia CC, Finnerty JR. 2023 Rampant asexual reproduction and limited dispersal in a mangrove population of the coral *Porites divaricata*. Figshare. (doi:10.6084/m9.figshare.c.6700115)

Downloaded from https://royalsocietypublishing.org/ on 05 July 2023