MOLECULAR ECOLOGY

Molecular Ecology (2013) **22**, 56–73 doi: 10.1111/mec.12104

Range-wide population genetic structure of the Caribbean sea fan coral, *Gorgonia ventalina*

JASON P. ANDRAS,* KRYSTAL L. RYPIEN† and CATHERINE D. HARVELL

Department of Ecology and Evolutionary Biology, Cornell University, Dale R. Corson Hall, Ithaca, NY 14853, USA

Abstract

The population structure of benthic marine organisms is of central relevance to the conservation and management of these often threatened species, as well as to the accurate understanding of their ecological and evolutionary dynamics. A growing body of evidence suggests that marine populations can be structured over short distances despite theoretically high dispersal potential. Yet the proposed mechanisms governing this structure vary, and existing empirical population genetic evidence is of insufficient taxonomic and geographic scope to allow for strong general inferences. Here, we describe the range-wide population genetic structure of an ecologically important Caribbean octocoral, *Gorgonia ventalina*. Genetic differentiation was positively correlated with geographic distance and negatively correlated with oceanographically modelled dispersal probability throughout the range. Although we observed admixture across hundreds of kilometres, estimated dispersal was low, and populations were differentiated across distances <2 km. These results suggest that populations of *G. ventalina* may be evolutionarily coupled via gene flow but are largely demographically independent. Observed patterns of differentiation corroborate biogeographic breaks found in other taxa (e.g. an east/west divide near Puerto Rico), and also identify population divides not discussed in previous studies (e.g. the Yucatan Channel). High genotypic diversity and absence of clonemates indicate that sex is the primary reproductive mode for *G. ventalina*. A comparative analysis of the population structure of *G. ventalina* and its dinoflagellate symbiont, *Symbiodinium*, indicates that the dispersal of these symbiotic partners is not coupled, and symbiont transmission occurs horizontally.

Keywords: Caribbean, coral, *Gorgonia ventalina*, population genetics, seascape genetics *Symbiodinium*

Received 19 May 2011; revision received 19 September 2012; accepted 24 September 2012

Introduction

Larval dispersal is the primary means of gene flow among populations of most benthic and demersal marine organisms (Hedgecock 1986). Many species have long-lived, pelagic propagules that can be entrained by ocean currents and disperse across great distances, and the amount of time larvae spend in the water column is generally correlated with dispersal distance (Bohonak 1999). Although examples of substantial long-distance gene flow and panmixia do exist (Shulman & Bermingham 1995; Lessios *et al.* 2001; Neethling *et al.* 2008), exceptions are not uncommon, and it has become increasingly clear that even marine species with theoretically high dispersal potential can exhibit strong population differentiation over relatively small spatial scales (Quesada *et al.* 1995; Barber *et al.* 2000; Taylor & Hellberg 2003a). A number of mechanisms have been proposed to explain such population structure, including spatially divergent selection (Bongaerts *et al.* 2010), physical oceanographic barriers (Cowen *et al.* 2000) or larval behaviour/mortality that results in local retention

*Correspondence: Jason Andras, Evolutionsbiologie, Zoologisches Institut, Universität Basel, Vesalgasse 1, CH-4051, Basel, Switzerland. Fax: +41 61 267 0362; E-mail: jpa24@cornell.edu

†Present address: Section of Cell and Developmental Biology, University of California San Diego, 9500 Gilman Drive, La Jolla, CA 92093, USA

(Burton & Feldman 1982). The relative importance of each of these explanations is a matter of ongoing debate (Colin 2003; Taylor & Hellberg 2003b; Warner & Palumbi 2003), and additional empirical studies from a broader diversity of taxa will help to identify general mechanisms that govern the structure of benthic marine populations.

Geographic surveys of genetic variation are a particularly useful approach for mapping patterns of connectivity among populations of marine organisms (Hellberg *et al.* 2002). The small size and broad geographic extent of most planktonic propagules precludes direct estimates of migration by tracking of individuals or mark–recapture studies. However, population subdivision can be inferred from the distribution of selectively neutral diversity, and genetic admixture among differentiated populations provides a signal from which one can estimate the extent and distance of dispersal. The population genetic structure of a species can also shed light on fundamental aspects of its basic biology and life history. Structured populations have the potential to differentiate and adapt to local selective pressures without the diluting effects of genetic input from disparate regions, whereas panmictic species should be more resistant to local selection (Kawecki & Ebert 2004). Moreover, an accurate understanding of population connectivity is essential for the design of effective conservation and management strategies for threatened species. For example, marine reserve networks, one of the most important tools for managing marine systems, require spatially explicit knowledge of the structure of populations they aim to protect (Palumbi 2003).

Tropical shallow-water corals are among the marine taxa most threatened by anthropogenic disturbance. In just the past few decades, reefs have suffered massive and accelerating losses worldwide due to numerous threats including climate warming (Hoegh-Guldberg 1999), ocean acidification (Hoegh-Guldberg *et al.* 2007), disease (Harvell *et al.* 2002), eutrophication (McCook *et al.* 2001) and overfishing (Jackson *et al.* 2001). A global initiative is underway to protect reef ecosystems through coordinated networks of marine reserves (Kelleher *et al.* 1995), yet our knowledge of the population structure of most coral species is inadequate to inform management plans (Van Oppen & Gates 2006; Baums 2008). Corals exhibit a diversity of reproductive strategies, ranging from hermaphroditic brooders with crawl-away juveniles to gonochoric broadcast spawners with positively buoyant larvae that remain viable for months (Harrison & Wallace 1990). In general, coral population structure tends to correlate with reproductive mode, with brooding corals exhibiting more genetic subdivision than broadcast spawners (Hellberg 1996; Ayre & Hughes 2000; Nishikawa *et al.* 2003; Miller & Ayre 2008b; Underwood *et al.* 2009). However, coral life history characteristics have, in some cases, been found to be poor predictors of genetic structure (Miller & Ayre 2008a), and several studies have shown that population subdivision can exist even in coral species with long pelagic larval duration. For example, the Caribbean coral, *Acropora palmata*, is divided into two large regional populations in the Eastern and Western Caribbean (Baums *et al.* 2005). *Acropora cervicornis* has been divided into at least six regional populations throughout the Caribbean (Galindo *et al.* 2006). And at least five species of broadcasting corals (*Acropora hyacinthus*, *A. cytherea*, *A. millepora*, *A. valida* and *A. tenuis*) are differentiated across distances <10 km on reefs in Australia (Ayre & Hughes 2000; Underwood *et al.* 2009).

Here, we investigate the population genetic structure of *Gorgonia ventalina*, one of the most abundant species of octocoral in the Caribbean. *G. ventalina* has been heavily impacted over the past two decades by the fungal disease aspergillosis (Kim & Harvell 2004), and numerous studies have investigated the ecology (Kim *et al.* 2006), epidemiology (Jolles *et al.* 2002) and immunology (Couch *et al.* 2008) of this coral. Yet there is little information available regarding the population biology of *G. ventalina*, or most octocorals, for that matter. All population genetic studies of gorgonian corals to date have observed high levels of differentiation across short distances (*Briareum asbestinum* <10 km, Brazeau & Harvell 1994; *Pseudopterogorgia elisabethae* <10 km, Gutierrez-Rodriguez & Lasker 2004; *Corallium rubrum* <1 m, Ledoux *et al.* 2010a; *Paramuricea clavata* ~20 m, Mokhtar-Jamai *et al.* 2011). However, these studies all focused on species of brooding corals with larvae that settle close to the maternal colony—a relatively uncommon reproductive mode among Caribbean gorgonians. Observations of spawning or planktonic larvae of *G. ventalina* have never been reported, so time of spawning, reproductive mode and larval duration are not definitively known. However, *G. ventalina* colonies are dioecious (Petes *et al.* 2003; Fitzsimmons-Sosa *et al.* 2004), have never been observed with surface-brooded larvae, and their eggs and polyps are much smaller than those of most brooding corals (C. D. Harvell, unpublished data), suggesting that *G. ventalina* is likely an outcrossing broadcast spawner.

Like most tropical shallow-water corals, *G. ventalina* exists in obligate symbiosis with photosynthetic dinoflagellates of the genus *Symbiodinium*, which provide the majority of the coral's nutrition (Muscatine & Porter 1977). Some corals transmit their *Symbiodinium* vertically from the maternal colony to eggs or larvae. In such cases of tightly coupled dispersal, the population structure of host and symbiont should be highly congruent (Bongaerts *et al.* 2010). More commonly, though, coral larvae do not carry with them the *Symbi-*

odinium of their maternal colony and must acquire symbionts anew each generation (Knowlton & Rohwer 2003). In such cases of horizontal transmission, the dispersal of host and symbiont is independent, adding an important dimension of complexity to the consideration of coral population biology. As most broadcast-spawning corals do not transmit their symbionts vertically (Knowlton & Rohwer 2003), it is likely that *G. ventalina* larvae acquire *Symbiodinium* from the environment where they settle.

We used seven polymorphic microsatellite markers to describe the population genetic structure of *G. ventalina* at 35 localities spanning the species range throughout the Caribbean Sea and western North Atlantic Ocean. Given the differentiation observed among populations of other Caribbean organisms with high dispersal potential, we expected that populations of *G. ventalina* would be structured across the range. The range-wide population structure of *Symbiodinium* hosted by *G. ventalina* has recently been described using the same samples as the current study (Andras *et al.* 2011), and strong differentiation was observed between localities <10 km apart. Here, we compare the population structure of the host with those published results. Based on the known or estimated life history characteristics of *G. ventalina* and its *Symbiodinium*, we hypothesized that the population structures of these symbiotic partners would be distinct. We expected that populations of *G. ventalina* would be connected across larger distances than its symbiont, reflecting the longer pelagic duration and broader dispersal potential of its propagules. Taken together, the present study of the coral host, in conjunction with previous results for its algal symbiont, provides a unique opportunity to explore the population biology of both partners composing the ecologically functional coral entity.

Methods

Population sampling

A total of 1607 samples were collected from 35 localities spanning the range of *Gorgonia ventalina* in the Caribbean and Western Atlantic (Fig. 1, Table 1). Localities ranged in depth from 5 to 24 m, with a median of 8 m. Where possible, localities were chosen for consistency in habitat characteristics, namely, hard-bottom fore-reef sites dominated by gorgonian communities. Distances between localities ranged from 0.8 to 3124 km. At each locality, adult colonies of *G. ventalina* (>30 cm height) were haphazardly sampled along several swimming transects across an area measuring approximately 25 × 25 m^2. From each sampled colony, a 4-cm^2 tissue explant was cut from the apical colony edge and transferred to a labelled bag. The number of individuals sampled per locality (Table 1) varied based on availability, with an average of 46. After collection, samples were transferred to

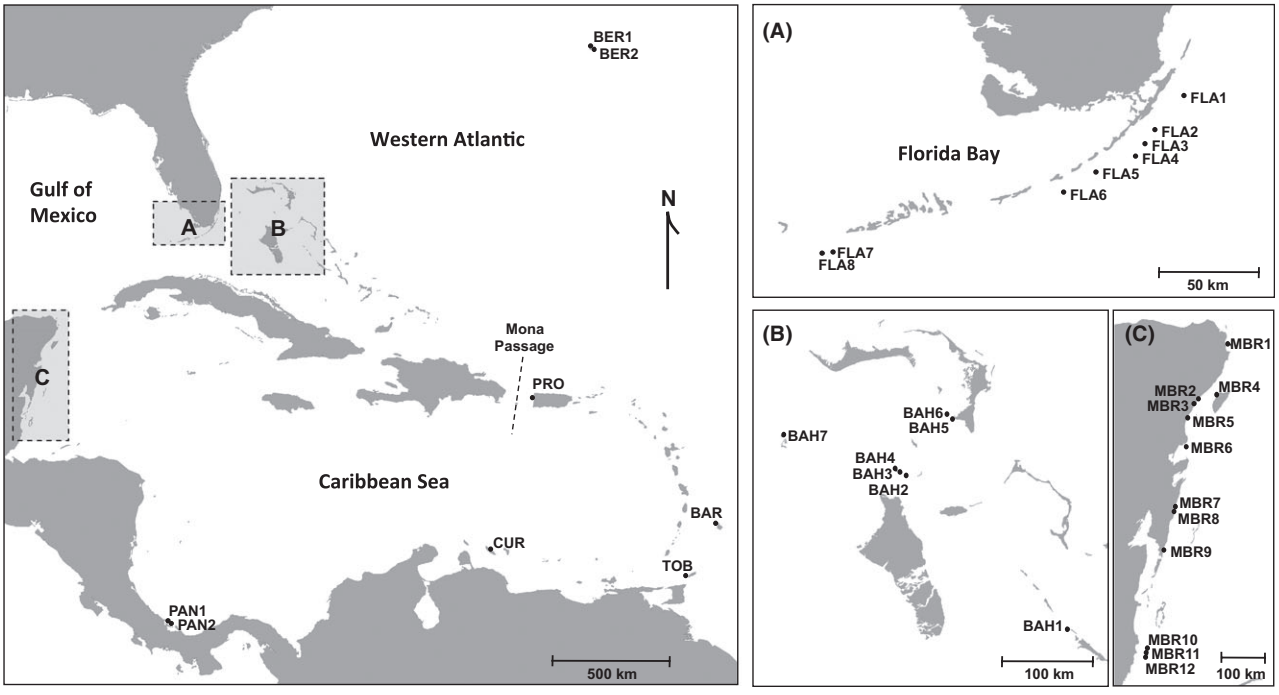

Fig. 1 Map of 35 sample localities across the Caribbean Sea and Western Atlantic, with enlarged regional maps of the Florida Keys (A), Bahamas (B) and Mesoamerican Barrier Reef (C).

Table 1 Name; abbreviation; regional designation; coordinates; collection date; sample size (n); average allelic richness (Na); expected and observed heterozygosity (H_E, H_O); inbreeding coefficient (F_{IS}); and probability of identity (PI) for all 35 sample localities included in this study

Region	Site	Site code	Depth (m)	GPS	Date collected	n	Na	H_E	H_O	F_{IS}	PI
Florida Keys	Florida, Carysfort	FLA1	5	N 25.22°, W 80.21°	8/03	86	13.6	0.68	0.61	0.08*	1.7E−11
	Florida, Molasses	FLA2	6	N 25.00°, W 80.37°	8/03	72	13.4	0.58	0.63	0.07*	4.1E−11
	Florida, Pickles	FLA3	6	N 24.98°, W 80.41°	8/03	181	15	0.60	0.66	0.02	3.6E−10
	Florida, Conch	FLA4	8	N 24.95°, W 80.45°	8/03	55	12.1	0.62	0.65	0.03	2.1E−11
	Florida, Alligator	FLA5	5	N 24.84°, W 80.62°	8/03	68	12.6	0.62	0.62	0.05	1.9E−11
	Florida, Tennessee	FLA6	6	N 24.74°, W 80.78°	8/03	75	13.4	0.62	0.65	0.05	2.6E−11
	Florida, Western Dry Rocks	FLA7	6	N 24.44°, W 81.92°	8/03	39	11	0.65	0.62	0.05	1.9E−10
	Florida, Sand Key	FLA8	5	N 24.45°, W 81.87°	8/03	30	10.7	0.65	0.68	0.01	7.4E−11
Mesoamerican Barrier Reef	Mexico, Isla Mujeres, Tavos	MBR1	9	N 21.24°, W 86.73°	4/03	46	11.7	0.65	0.67	0.02	1.5E−10
	Mexico, Akumal, Media Luna	MBR2	9	N 20.40°, W 87.30°	4/03	86	13.7	0.66	0.65	0.05	2.0E−11
	Mexico, Akumal, South Point	MBR3	9	N 20.38°, W 87.31°	4/03	10	5.57	0.67	0.64	0	4.8E−08
	Mexico, Cozumel, Paradise	MBR4	8	N 20.51°, W 86.94°	4/03	61	11.9	0.67	0.69	0.01	6.5E−10
	Mexico, Tulum, La Piscina	MBR5	12	N 20.22°, W 87.74°	5/03	45	10.9	0.67	0.62	0.09*	2.9E−10
	Mexico, Punta Allen	MBR6	9–12	N 19.78°, W 87.43°	7/06	30	10.3	0.67	0.63	0.06	1.6E−10
	Mexico, Mahahual, El Jardin	MBR7	17	N 18.85°, W 87.63°	5/03	37	11.1	0.68	0.65	0.05	6.0E−11
	Mexico, Mahahual, Site 2	MBR8	8	N 18.84°, W 87.64°	5/03	51	12	0.68	0.65	0.04	1.1E−09
	Mexico, Xcalak, Dona Nica	MBR9	11	N 18.29°, W 87.81°	5/03	44	12.7	0.68	0.64	0.09*	4.4E−11
	Belize, Southwater Caye, Long Reef	MBR10	5	N 16.77°, W 88.08°	5/03	42	12	0.68	0.65	0.05	5.4E−10
	Belize, Carrie Bow Caye	MBR11	5	N 16.80°, W 88.08°	5/03	23	10.1	0.69	0.65	0.04	3.9E−10
	Belize, Southwater Caye, East Side	MBR12	9	N 16.81°, W 88.07°	5/03	43	12.4	0.69	0.62	0.11*	4.7E−11
Panama	Panama, Bocas del Toro, Punta Vieja	PAN1	5–8	N 9.260°, W 82.12°	10/05	28	8.71	0.69	0.57	0.08	8.2E−10
	Panama, Bocas del Toro, Hospital Point	PAN2	5–8	N 9.333°, W 82.21°	10/05	17	6.71	0.69	0.60	0	2.4E−08
Curacao	Curacao	CUR	9–12	N 12.11°, W 68.97°	7/06	50	10.1	0.69	0.59	0.1*	2.0E−09
Tobago	Tobago	TOB	9–12	N 11.19°, W 60.79°	4/08	50	7.29	0.69	0.58	0	2.5E−08
Barbados	Barbados	BAR	9–12	N 13.17°, W 59.64°	9/06	61	11.3	0.69	0.56	0.09*	3.7E−10
Puerto Rico	Puerto Rico, Steps Beach, Rincon	PRO	5–6	N 18.35°, W 67.26°	8/06	51	12	0.69	0.65	0.04	1.3E−10
Bahamas	Bahamas, Lee Stocking Island	BAH1	5–6	N 23.78°, W 76.13°	5/03	26	8.86	0.69	0.60	0.09*	1.0E−10
	Bahamas, Chub Cay	BAH2	9–12	N 25.40°, W 77.92°	5/05	21	9.29	0.69	0.63	0.04	7.7E−10
	Bahamas, GPS121	BAH3	11–12	N 25.42°, W 77.98°	5/04	16	8	0.69	0.73	−0.01	1.1E−09
	Bahamas, Rum Cay	BAH4	12–15	N 25.45°, W 78.03°	5/04	10	6.57	0.70	0.74	0	5.2E−10
	Bahamas, Sandy Point	BAH5	8–9	N 25.99°, W 77.42°	5/04	21	9.71	0.70	0.66	0.06	6.5E−11
	Bahamas, Gorda Rock	BAH6	5–6	N 26.04°, W 77.47°	5/04	18	8	0.71	0.64	0.01	1.1E−09

Table 1 *Continued*

Region	Site	Site code	Depth (m)	GPS	Date collected	*n*	Na	H_E	H_O	F_{IS}	PI
	Bahamas, Bimini	BAH7	21–24	N 25.81°, W 79.28°	5/05	14	7.57	0.71	0.58	0.15*	1.6E−08
Bermuda	Bermuda, Castle Harbour	BER1	5–6	N 32.33°, W 64.67°	5/07	50	9.57	0.71	0.65	0.06	3.9E−10
	Bermuda, Crescent	BER2	5–6	N 32.39°, W 64.79°	5/07	50	10	0.73	0.67	0.02	6.8E−11

*Significant values of F_{IS}.

individual 2-mL plastic tubes containing a 20% salt-saturated dimethyl sulfoxide solution for preservation (Dawson *et al.* 1998).

DNA Extraction, amplification and genotyping

Whole genomic DNA was extracted from 1-cm^2 tissue subsamples using DNeasy Tissue Kits (Qiagen). Each sample was genotyped via polymerase chain reaction (PCR) using primers and run conditions for 10 previously reported microsatellite loci (Andras & Rypien 2009). PCR products were analysed on an ABI 3100 Automated Capillary DNA Sequencer using the GeneScan-500 LIZ size standard (Applied Biosystems). Allele sizes were scored using GeneMapper 3.5 (Applied Biosystems) and validated by eye.

Genetic diversity

All loci were tested for evidence of null alleles with the program MICRO-CHECKER (Van Oosterhout *et al.* 2004). We used the program GENODIVE 2.0b22 (Meirmans & van Tienderen 2004) to calculate observed and expected heterozygosities (Nei 1987), inbreeding coefficients (F_{IS}, Weir & Cockerham 1984) and to test for deviations from Hardy–Weinberg equilibrium (1×10^4 permutations to assess significance). Linkage disequilibrium between loci within each locality was tested using Arlequin 3.0 (Excoffier *et al.* 2005; 1×10^4 permutations to assess significance). We used the program GENALEX 6.41 (Peakall & Smouse 2006) to calculate the probability that two individuals drawn from the same locality will have the same multilocus genotype (probability of identity). Finally, we used GENODIVE to survey the data set for identical multilocus genotypes (clonemates) and to perform significance tests for clonal population structure, using Nei's diversity index (Nei 1987) as the test statistic (1×10^4 permutations to assess significance).

Population structure and connectivity

To investigate the partitioning of genetic diversity among localities and regions, we performed analyses of molecular variance (AMOVA; Excoffier *et al.* 1992) using the program Arlequin 3.0 (Excoffier *et al.* 2005). Samples were grouped by collection locality nested within region. Regional designations (Table 1) were defined based on the geographic proximity of sampling localities and oceanographic barriers between them. Separate AMOVAs were performed assuming either an infinite allele model (IAM; Kimura & Crow 1964) or a stepwise mutation model (SMM; Ohta & Kimura 1973). The SMM assumes that relatedness between two alleles is inversely proportional to their difference in length and may thus be a more appropriate model for microsatellites, which are thought to mutate via the incremental gain or loss of single repeat motifs (Ellegren 2004). To estimate the degree of differentiation among all localities, pairwise measures of F_{ST} (Weir & Cockerham 1984), which assumes an IAM, and R_{ST} (Slatkin 1995), an F_{ST} analogue based on a SMM, were also calculated using Arlequin.

We inferred population structure in our data using a Bayesian clustering approach implemented by the program Structure 2.3 (Pritchard *et al.* 2000). This program probabilistically assigns individuals membership among K populations (where K is specified by the user) without regard to collection locality. We employed a model that allowed admixture and assumed correlated allele frequencies among populations. We conducted 10 independent runs at each K from 1 to 35. Each run consisted of 2×10^6 Markov chain Monte Carlo (MCMC) iterations after a burn-in of 2×10^6 steps. This run length was sufficient to achieve stabilization of all relevant summary statistics. We chose the optimal number of genetic clusters as the value of K that achieved the highest posterior probability while maximizing average cluster membership coefficients (Q; Pritchard *et al.* 2000). In essence, this approach aims to identify the value of K at which the posterior probability 'more or less plateaus' (Pritchard *et al.* 2010). For the chosen value of K, cluster membership coefficients were matched and averaged across the 10 independent runs by the program CLUMPP (Jakobsson & Rosenberg 2007), using the greedy algorithm with 1×10^5 random input orders.

We estimated recent migration rates between localities (i.e. within the past several generations) using the program BAYESASS 3.0 (Wilson & Rannala 2003). This program employs a Bayesian MCMC approach to identify migrants or recent descendants of migrants based on transient linkage disequilibrium among multilocus genotypes from different source populations. We performed 10 separate runs of 2×10^7 iterations, with a burn-in of 1×10^6 and a sampling frequency of 1000. This run length was sufficient for the posterior probability to achieve convergence. The MCMC mixing parameters for allele frequency, level of inbreeding and migration rate, which define the maximum amount each parameter can change after each iteration, were adjusted to 0.75, 0.95 and 0.60, respectively. These values resulted in acceptance ratios between 40% and 60%, which tend to maximize log likelihood values (Wilson & Rannala 2003). Migration rates were averaged over the 10 independent runs and compared to average migration rates of 10 randomly permuted data sets (generated in GENODIVE) to assess significance. Estimated migration rates were considered significant when the 95% confidence interval (CI) did not overlap with the 95% CI of the randomly permuted data.

Geographic and oceanographic correlation analyses

To infer mechanisms that may be responsible for the observed patterns of population structure, we compared estimates of genetic differentiation to geographic distances among localities as well as estimates of connectivity among regions derived from an oceanographic model. We used a Mantel test (Mantel 1967) to evaluate the correlation between linearized genetic differentiation ($F_{ST}/1 - F_{ST}$) and the logarithm of the straight-line geographic distance between localities. This relationship is expected to be positive and linear in the context of a two-dimensional isolation-by-distance (IBD) model (Rousset 1997), and the slope of this correlation (*blog*) can be used to estimate the dispersal neighbourhood in terms of the number of individual nearest neighbours (Nb = 1/*blog*).

We also used Mantel tests to compare genetic differentiation of *G. ventalina* to estimates of connectivity among regions derived from an oceanographic model. Connectivity estimates were derived from simulations reported by Galindo *et al.* (2006) and used with the authors' permission. These simulations, implemented by the Miami Isopycnic Coordinate Ocean Model, use historical wind data to estimate near-surface ocean currents. Specifically, Galindo *et al.* (2006) estimated dispersal among 87 randomly chosen localities across the Caribbean by tracking the movements of simulated passively drifting particles. The proportion of particles released at one locality that arrived at another (including 50-km buffer zones around all localities) represents the probability of passive directional dispersal between those localities. Simulations were repeated in the winter (Julian days 15–57), spring (Julian days 135–177) and summer (Julian days 205–247) of each year from 1982 to 1986 (see Galindo *et al.* 2006 for full details). For our analysis, we selected localities from the model that were closest to our sampling localities and compared the corresponding seasonal dispersal probabilities averaged across all five modelled years to linearized estimates of genetic differentiation ($F_{ST}/1 - F_{ST}$). As corresponding model localities were not available for each of our sampling localities, comparisons were performed among mean values for regional groups of localities (designated in Table 1). Because dispersal probabilities were bidirectional and asymmetric, we averaged dispersal in both directions to facilitate comparison with our estimates of differentiation. Sampling localities in Bermuda were omitted from the analysis, as this region was not included in the oceanographic model. To determine whether geographic distance and dispersal probability between localities were independently correlated with genetic differentiation, we performed partial Mantel tests, which evaluate the association between two matrices while controlling for a third (Smouse *et al.* 1986). All Mantel tests were performed using the program GENODIVE with 1×10^5 random permutations to assess significance.

We performed tests of spatial autocorrelation using the program GENALEX 6.41 (Peakall & Smouse 2006) to evaluate whether the degree of genetic similarity between localities was correlated with the geographic distance between them. Unlike Mantel tests, which identify strong patterns of differentiation extending over the full geographic sample range, spatial autocorrelation analyses allow for the independent comparison of individuals or populations within different distance classes, thereby providing greater resolution of spatial genetic structure (Clark & Richardson 2002; Epperson 2005). Specifically, we used pairwise matrices of genetic distance (as calculated by Peakall *et al.* 1995) and pairwise geographic distance between localities to calculate the spatial autocorrelation coefficient of genetic distance (r) for 64 geographic distance classes of increasing size, ranging from 50 to 3200 km, the maximum distance between sampling localities. For each distance class, 95% CI about r were generated based on 1000 bootstrap replicates. The behaviour of r over increasing distance can illustrate the shifting balance between gene flow and genetic drift. In cases where positive spatial structure is present, r will decrease with increasing distance class size, and the distance class at which r becomes not significantly different from zero provides an estimate of

the extent of positive spatial genetic structure (Peakall *et al.* 2003).

Results

Genetic diversity

Of the 10 microsatellite loci developed for this study (Andras & Rypien 2009), three (SYM203, GV31 and GVc9) showed significant deviations from Hardy–Weinberg equilibrium at nearly all sampling localities and appeared to suffer from substantial null alleles. Consequently, these loci were excluded from all analyses (although their inclusion did not alter the results substantially—data not shown). For the remaining seven loci, inbreeding coefficients were generally low (global $F_{IS} = 0.04$, not significant), and 27 of the 35 localities had F_{IS} values not significantly different from zero (Table 1), indicating that most localities were at or near Hardy–Weinberg equilibrium. Less than 9% (21/245) of tests for null alleles within localities were significant (Table S1, Supporting Information), and positive tests were distributed evenly across loci and throughout localities, suggesting that there is likely no systematic bias introduced by null alleles. Only 2.6% of all pairwise comparisons between loci within populations exhibited significant evidence of linkage disequilibrium. The probability of identity over the 7 loci used in this study was quite low (10^{-8}–10^{-11} per locality, Table 1), and there were no clonal multilocus genotypes detected throughout the entire data set, indicating that clones are rare or nonexistent in *Gorgonia ventalina* populations. In support of this, tests of clonal population structure were not significant for any locality ($P = 1.0$). Mean gene diversity (H_E) for each locality was high (0.58–0.73, Table 1) and was positively correlated with latitude ($R^2 = 0.303$, $P = 0.0006$; Fig. S1, Supporting Information). All measures of genetic diversity are summarized per locus for each locality in Table S1 (Supporting Information).

Population structure and connectivity

AMOVAs based on both an IAM and SMM detected significant differentiation among regions and populations within regions (Table 2). Pairwise F_{ST} comparisons between localities (Table S2, below diagonal, Supporting Information) ranged from 0.010 to 0.192 (overall $F_{ST} = 0.077$), and nearly all were significant (98.5%). Estimates of R_{ST} (Table S2, above diagonal, Supporting Information) were higher than F_{ST} (overall $R_{ST} = 0.16$; range = 0.010–0.550), although fewer pairwise comparisons were significant (84.7%).

For the Bayesian clustering analyses run with Structure, the posterior probability rose sharply over K 1–5 and settled into a more gradual yet consistent ascent thereafter (Fig. S2, Supporting Information). Cases where the model choice criterion continues to rise with increasing K typically correspond to complex patterns of structure, such as IBD, where populations are not discrete (Pritchard *et al.* 2010). One of the most commonly used approaches to select the optimal number of populations for Bayesian clustering analyses run with Structure is the ΔK method described by Evanno *et al.* (2005). However, this method was designed for a hierarchical island model of gene flow and identifies an optimal clustering solution corresponding to the highest hierarchical level of population structure. Consequently, the ΔK method frequently underestimates the true number of population clusters, which can lead to spurious clustering results, particularly when the true population structure is not hierarchical (Kalinowski 2011). Because our data showed definitive evidence of not conforming to the hierarchical island model (see IBD results below), and because we felt the ΔK method significantly underestimated K (results not shown), we chose to follow the more heuristic method described in the Structure user's manual (Pritchard *et al.* 2010). This approach identifies the optimal number of genetic clusters as the value of K that achieves the highest posterior probability while maximizing average cluster membership coefficients (Q;

Table 2 Results from AMOVAs implementing either an infinite allele model (IAM, A) or a stepwise mutation model (SMM, B)

Model used	Source of variation	d.f.	Sum of squares	Variance component	% Variation	Fixation indices
(A) IAM	Among regions	8	498.91	$V_a = 0.157$	4.31	$F_{CT} = 0.043$*
	Among localities within regions	26	385.10	$V_b = 0.122$	3.36	$F_{SC} = 0.035$*
	Among individuals within a locality	1572	6297.06	$V_c = 3.001$	17.97	$F_{ST} = 0.077$*
	Within individuals	1607	4340.00	$V_d = 2.701$	74.36	
(B) SMM	Among regions	8	68102.65	$V_a = 24.887$	11.24	$R_{CT} = .112$*
	Among localities within regions	26	27116.21	$V_b = 9.326$	4.21	$R_{SC} = 0.047$*
	Among individuals within a locality	1572	342263.16	$V_c = 30.614$	13.83	$R_{ST} = 0.155$*
	Within individuals	1607	251491.50	$V_d = 156.497$	70.71	

*$P < 0.001$.

Pritchard *et al.* 2000), which generally corresponds to the value of K at which the posterior probability 'more or less plateaus' (Pritchard *et al.* 2010). Based on this criterion, we chose a seven-population model as the best solution for the Bayesian clustering analysis, as values of $K < 7$ failed to capture certain features of biogeographically sensible structure, and values of $K > 7$ reduced average cluster membership values.

In the $K = 7$ solution, a total of 1250 individuals (77%) were assigned to one of the seven clusters with a probability of at least 0.6. The clusters were generally distributed cohesively across contiguous or adjacent localities and identify five broad genetically differentiated regions (Fig. 2):

1 The large majority of individuals from *Bermuda* were assigned to the Yellow Cluster, which is relatively uncommon across the rest of the range.
2 Localities in the *Florida Keys* were dominated by either the Orange Cluster or Red Cluster.
3 The Brown and Green Clusters were almost exclusively limited to localities from the *Mesoamerican* Barrier Reef and Panama.
4 The Purple Cluster was restricted to the *Windward Islands* of Barbados and Tobago in the east.
5 Most individuals from the *Bahamas*, *Puerto Rico*, and *Curacao* were assigned to the Blue Cluster, although members of the Yellow and Red Clusters are not uncommon among these localities, indicating some connectivity with Bermuda and the Florida Keys.

In contrast to the patterns of admixture within regions, there was little evidence of recent migration between localities as estimated by BAYESASS. Of the 1190 bidirectional estimates of migration between localities, only four were significant (Table 3). Three of these

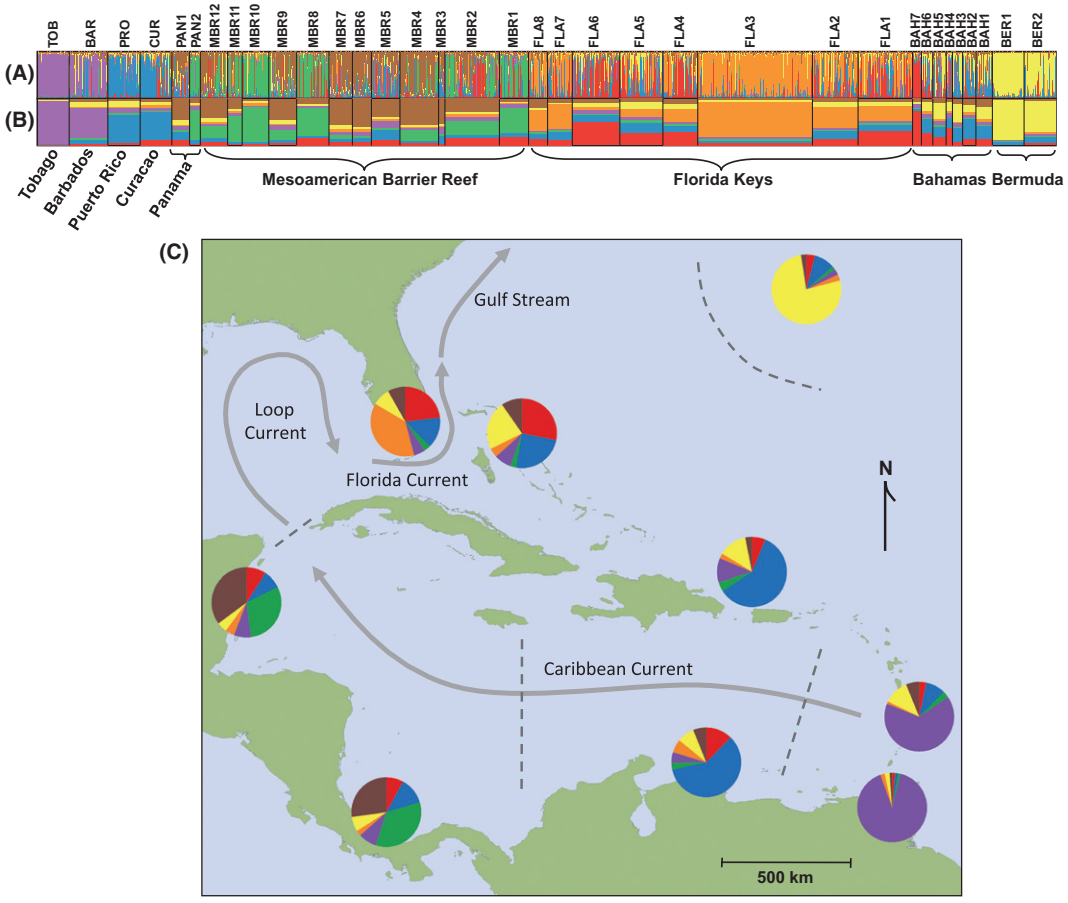

Fig. 2 Graphical summary of Bayesian clustering results. Samples were assigned among seven colour-coded genetic clusters (Red, Orange, Yellow, Green, Blue, Purple, Brown). (A) Cluster assignments of individual samples, where each thin vertical line represents a single *Gorgonia ventalina* colony. Individuals are grouped by locality (labels above, see codes in Table 1) and region (labels below). (B) Average cluster assignments for each locality. (C) Cluster assignments are averaged for each region and displayed as pie charts. Arrows denote major current patterns discussed in the text. Dashed lines denote divisions between regional populations.

Table 3 Recent migration rates between localities as estimated by BAYESASS

Source locality	Recipient locality	Migration rate ± 95% CI	Geographic distance (km)
FLA1 (Florida, Carysfort)	FLA3 (Florida, Pickles)	0.083 ± 0.049	33.3
FLA7 (Florida, Western Dry Rocks)	FLA3 (Florida, Pickles)	0.095 ± 0.062	163.6
FLA5 (Florida, Alligator)	FLA6 (Florida, Tennessee)	0.098 ± 0.058	19.4
BER1 (Bermuda, Castle Harbour)	BER2 (Bermuda, Crescent)	0.112 ± 0.053	12.6

All pairwise estimates between localities that are not shown were not significantly different from zero.

instances of migration were between localities in the Florida Keys (8.3–9.8% migrants, between 19 and 164 km apart), and one was between localities in Bermuda (11.2% migrants, 13 km apart).

Geographic and oceanographic correlation analyses

Genetic differentiation between localities ($F_{ST}/1 - F_{ST}$) was positively correlated with the geographic distance between them (Mantel's $R^2 = 0.168$, $P = 0.002$; Fig. 3A), suggesting that geographic distance serves as an isolating mechanism for populations of *G. ventalina*. In addition, F_{ST} between regions was negatively correlated with dispersal probability in winter ($R^2 = 0.112$, $P = 0.008$), spring ($R^2 = 0.136$, $P = 0.009$) and summer ($R^2 = 0.161$, $P = 0.002$; Fig. 3B), indicating that ocean currents likely serve as a means of connectivity. Although dispersal probability and geographic distance were correlated with each other, partial Mantel tests, which evaluate the association between two matrices while controlling for a third, identified that both of these variables were independently correlated with genetic differentiation (seasonally averaged dispersal probability controlling for geographic distance: $P = 0.046$; geographic distance controlling for seasonally averaged dispersal probability: $P = 0.040$).

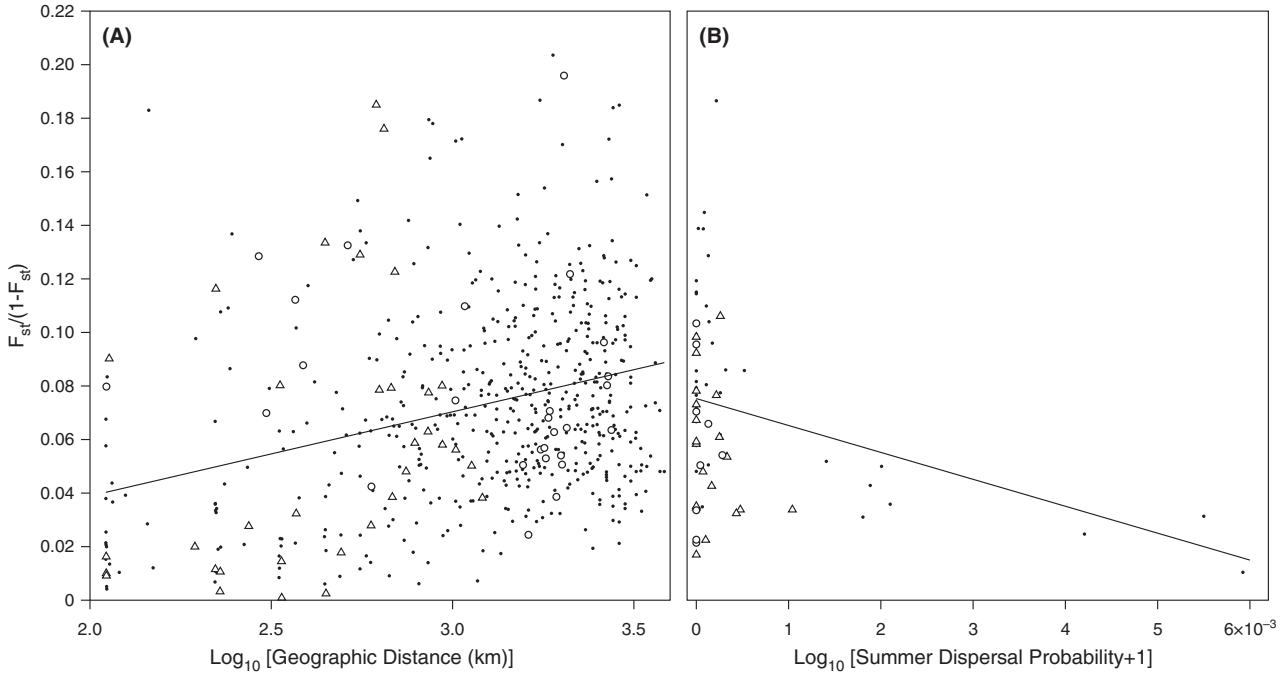

Fig. 3 (A) Genetic differentiation [$(F_{ST}/(1 - F_{ST})$] of *Gorgonia ventalina* between localities versus the logarithm of geographic distance. (B) Genetic differentiation between regions versus the logarithm of oceanographically modelled dispersal probability in summer. Subsets of the data discussed in the text are marked with different icons: △, comparisons between the Bahamas and other localities. ○, comparisons between Panama and other localities. ●, comparisons between all localities except the Bahamas and Panama. Localities from Bermuda are not shown in the panel B, as this region was not included in the dispersal model.

Analyses of spatial autocorrelation also identified significant positive genetic structure and provide a detailed view of how this structure changes over increasing geographic distance (Fig. 4). Spatial autocorrelation was strongest for the shortest distance classes and decreased progressively until r became not significantly different from zero at the 0–1050 km distance class. Thus, the limit of detectable positive spatial genetic structure for *G. ventalina* occurs at approximately 1000 km. The dispersal neighbourhood, defined as the region throughout which the larval pool is well mixed, can also be estimated from analyses of spatial autocorrelation, provided the scale of spatial sampling is sufficiently fine. The dispersal neighbourhood is identified as the distance over which the autocorrelation coefficient (r) remains approximately constant, before it begins to decline (Epperson 2005). Based on the sampling scheme of this study, the autocorrelation coefficient of *G. ventalina* populations shows no initial plateau, but declines progressively from the first distance class. This pattern held for distance classes as small as 2 km (results not shown), the maximum spatial resolution possible with this data set, indicating that the spatial scale of sampling of this study is inadequate to resolve the precise dispersal neighbourhood. Nonetheless, these results suggest that the dispersal neighbourhood is smaller than 2 km. In agreement with this upper bound, the density-dependant dispersal neighbourhood estimated from the slope of the regression between $F_{ST}/(1 - F_{ST})$ and the logarithm of geographic distance ($Nb = 1/blog$) was found to be approximately 212 individuals, a number commonly encountered within a radius of 30–70 m on a typical reef (Kim & Harvell 2004).

Discussion

The analyses of population structure presented here illustrate that, although dispersal by *Gorgonia ventalina* results in significant admixture across thousands of kilometres and gene pools are well mixed within individual sampling localities, populations can be differentiated across distances <2 km. Throughout the range, genetic differentiation among localities was positively correlated with geographic distance and negatively correlated with oceanographically modelled dispersal probability. These trends suggest that distance is an important isolating mechanism for *G. ventalina*, while dispersal via ocean currents is a likely means of connectivity among populations.

Differentiation and connectivity of G. ventalina populations

The dominant ocean currents throughout the Caribbean and western North Atlantic are largely continuous and

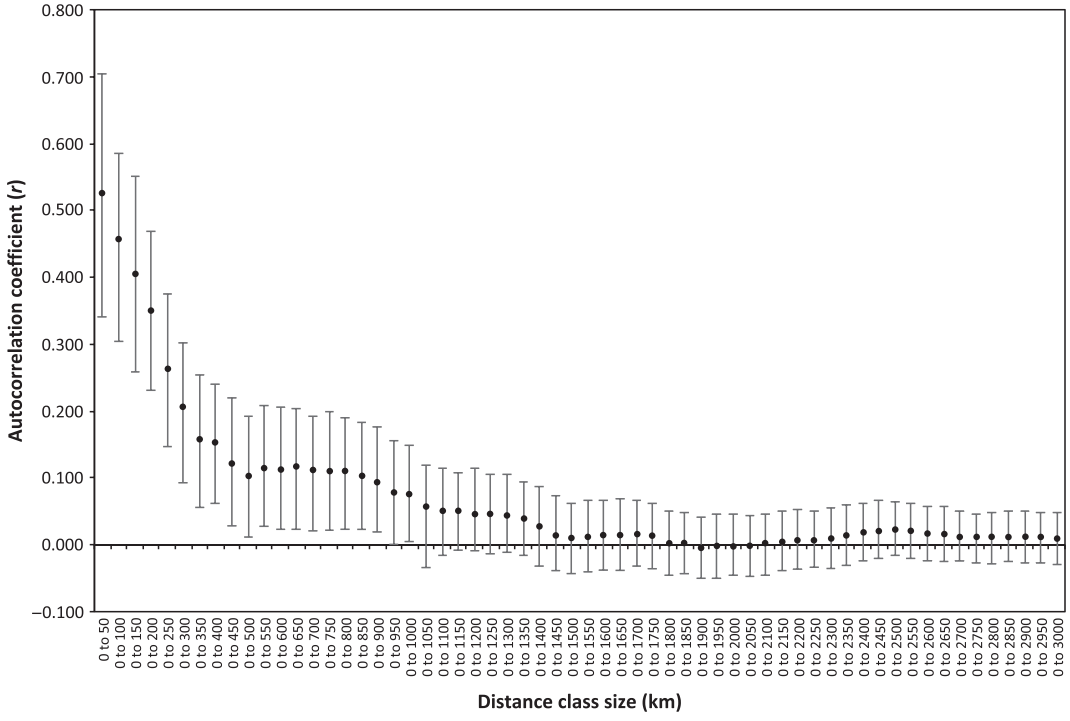

Fig. 4 Plot of the autocorrelation coefficient of *Gorgonia ventalina* (r) versus distance classes of progressively increasing size. Error bars about r depict 95% confidence intervals based on 1×10^3 bootstrap trials.

unidirectional (Joyce *et al.* 2001; Fig. 2), and the range of *G. ventalina* can be construed along the trajectory of these currents. Most flow enters the Caribbean between the Windward Islands in the east, moves west/northwest across the Caribbean Basin (Caribbean Current), through the Gulf of Mexico (Loop Current) and Straits of Florida (Florida Current), and joins the Gulf Stream heading north/northeast. Along this route, the contiguous distribution of genetic groups identified by Bayesian clustering loosely delimits five interconnected regional populations of *G. ventalina* (Fig. 2). At the opposite ends of the range, the Windward Islands (Tobago and Barbados) and Bermuda (Fig. 2—Purple & Yellow Clusters, respectively) were differentiated from localities in the centre of the range. In general, localities in the middle of the range showed greater admixture and shared cluster membership, although regional patterns of differentiation were still clear.

The Windward Islands had markedly different cluster membership than Puerto Rico and Curacao immediately to the west. This break is noteworthy, as several oceanographic models (Baums *et al.* 2006; Cowen *et al.* 2006; Galindo *et al.* 2006) along with empirical studies of fish (Taylor & Hellberg 2003a, 2006; Eytan & Hellberg 2010) and corals (Baums *et al.* 2005, 2006; Galindo *et al.* 2006) have identified a similar juncture near Puerto Rico, suggesting that this may be a common biogeographic divide for many Caribbean organisms. Studies of fish and oceanographic models have consistently placed this divide in the Mona Passage, where strong currents flow between Puerto Rico and Hispaniola. In contrast, Baums *et al.* (2005) found that colonies of the coral, *Acropora palmata*, sampled from Puerto Rico were genetically clustered with other localities in the western Caribbean, similar to the results we report here. However, in a second study, when more sampling localities were added in the vicinity of the Mona Passage, *A. palmata* colonies from Puerto Rico changed cluster membership and were grouped with localities to the east (Baums *et al.* 2006). The authors attribute the change in population assignment of Puerto Rico to insufficient sampling density in the first study, which has the potential to bias the outcome of Bayesian clustering (Beerli 2004), and conclude that the Mona Passage represents an oceanographic filter to the dispersal of *A. palmata* larvae (Baums *et al.* 2006). Our study has only one sampling locality in the vicinity of this biogeographic divide, and it lies on the western-most point of Puerto Rico, directly in the Mona Passage. It is possible that the addition of sampling localities in this vicinity could alter the cluster membership of *G. ventalina* from Puerto Rico, as it did for *A. palmata*. Despite the population break, there was evidence of significant admixture among *A. palmata* populations across the Mona Passage (Baums *et al.* 2006), indicating that this barrier is not impermeable. Hence, it is possible that *G. ventalina* is capable of dispersing across the Mona Passage, and the biogeographic break for *G. ventalina* truly does occur somewhere farther to the east. This issue will be resolved by future studies that increase the spatial resolution of sampling in this region.

The Florida Keys were united by the dominance of a single cluster uncommon throughout the rest of the range (Fig. 2—Orange Cluster), yet there was substantial admixture apparent with the Bahamas (Fig. 2—Red & Blue Clusters). The shared cluster membership between the Florida Keys and the Bahamas is notable, given that these regions are separated by the strong Florida Current, which has been identified as a barrier to gene flow for other coral species (Vollmer & Palumbi 2007; Baums *et al.* 2010) and for *Symbiodinium* hosted by *G. ventalina* (Andras *et al.* 2011). In the western Caribbean, localities from Panama and the Mesoamerican Barrier Reef were dominated by two clusters that rarely occurred elsewhere (Fig. 2—Brown & Green Clusters). The apparent admixture throughout this region is consistent with a high potential for larval dispersal among localities via the rapid boundary currents and seasonally variable eddies that occur in the western Caribbean (Andrade & Barton 2000; Cowen *et al.* 2003; Richardson 2005).

Based on spatial autocorrelation (Fig. 4), the limit of positive genetic structure for *G. ventalina* occurs around 1000 km. This distance represents the point at which genetic drift overwhelms the signature of gene flow, and it is based on the integrated signal of direct dispersal as well as stepping-stone dispersal over multiple generations. The actual dispersal distance of *G. ventalina* larvae is certainly much smaller. Although our sampling scheme was too coarse to allow a specific estimate of the dispersal neighbourhood based on spatial autocorrelation, it appears to be <2 km—the smallest scale of spatial resolution possible with the present data set. The density-dependant dispersal neighbourhood, estimated from the slope of the IBD correlation, is just 212 individuals, many times smaller than the number of *G. ventalina* colonies encountered on a typical patch reef. Rates of recent migration (i.e. over the previous two generations), as estimated by BAYEASS, were not significantly different from zero between most localities, and the few instances of significant migration occurred between localities within the same region, <165 km apart (Table 3). These independent estimates of migration indicate that dispersal is spatially limited and may commonly not extend beyond the reef of origin. These results do not contradict the results of Bayesian clustering, which illustrate patterns of admixture across

broader regional populations, as even low rates of migration are sufficient to generate a signal of admixture (Slatkin 1987). However, low migration rates are typically of little consequence for the demography of populations. Together, our estimates of dispersal and population structure indicate that, although regional populations of *G. ventalina* are evolutionarily coupled via gene flow, they are likely to be demographically and, hence, ecologically independent.

Isolation by distance and seascape genetics of G. ventalina

Genetic differentiation of *G. ventalina* was positively correlated with geographic distance throughout the range (Fig. 3A). A similar pattern has been observed across the Caribbean basin for at least two species of reef fish with pelagic larvae (Purcell *et al.* 2006; Puebla *et al.* 2009), as well as the *Symbiodinium* hosted by *G. ventalina* (Andras *et al.* 2011). This range-wide pattern of IBD is noteworthy, given that this pattern was not observed in numerous other large-scale population genetic surveys of Caribbean species, including several broadcast-spawning corals (Baums *et al.* 2005, 2010; Severance & Karl 2006; Nunes *et al.* 2009), a sponge (Lopez-Legentil & Pawlik 2009) and several fish (Purcell *et al.* 2006, 2009).

Seascape genetic models use empirical estimates of the composition and configuration of oceanographic features (e.g. currents, barriers, gradients, etc.) to elucidate spatial patterns of genetic differentiation. These models have recently been used to successfully explain the population structure of a number of marine species, including corals (Galindo *et al.* 2006), barnacles (Galindo *et al.* 2010), whelks (White *et al.* 2010), lobster and fish (Selkoe *et al.* 2010). Here, we compare the population genetic structure of *G. ventalina* to an oceanographic model of dispersal that was previously shown to predict many features of the population structure of the staghorn coral, *Acropora cervicornis*, across the Caribbean (Galindo *et al.* 2006). Genetic differentiation of *G. ventalina* was negatively correlated with dispersal probability in all seasons, with summer dispersal (Fig. 3B, $R^2 = 0.161$) explaining a greater portion of variation than winter or spring dispersal ($R^2 = 0.112$ and $R^2 = 0.136$, respectively). These results are consistent with observations that *G. ventalina* colonies can be reproductively competent throughout the year, but the highest proportion of colonies with eggs or sperm occurs in late spring/early summer (Fitzsimmons-Sosa *et al.* 2004). Interestingly, dispersal probabilities did not explain the genetic structure of *G. ventalina* much better than the simple IBD model. However, partial Mantel tests indicate these two models each independently explain significant variation in genetic differentiation, demonstrating that both geographic distance and ocean currents play an important role in determining the population structure of *G. ventalina*.

It is noteworthy that the correlation between genetic differentiation and dispersal probability is reduced considerably in certain subsets of the data. Namely, localities in Panama and the Bahamas tend to have lower F_{ST} values than dispersal estimates would predict (Fig. 3B). The connectivity estimates employed here reflect the probability of direct dispersal between localities in a single generation, while genetic structure is the result of integrated gene flow across multiple generations and intermediate locations. It is possible that the deviation of localities such as the Bahamas and Panama might be improved if multigenerational dispersal was incorporated into the oceanographic model, especially given the fact that these regions appear to have relatively high levels of admixture with other nearby regions (Fig. 2). For example, genetic structure of the subtidal whelk *Kelletia kelletii* in the Santa Barbara Channel was better explained by models incorporating migration over multiple generations compared to single generation dispersal (White *et al.* 2010). Future models of dispersal in the Caribbean might be improved by considering such stepping-stone migration.

Genetic diversity of G. ventalina populations

Gene diversity varied by as much as 17% throughout the range (Table 1, $H_E = 0.58–0.73$) and was positively correlated with latitude (Fig. S1, Supporting Information). One striking feature of this trend is the relatively high diversity of Bermuda. The combination of isolation, extreme environmental conditions and genetic drift associated with low population densities is expected to result in reduced genetic diversity at the edges of species ranges (Hoffmann & Blows 1994). Moreover, sea temperature variability is much greater in Bermuda than the Caribbean Basin (Sheppard & Rioja-Nieto 2005) and routinely approaches the lower tolerance limit of tropical corals (~18 °C). However, substantial immigration can maintain high diversity in peripheral populations (Lesica & Allendorf 1995). Based on the dominant ocean current patterns discussed above, Bermuda is the farthest 'downstream' region in the range and may therefore act as a sink for genetic diversity. In agreement with a source/sink dynamic driven by prevailing current patterns, Tobago and Barbados, the farthest 'upstream' localities at the eastern limit of the species range, had among the lowest values of gene diversity and allelic richness observed (Table 1; Fig. S1, Supporting Information).

Within localities, inbreeding coefficients were low, and most were not significantly different from zero, indicating that most localities were at or near Hardy–Weinberg equilibrium. These results stand in contrast to many other species of broadcast-spawning marine invertebrates that exhibit significant heterozygote deficits (Addison & Hart 2005) and indicate that gene pools are well mixed at the level of the locality.

The probability of identity over all seven loci was quite low, and there were no duplicate multilocus genotypes observed throughout the entire data set, indicating that sexual outcrossing is the predominant, if not exclusive, mode of reproduction for *G. ventalina*. This pattern differs from numerous other coral species for which clonal reproduction and/or self-fertilization are common (Highsmith 1982; Heyward & Babcock 1986; Fautin 2002). Most reported asexual reproduction in corals occurs via disturbance-mediated fragmentation of brittle adult colonies. Given that *G. ventalina* colonies are flexible and not easily broken, the absence of clones is perhaps not surprising. Moreover, as *G. ventalina* is dioecious (Petes *et al.* 2003; Fitzsimmons-Sosa *et al.* 2004), self-fertilization is not possible. Asexual reproduction can also occur via budding, fission and the release of clonal planulae (Simpson 2009), and our results indicate that none of these mechanisms are likely for *G. ventalina*. The high genotypic diversity resulting from sexual recombination may provide greater adaptive potential and resilience in the face of selective pressures such as disease. However, sexual species will be more susceptible than clonal species to density-dependent phenomena such as the Allee effect (Allee 1949) and may recover from disturbance more slowly.

Comparative population structure of G. ventalina and its Symbiodinium

The population genetic structure of *Symbiodinium* B1/184 associated with *G. ventalina* has been previously described based on the same tissue samples used in this study (Andras *et al.* 2011), and there are several features common to both symbiotic partners. Both exhibit a positive correlation between geographic and genetic distance, and the maximum extent of spatial structure is similar for both (900–1000 km). More over, pairwise estimates of F_{ST} among localities are strongly correlated between *G. ventalina* and its *Symbiodinium* (Fig. 5), and some patterns of inter-regional connectivity are common to host and symbiont. For example, both *G. ventalina* and *Symbiodinium* showed little connectivity between the Mesoamerican Barrier Reef and the Florida Keys, suggesting that the Yucatan Channel may represent an important divide between the Caribbean Basin and localities further downstream. Additionally, populations of both symbiotic partners are strongly differentiated between the Windward Islands and Puerto Rico.

Despite these similarities, the population structures of *G. ventalina* and its algal symbiont are not completely congruent. Most significantly, the degree of population differentiation is dramatically higher for *Symbiodinium* than for *G. ventalina*. This disparity is most apparent in estimates of F_{ST}, which are, on average, more than four times higher for *Symbiodinium* than *G. ventalina* (Fig. 5; global F_{ST} of *G. ventalina* = 0.077; global F_{ST} of *Symbiodinium* = 0.315). Overall levels of gene diversity were also different between these two symbiotic partners (H_E of *G. ventalina* = 0.67, H_E of *Symbiodinium* = 0.60). Higher gene diversity results in a relative reduction in F_{ST} (Hedrick 2005), which could affect comparisons between

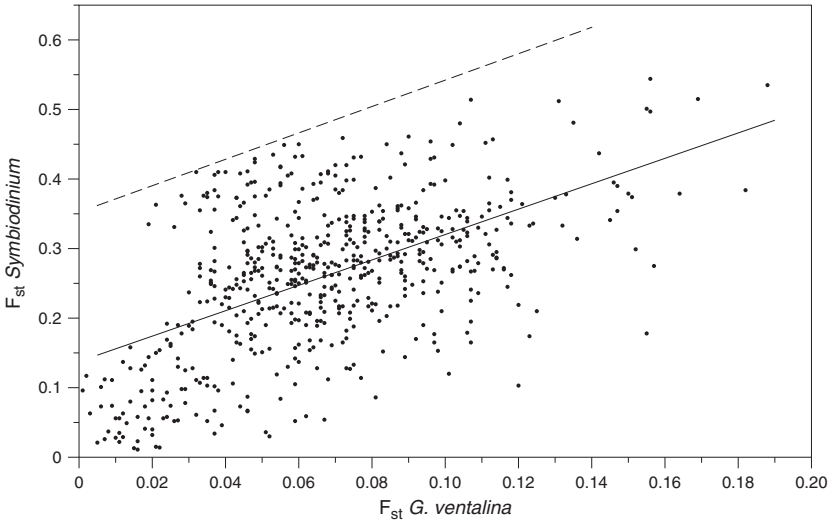

Fig. 5 Pairwise genetic differentiation of *Gorgonia ventalina* between localities versus pairwise genetic differentiation of *Symbiodinium* hosted by *G. ventalina*. Solid line represents the correlation of F_{ST} values (solid dots). Dashed line represents the correlation of Jost's *D* (points not shown). Estimates of differentiation are based on the same samples from the same localities across the Caribbean and Western Atlantic.

data sets with differing levels of diversity. To ascertain this possibility, we also compared the differentiation of *G. ventalina* and its *Symbiodinium* using Jost's *D*, a standardized measure of differentiation that controls for different levels of diversity (Jost 2008). Although the absolute values of Jost's *D* were substantially higher than F_{ST}, the slope of the correlation is nearly identical (Fig. 5), indicating that the higher degree of population structure observed for *Symbiodinium* is not an artefact of differing levels of diversity but is a genuine characteristic of these symbiotic partners.

There are also key connectivity patterns that differ between host and symbiont. For example, populations of *G. ventalina* in the Bahamas and the Florida Keys appear to be connected by substantial gene flow, whereas *Symbiodinium* populations from these two regions are among the most highly differentiated in the range. In contrast, *Symbiodinium* is connected across regions that divide populations of the host. One occurs in the southeastern Caribbean between the Windward Islands and Curacao. A second occurs in the north, between Florida and Bermuda, although some evidence suggests that this apparent connectivity may be due to founder effects among *Symbiodinium* populations in Bermuda, and not substantial ongoing gene flow (Andras *et al.* 2011). Finally, in contrast to the positive correlation between gene diversity and latitude observed for *G. ventalina*, *Symbiodinium* showed the opposite trend. The positive correlation observed for *G. ventalina* is concordant with a range-wide source/sink dynamic driven by ocean currents, whereas the negative trend of *Symbiodinium* is more consistent with a tropical centre of distribution with reduced diversity near latitudinal range limits. The contravening geographic trends of host and symbiont diversity may have complex consequences for the adaptive capacity of the intact symbiosis. Assuming individual variants of host and symbiont can freely combine, the genetic diversity of each partner will have a multiplicative effect on the diversity of the holobiont, which would be predicted to be highest in the middle of the range of *G. ventalina*.

Taken together, the similarities between the population structure of *G. ventalina* and the *Symbiodinium* it harbours suggest that ocean currents are a likely means of connectivity for both partners. In contrast, the disparities in population structure provide strong evidence that the dispersal mechanisms of host and symbiont are not coupled and that symbiont transmission occurs horizontally. These observations are consistent with a number of other aspects of the biology of these organisms. Histological evidence suggests that *G. ventalina* is a dioecious broadcast spawner (Petes *et al.* 2003; Fitzsimmons-Sosa *et al.* 2004), a reproductive mode that is correlated with aposymbiotic larvae and a long pelagic larval duration relative to species of brooding corals (Knowlton & Rohwer 2003). *Symbiodinium* are capable of active motility (Freudenthal 1962) and have been detected in the water column (Coffroth *et al.* 2006; Littman *et al.* 2008; Manning & Gates 2008; Porto *et al.* 2008), but are much more common in sediments immediately surrounding reefs (Littman *et al.* 2008). These characteristics would provide opportunities for both symbiotic partners to disperse via ocean currents, but the probability of dispersal would be greater for the host.

Conclusions

The results presented here add to the growing evidence that, despite theoretically high dispersal potential, populations of many marine species are not well mixed and show considerable structure over short distances. The specific population structure of *Gorgonia ventalina* and its *Symbiodinium* corroborate previously reported biogeographic breaks in the Caribbean (e.g. an east/west divide near Puerto Rico), and identify new breaks that warrant further study in additional taxa (e.g. a divide near the Yucatan Channel, and the isolation of Bermuda). Population subdivision has both fundamental and applied implications for the biology of a species. To the extent that subpopulations are demographically independent, their ecological and evolutionary dynamics will be uncoupled. Species with subdivided populations have greater capacity to adapt to local conditions but may be more sensitive to disturbance. The independent population structure of *G. ventalina* and its *Symbiodinium* highlights the importance of considering both symbiotic partners when designing conservation and management plans for corals. For example, an adequate management strategy for *G. ventalina* might, at a minimum, include a network of protected areas that cover the major regional populations of host and symbiont and are spaced closely enough to accommodate the small estimated dispersal neighbourhoods. Such considerations will become increasingly important as spatially explicit management plans are more broadly implemented for the protection of threatened marine taxa.

Acknowledgements

This work was funded by a National Science Foundation grant to C.D. Harvell (OCE-0326705), an NSF Graduate Research Fellowship (J.P.A.) and research grants from the Theresa Heinz Scholars for Environmental Research (J.P.A.) and the Andrew W. Mellon Foundation (J.P.A.). The authors would like to thank Richard Harrison, James Morin, Monica Geber and four anonymous reviewers for comments on this manuscript and would also like to thank David Baker, Eric Jordan Dahlgren, Guillermo Jordan Garza, Rosa Rodriguez Martinez, Jessica

Ward, Kiho Kim, Ross Jones, Alexandre Menard, Richard Parkinson, Clayton Ball and Erich Bartels for help with sample collection.

References

Addison JA, Hart MW (2005) Spawning, copulation and inbreeding coefficients in marine invertebrates. *Biology Letters*, **1**, 450–453.

Allee WC (1949) Principles of Animal Ecology. Saunders Co., Philadelphia, Pennsylvania.

Andrade CA, Barton ED (2000) Eddy development and motion in the Caribbean Sea. *Journal of Geophysical Research-Oceans*, **105**, 26191–26201.

Andras JP, Rypien KL (2009) Isolation and characterization of microsatellite loci in the Caribbean sea fan coral, *Gorgonia ventalina*. *Molecular Ecology Resources*, **9**, 1036–1038.

Andras JP, Kirk NL, Harvell CD (2011) Range-wide population genetic structure of *Symbiodinium* associated with the Caribbean Sea fan coral, *Gorgonia ventalina*. *Molecular Ecology*, **20**, 2525–2542.

Ayre DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution*, **54**, 1590–1605.

Barber PH, Palumbi SR, Erdmann MV, Moosa MK (2000) Biogeography: a marine Wallace's line? *Nature (London)*, **406**, 692–693.

Baums IB (2008) A restoration genetics guide for coral reef conservation. *Molecular Ecology*, **17**, 2796–2811.

Baums IB, Miller MW, Hellberg ME (2005) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology*, **14**, 1377–1390.

Baums IB, Paris CB, Cherubin LM (2006) A bio-oceanographic filter to larval dispersal in a reef-building coral. *Limnology and Oceanography*, **51**, 1969–1981.

Baums IB, Johnson ME, Devlin-Durante MK, Miller MW (2010) Host population genetic structure and zooxanthellae diversity of two reef-building coral species along the Florida Reef Tract and wider Caribbean. *Coral Reefs*, **29**, 835–842.

Beerli P (2004) Effect of unsampled populations on the estimation of population sizes and migration rates between sampled populations. *Molecular Ecology*, **13**, 827–836.

Bohonak AJ (1999) Dispersal, gene flow, and population structure. *The Quarterly Review of Biology*, **74**, 21–45.

Bongaerts P, Riginos C, Ridgway T *et al.* (2010) Genetic divergence across habitats in the widespread coral seriatopora hystrix and its associated *Symbiodinium*. *PLoS ONE*, **5**, e10871.

Brazeau DA, Harvell CD (1994) Genetic Structure of local populations and divergence between growth forms in a clonal invertebrate, the Caribbean octocoral *Briareum asbestinum*. *Marine Biology*, **119**, 53–60.

Burton RS, Feldman MW (1982) Population genetics of coastal and estuarine invertebrates: does larval behavior influence population structure? In: *Estuarine Comparisons* (ed. Kennedy VS), pp. 537–551. Academic Press, San Diego, California.

Clark SA, Richardson BJ (2002) Spatial analysis of genetic variation as a rapid assessment tool in the conservation management of narrow-range endemics. *Invertebrate Systematics*, **16**, 583–587.

Coffroth MA, Lewis CF, Santos SR, Weaver JL (2006) Environmental populations of symbiotic dinoflagellates in the genus *Symbiodinium* can initiate symbioses with reef cnidarians. *Current Biology*, **16**, R985–R987.

Colin PL (2003) Larvae retention: genes or oceanography? *Science*, **300**, 1657.

Couch CS, Mydlarz LD, Harvell CD, Douglas NL (2008) Variation in measures of immunocompetence of sea fan coral, *Gorgonia ventalina*, in the Florida Keys. *Marine Biology*, **155**, 281–292.

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science (Washington DC)*, **287**, 857–859.

Cowen RK, Paris CB, Olson DB, Fortuna JL (2003) The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf and Caribbean Research*, **14**, 129–137.

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science*, **311**, 522–527.

Dawson MN, Raskoff KA, Jacobs DK (1998) Field preservation of marine invertebrate tissue for DNA analyses. *Molecular Marine Biology and Biotechnology*, **7**, 145–152.

Ellegren H (2004) Microsatellites: simple sequences with complex evolution. *Nature Reviews Genetics*, **5**, 435–445.

Epperson BK (2005) Estimating dispersal from short distance spatial autocorrelation. *Heredity*, **95**, 7–15.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, **14**, 2611–2620.

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes, application to human mitochondrial DNA restriction data. *Genetics*, **131**, 479–491.

Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.

Eytan RI, Hellberg ME (2010) Nuclear and mitochondrial sequence data reveal and conceal different demographic histories and population genetic processes in Caribbean reef fishes. *Evolution*, **64**, 3380–3397.

Fautin DG (2002) Reproduction of Cnidaria. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **80**, 1735–1754.

Fitzsimmons-Sosa K, Hallock P, Wheaton J, Hackett KE, Callahan MK (2004) Annual cycles of gonadal development of six common Gorgonians from Biscayne National Park, Florida, USA. *Caribbean Journal of Science*, **40**, 144–150.

Freudenthal H (1962) *Symbiodinium* gen. nov. and *Symbiodinium microadriaticum* sp. nov, a zooxanthella: taxonomy, life cycle, and morphology. *Journal of Protozoology*, **9**, 45–52.

Galindo HM, Olson DB, Palumbi SR (2006) Seascape genetics: a coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology*, **16**, 1622–1626.

Galindo HM, Pfeiffer-Herbert AS, McManus MA, Chao Y, Chai F, Palumbi SR (2010) Seascape genetics along a steep cline: using genetic patterns to test predictions of marine larval dispersal. *Molecular Ecology*, **19**, 3692–3707.

Gutierrez-Rodriguez C, Lasker HR (2004) Microsatellite variation reveals high levels of genetic variability and population structure in the gorgonian coral *Pseudopterogorgia elisabethae* across the Bahamas. *Molecular Ecology*, **13**, 2211–2221.

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: *Ecosystems of the World: Coral Reefs* (ed Dubinsky Z), pp. 133–207. Elsevier Publishers, Amsterdam, The Netherlands.

Harvell CD, Mitchell CE, Ward JR, *et al.* (2002) Ecology—Climate warming and disease risks for terrestrial and marine biota. *Science*, **296**, 2158–2162.

Hedgecock D (1986) Is gene flow from pelagic larval dispersal important in the adaptation and evolution of marine invertebrates? *Bulletin of Marine Science*, **39**, 550–564.

Hedrick PW (2005) A standardized genetic differentiation measure. *Evolution*, **59**, 1633–1638.

Hellberg ME (1996) Dependence of gene flow on geographic distance in two solitary corals with different larval dispersal capabilities. *Evolution*, **50**, 1167–1175.

Hellberg ME, Burton RS, Neigel JE, Palumbi SR (2002) Genetic assessment of connectivity among marine populations. *Bulletin of Marine Science*, **70**, 273–290.

Heyward AJ, Babcock RC (1986) Self-fertilization and cross-fertilization in scleractinian corals. *Marine Biology*, **90**, 191–195.

Highsmith RC (1982) Reproduction by fragmentation in corals. *Marine Ecology Progress Series*, **7**, 207–226.

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Hoffmann AA, Blows MW (1994) Species borders—ecological and evolutionary perspectives. *Trends in Ecology & Evolution*, **9**, 223–227.

Jackson JBC, Kirby MX, Berger WH *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science (Washington DC)*, **293**, 629–638.

Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics (Oxford)*, **23**, 1801–1806.

Jolles AE, Sullivan P, Alker AP, Harvell CD (2002) Disease transmission of aspergillosis in sea fans: inferring process from spatial pattern. *Ecology*, **83**, 2373–2378.

Jost L (2008) G(ST) and its relatives do not measure differentiation. *Molecular Ecology*, **17**, 4015–4026.

Joyce TM, Hernandez-Guerra A, Smethie WM (2001) Zonal circulation in the NW Atlantic and Caribbean from a meridional World Ocean Circulation Experiment hydrographic section at 66 degrees W. *Journal of Geophysical Research-Oceans*, **106**, 22095–22113.

Kalinowski ST (2011) The computer program STRUCTURE does not reliably identify the main genetic clusters within species: simulations and implications for human population structure. *Heredity*, **106**, 625–632.

Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecology Letters*, **7**, 1225–1241.

Kelleher G, Bleakley C, Wells S (1995) A Global Representative System of Marine Protected Areas. Great Barrier Reef Marine Park Authority, The World Bank, Washington, District of Columbia, and IUCN, Gland, Switzerland.

Kim K, Harvell CD (2004) The rise and fall of a six-year coral-fungal epizootic. *The American Naturalist*, **164**, S52–S63.

Kim K, Alker AP, Shuster K, Quirolo C, Harvell CD (2006) Longitudinal study of aspergillosis in sea fan corals. *Diseases of Aquatic Organisms*, **69**, 95–99.

Kimura M, Crow JF (1964) The number of alleles that can be maintained in a finite population. *Genetics*, **49**, 725–738.

Knowlton N, Rohwer F (2003) Multispecies microbial mutualisms on coral reefs: the host as a habitat. *The American Naturalist*, **162**, S51–S62.

Ledoux JB, Garrabou J, Bianchimani O, Drap P, Féral JP, Aurelle D (2010a) Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum*. *Molecular Ecology*, **19**, 4204–4216.

Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? *Conservation Biology*, **9**, 753–760.

Lessios HA, Kessing BD, Pearse JS (2001) Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, **55**, 955–975.

Littman RA, van Oppen MJH, Willis BL (2008) Methods for sampling free-living *Symbiodinium* (zooxanthellae) and their distribution and abundance at Lizard Island (Great Barrier Reef). *Journal of Experimental Marine Biology and Ecology*, **364**, 48–53.

Lopez-Legentil S, Pawlik JR (2009) Genetic structure of the Caribbean giant barrel sponge *Xestospongia muta* using the I3–M11 partition of COI. *Coral Reefs*, **28**, 157–165.

Manning MM, Gates RD (2008) Diversity in populations of free-living *Symbiodinium* from a Caribbean and Pacific reef. *Limnology and Oceanography*, **53**, 1853–1861.

Mantel N (1967) The detection of disease clustering and generalized regression approach. *Cancer Research*, **27**, 209–220.

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, **19**, 400–417.

Meirmans PG, van Tienderen PH (2004) GENOTYPE and GENODIVE: two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes*, **4**, 792–794.

Miller KJ, Ayre DJ (2008a) Population structure is not a simple function of reproductive mode and larval type: insights from tropical corals. *Journal of Animal Ecology*, **77**, 713–724.

Miller KJ, Ayre DJ (2008b) Protection of genetic diversity and maintenance of connectivity among reef corals within marine protected areas. *Conservation Biology*, **22**, 1245–1254.

Mokhtar-Jamai K, Pascual M, Ledoux JB *et al.* (2011) From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: the interplay between oceanographic conditions and limited larval dispersal. *Molecular Ecology*, **20**, 3291–3305.

Muscatine L, Porter JW (1977) Reef corals, mutualistic symbioses adapted to nutrient-poor environments. *BioScience*, **27**, 454–460.

Neethling M, Matthee CA, Bowie RCK, von der Heyden S (2008) Evidence for panmixia despite barriers to gene flow in the southern African endemic, *Caffrogobius caffer* (Teleostei: Gobiidae). *Bmc Evolutionary Biology*, **8**, 325.

Nei M (1987) Molecular Evolutionary Genetics. Columbia University Press, New York.

Nishikawa A, Katoh M, Sakai K (2003) Larval settlement rates and gene flow of broadcast-spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. *Marine Ecology Progress Series*, **256**, 87–97.

Nunes F, Norris RD, Knowlton N (2009) Implications of isolation and low genetic diversity in peripheral populations of an amphi-Atlantic coral. *Molecular Ecology*, **18**, 4283–4297.

Ohta T, Kimura M (1973) A model of mutation appropriate to estimate the number of electrophoretically detectable alleles in a finite population. *Genetical Research*, **22**, 201–204.

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications*, **13**, S146–S158.

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, **6**, 288–295.

Peakall R, Smouse PE, Huff DR (1995) Evolutionary implications of allozyme and RAPD variation in diploid populations of dioecious buffalograss *Buchloe dactyloides*. *Molecular Ecology*, **4**, 135–147.

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution*, **57**, 1182–1195.

Petes LE, Harvell CD, Peters EC, Webb MAH, Mullen KM (2003) Pathogens compromise reproduction and induce melanization in Caribbean sea fans. *Marine Ecology Progress Series*, **264**, 167–171.

Porto I, Granados C, Restrepo JC, Sanchez JA (2008) Macroalgal-associated dinoflagellates belonging to the genus *Symbiodinium* in Caribbean reefs. *PLoS ONE*, **3**, e2160.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Pritchard JK, Wen X, Falush D (2010) Documentation for STRUCTURE Software: Version 2.3 http://pritch.bsd.uchicago.edu/structure.html.

Puebla O, Bermingham E, Guichard F (2009) Estimating dispersal from genetic isolation by distance in a coral reef fish (*Hypoplectrus puella*). *Ecology*, **90**, 3087–3098.

Purcell JFH, Cowen RK, Hughes CR, Williams DA (2006) Weak genetic structure indicates strong dispersal limits: a tale of two coral reef fish. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **273**, 1483–1490.

Purcell JFH, Cowen RK, Hughes CR, Williams DA (2009) Population structure in a common Caribbean coral-reef fish: implications for larval dispersal and early life-history traits. *Journal of Fish Biology*, **74**, 403–417.

Quesada H, Zapata C, Alvarez G (1995) A multilocus allozyme discontinuity in the mussel *Mytilus galloprovincialis*: the interaction of ecological and life-history factors. *Marine Ecology Progress Series*, **116**, 99–115.

Richardson PL (2005) Caribbean Current and eddies as observed by surface drifters. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **52**, 429–463.

Rousset F (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

Selkoe KA, Watson JR, White C, *et al.* (2010) Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology*, **19**, 3708–3726.

Severance EG, Karl SA (2006) Contrasting population genetic structures of sympatric, mass-spawning Caribbean corals. *Marine Biology*, **150**, 57–68.

Sheppard C, Rioja-Nieto R (2005) Sea surface temperature 1871–2099 in 38 cells in the Caribbean region. *Marine Environmental Research*, **60**, 389–396.

Shulman MJ, Bermingham E (1995) Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution*, **49**, 897–910.

Simpson A (2009) Reproduction in Octocorals (Subclass Octocorallia): a review of published literature. Version 16 July 2009 In Deep-Sea Corals Portal, http://www.ucs.louisiana.edu/~scf4101/Bambooweb/

Slatkin M (1987) Gene flow and the geographic structure of natural-populations. *Science*, **236**, 787–792.

Slatkin M (1995) A measure of population subdivision based on microsatellite allele frequencies. *Genetics*, **139**, 457–462.

Smouse PE, Long JC, Sokal RR (1986) Multiple-regression and correlation extensions of the mantel test of matrix correspondence. *Systematic Zoology*, **35**, 627–632.

Taylor MS, Hellberg ME (2003a) Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science (Washington DC)*, **299**, 107–109.

Taylor MS, Hellberg ME (2003b) Response. *Science (Washington DC)*, **300**, 1657–1658.

Taylor MS, Hellberg ME (2006) Comparative phylogeography in a genus of coral reef fishes: biogeographic and genetic concordance in the Caribbean. *Molecular Ecology*, **15**, 695–707.

Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2009) Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecological Applications*, **19**, 18–29.

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, **4**, 535–538.

Van Oppen MJH, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. *Molecular Ecology*, **15**, 3863–3883.

Vollmer SV, Palumbi SR (2007) Restricted gene flow in the Caribbean staghorn coral Acropora cervicomis: implications for the recovery of endangered reefs. *Journal of Heredity*, **98**, 40–50.

Warner RR, Palumbi SR (2003) Larvae retention: genes or oceanography? Response. *Science*, **300**, 1658.

Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ (2010) Ocean currents help explain population genetic structure. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **277**, 1685–1694.

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, **163**, 1177–1191.

This research represents part of J.P.A.'s PhD dissertation on the population structure of the Caribbean sea fan coral, *Gorgonia ventalina*. J.P.A. is currently a postdoctoral research associate in the laboratory of Dr. Dieter Ebert at the Universität Basel, Switzerland, where his research focuses on the biogeography and functional genomics of the *Daphnia magna*/*Pasteuria ramosa* pathosystem. The research presented here was conducted in the laboratory of C.D.H., which studies the ecology of coral communities, with a focus on species impacted by infectious disease. K.L.R. was a PhD student in the laboratory of C.D.H., and her research focuses on the ecology and evolution of interactions between microorganisms and their invertebrate hosts.

Data accessibility

Microsatellite genotype data, geographic distance matrix and average annual dispersal probability matrix available via DRYAD; doi:10.5061/dryad.c8m2k.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Geographic distribution of genetic diversity among *Gorgonia ventalina* populations.

Fig. S2 Mean ± standard deviation of the estimated posterior probability [ln $P(D)$] of the data for each value of K (1–35) tested with Structure.

Table S1 Number of alleles (Na); observed and expected heterozygosity (H_O, H_E); inbreeding coefficient (F_{IS}), probability of identity (PI); and significance fest for null alleles (Null) for each of the 7 loci at each of the 35 locations used in this study.

Table S2 Pairwise F_{ST} values (below diagonal) and R_{ST} values (above diagonal) for all loci. Site codes are given in Table 1. Nonsignificant values are shaded grey.