Journal of Biogeography (J. Biogeogr.) (2016) 43, 510–519

ORIGINAL ARTICLE

Population genetic structure of the stony coral *Acropora tenuis* shows high but variable connectivity in East Africa

Rosa M. van der Ven[1]*, Ludwig Triest[2], Dennis J. R. De Ryck[2], Jelvas M. Mwaura[3], Mohammed S. Mohammed[4] and Marc Kochzius[1]

[1]Marine Biology, Vrije Universiteit Brussel (VUB), 1050 Brussels, Belgium, [2]Laboratory of Plant Biology and Nature Management, Vrije Universiteit Brussel (VUB), 1050 Brussels, Belgium, [3]Kenya Marine and Fisheries Research Institute, Mombasa, Kenya, [4]Department of Natural Science, The State University of Zanzibar, Zanzibar, Tanzania

*Correspondence: Rosa M. van der Ven, Marine Biology, Vrije Universiteit Brussel (VUB), Pleinlaan 2, 1050 Brussels, Belgium. E-mail: rosa.vanderven@gmail.com

ABSTRACT

Aim The aim of this study is to determine the genetic diversity, population structure and connectivity of the broadcast-spawning coral *Acropora tenuis* (Cnidaria; Scleractinia; Acroporidae). Based on the long pelagic larval duration (PLD) of the species, long-distance dispersal resulting in high connectivity among populations is hypothesized.

Location East Africa (Kenya and Tanzania; 2.5°S ~ 10°S)

Methods A total of 269 samples were collected from 11 sample sites in Kenya and Tanzania spanning a distance of 900 km. The coral fragments were genotyped using seven microsatellite markers. Analyses included population genetic estimations of diversity and population differentiation, principal coordinate analysis (PCoA), Bayesian clustering approaches and testing for isolation by distance (IBD).

Results Moderate, but significant, genetic structure was found when comparing all sample sites, but IBD could not be detected. Based on Bayesian cluster analyses three groups of samples sites could be identified: (1) Kenya and northern Tanzania, (2) southern Tanzania and (3) sample sites located in the Zanzibar and Pemba channels.

Main conclusions High connectivity can be explained by the long-distance dispersal capacity of *A. tenuis* and by the influence of the northbound East African Coastal Current facilitating dispersal by effectively spreading larvae along the coast. Oceanographic characteristics rather than distance are factors that determine connectivity among populations of *A. tenuis* in Kenya and Tanzania. No clear genetic break was identified. However, variable connectivity between sample sites does occur, with limited connectivity of the sample sites Misali and Stonetown.

Keywords
acroporids, coral reef, dispersal, genetic structure, pelagic larval duration, population genetics, Western Indian Ocean

INTRODUCTION

Scleractinian corals are important ecosystem engineers, which form the foundation of one of the most productive and diverse marine ecosystems (Wilkinson, 2008). Coral reefs provide ecosystem goods and services such as fisheries and tourism to many coastal communities (Moberg & Folke, 1999). However, coral reefs are declining at an alarming rate, owing primarily to local disturbances (e.g. overexploitation, diseases, pollution and sedimentation), as well as global scale losses through increasing sea surface temperatures and ocean acidification (Pandolfi *et al.*, 2003; Bellwood *et al.*, 2004; Harvell *et al.*, 2004; Hoegh-Guldberg *et al.*, 2007; Wilkinson, 2008; Kleypas & Yates, 2009). Coral bleaching during the 1998 El Niño Southern Oscillation (ENSO) resulted in reduced coral cover in Kenya and Tanzania, from initial 38% in 1997, to 16% in 1999 (Ateweberhan *et al.*, 2011). Coral cover loss differed regionally, with substantial loss in Kenyan reefs, such as Watamu (decline from 37.7 to 9.0%) and Mombasa (decline from 42.0 to 18.8%) and in the Tanzanian reefs, such as Misali (from 53.7 to 12.3%), Mafia (from 73.3 to 19.4%) and Mnazi Bay (from 60.0 to 20.0%), although

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/jbi.12643

Journal of Biogeography

some sites seemed less effected as observed in Bawe (Zanzibar; decline from 53 to 45%) (Wilkinson, 2002; McClanahan *et al.*, 2007b). Immediately after the bleaching event the coral reefs showed signs of recovery and had returned back to 22% coral cover in Kenya and Tanzania in 2005 (Ateweberhan *et al.*, 2011). However, recovery seems to have slowed down, and especially acroporids remain at low abundances compared to the rest of the Western Indian Ocean (WIO) (McClanahan *et al.*, 2014).

Coral reef conservation is essential and marine protected area (MPA) networks are advocated world-wide to increase reef resilience (Bellwood *et al.*, 2004). However, to design and manage them, information on the scale of connectivity is important (Almany *et al.*, 2009). Connectivity between reefs determines gene flow, genetic diversity and genetic structure of populations, as well as the ability of coral reefs to persist and recover from current stressors, and to adapt to future climate change (Palumbi, 2003). Connec-

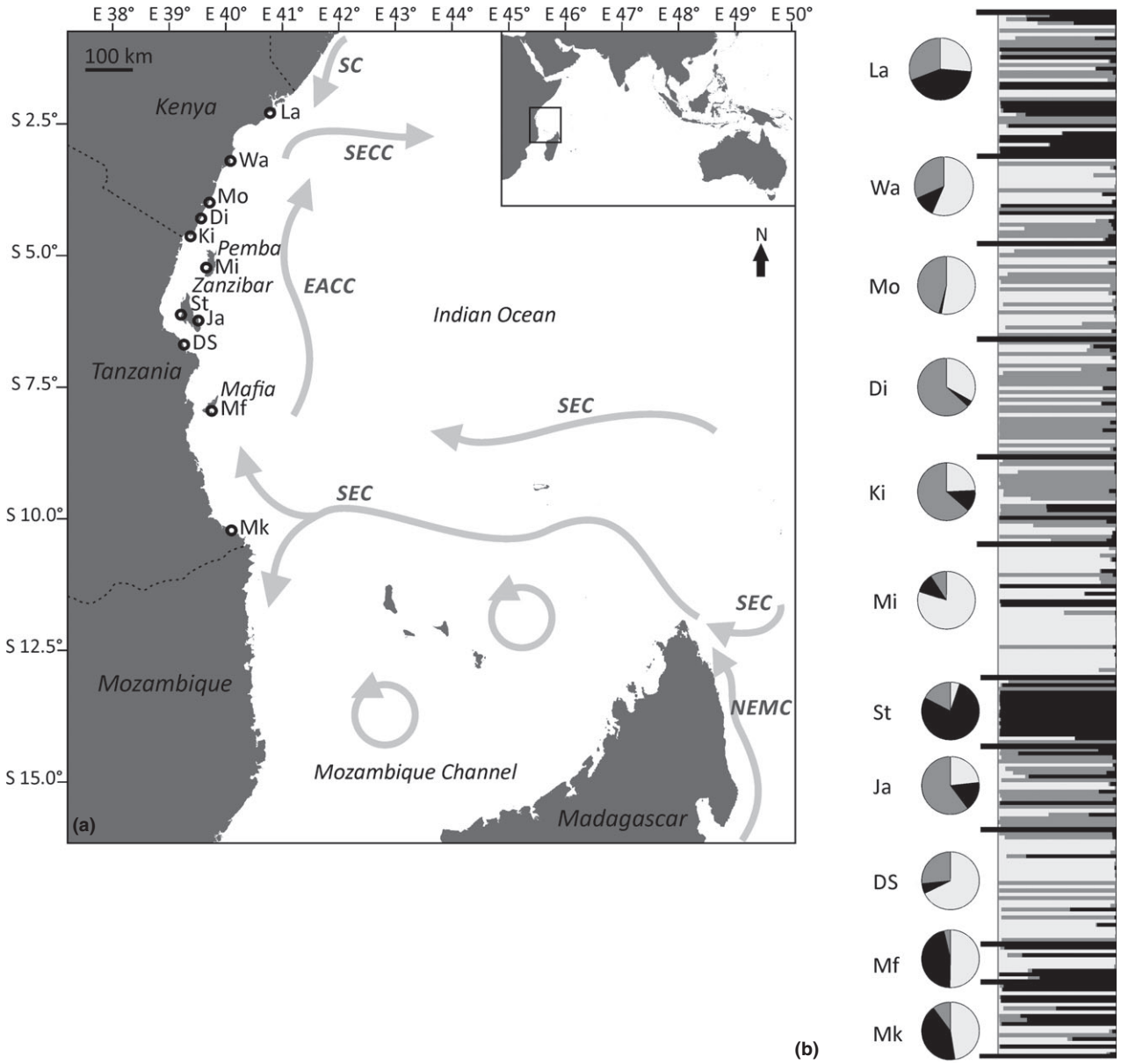

Figure 1 (a) Map of the East African coast (Kenya and Tanzania) showing sample sites of *Acropora tenuis*. Major ocean currents are indicated schematically (Schott & McCreary, 2001; Lutjeharms & Bornman, 2010; Hancke *et al.*, 2014). SEC: South Equatorial Current; NEMC: the Northeast Madagascar Current; EACC: East African Coastal Current; SECC: the South Equatorial Countercurrent; SC: Somali Current; for sample site codes see Table 1; (b) The pie charts show the distribution of three genetic clusters ($K = 3$) at sample sites as revealed in the Bayesian clustering implemented in STRUCTURE 2.3.4 (Pritchard *et al.*, 2000). The bar plot visualizes the individual's estimated membership fraction in each of the clusters, with each horizontal bar representing one individual.

Table 1 Genetic diversity in *Acropora tenuis* from East Africa.

Sample site	Site code	n	A_r	H_O	uH_E	F_{IS}	PVA
Lamu	La	37	5.9	0.364 ± 0.062	0.787 ± 0.014	0.540*	5
Watamu	Wa	22	5.6	0.329 ± 0.044	0.758 ± 0.027	0.572*	0
Mombasa	Mo	30	5.3	0.308 ± 0.059	0.735 ± 0.038	0.585*	2
Diani	Di	24	5.1	0.329 ± 0.033	0.722 ± 0.036	0.550*	2
Kisite	Ki	22	5.6	0.345 ± 0.053	0.728 ± 0.040	0.531*	5
Misali	Mi	34	4.8	0.352 ± 0.057	0.627 ± 0.050	0.443*	2
Stonetown	St	17	5.0	0.460 ± 0.050	0.664 ± 0.045	0.314*	2
Jambiani	Ja	21	6.1	0.388 ± 0.072	0.789 ± 0.029	0.515*	6
Dar es Salaam	DS	29	5.0	0.325 ± 0.066	0.713 ± 0.040	0.549*	1
Mafia	Mf	9	4.7	0.286 ± 0.090	0.740 ± 0.050	0.629*	0
Mikindani	Mk	20	5.1	0.343 ± 0.074	0.721 ± 0.024	0.531*	3

n: sample size, A_r: allelic richness, H_O: observed heterozygosity (±SD), uH_E: unbiased expected heterozygosity (±SD), F_{IS}: departure from Hardy–Weinberg equilibrium, positive values indicate a deficit of heterozygotes; *$P < 0.001$, significant departure from zero is based on 77,000 randomizations, P-values have been corrected for multiple tests; PVA: private alleles. Sites are in latitudinal order. For geographical location of the sample sites see Fig. 1 and Table S1.

tivity, or the 'movement of individuals within and among local or subpopulations' (Cowen & Sponaugle, 2009), is facilitated by dispersal of larvae. Connectivity between coral populations depends on the reproductive output, pelagic larval duration (PLD) and larval behaviour, as well as habitat suitability, ocean currents and oceanographic barriers (Graham *et al.*, 2008; Cowen & Sponaugle, 2009).

Broadcast spawners with long PLD generally show lower genetic subdivision than brooders with short PLD, as PLD is positively correlated with dispersal distance (Underwood *et al.*, 2009). Direct observation of larval dispersal is difficult, especially for coral species with longer PLD that disperse over larger distances. Connectivity is therefore mainly studied by measuring indirect effects, such as gene flow and genetic structure (van Oppen & Gates, 2006).

Acropora tenuis (Dana (1846); Cnidaria; Scleractinia; Acroporidae) is a branching scleractinian coral and is common in the Indo-Pacific (Veron, 2000). Acroporids are dominant species on East African reefs, but also highly susceptible to bleaching (Marshall & Baird, 2000; Obura, 2001; McClanahan *et al.*, 2007a). Sexual reproduction in *A. tenuis* occurs in synchronized mass-spawning events when buoyant eggs and sperm are released to the water column, where fertilization takes place. The PLD determines the dispersal potential and is variable between species of acroporids. *Acropora digitifera* has a maximum PLD of 45 days (Nishikawa & Sakai, 2005), while *Acropora latistella* has a maximum PLD of 209 days (Graham *et al.*, 2008). *Acropora tenuis* larvae are viable up to 69 days after spawning in laboratory experiments (Nishikawa *et al.*, 2003). Although the larval survival can be long enough for long-distance dispersal, early mortality is often considerable and highest settlement rates are on natal or nearby reefs, resulting in genetic structure on a small spatial scale (Ayre & Hughes, 2000; Graham *et al.*, 2008; Underwood *et al.*, 2009).

The coast of East Africa has a narrow band of almost continuous coral reefs, with patchy fringing reefs along the mainland coast of Kenya and Tanzania, and more extensive reefs found around the islands of Pemba, Zanzibar and Mafia (Wilkinson, 2002). The South Equatorial Current (SEC) carries water westwards towards the southern coast of Tanzania and the northern coast of Mozambique, where it splits into complex eddies in the Mozambique Channel and the northbound East African Coastal Current (EACC) along the coast of Tanzania and Kenya (Fig. 1) (Schott & McCreary, 2001; Ridderinkhof *et al.*, 2010; Hancke *et al.*, 2014).

In the North of Kenya the EACC converges during the northeast monsoon with the southward Somali Current (SC) forming the eastward South Equatorial Countercurrent (SECC) (Schott & McCreary, 2001). The largest coral species diversity is found in the northern Mozambique Channel (NMC), potentially because of genetic material transported by the SEC and subsequent recirculation by eddies in the channel (Obura, 2012).

The overall aim of this study is to investigate the genetic diversity, population structure, and connectivity of the stony coral *A. tenuis* along the coast of Kenya and Tanzania. Based on the long larval duration of the species, long-distance dispersal resulting in high connectivity among populations can be hypothesized. In addition, this study investigated whether bleaching events left signs of a genetic bottleneck.

MATERIAL AND METHODS

Coral sampling

A total of 269 individual *A. tenuis* colonies were sampled at five locations in Kenya and six locations in Tanzania (Fig. 1; Table 1). Fragments were collected between 3–15 m depth using scuba. Colonies were randomly selected while maintaining at least two metres between colonies to avoid sampling clones. Each sample was obtained by breaking a 1–2 cm fragment from a branch. The fragments were stored in a plastic container with sea water until fixation in absolute ethanol. Samples were stored in the dark at 7 °C until extraction.

Table 2 Characteristics of the used microsatellite loci for the analysis of *Acropora tenuis*.

Locus name	Primer sequence (5′–3′)	Repeat motif	Genbank accession number	Fluorescent label	Product size (bp)
Amil2_006[1]	F-CTTGACCTAAAAAACTGTCGTACAA R-GTTATTACTAAAAAGGACGAGAGAATAACTTT	(CA)4TA(CA)4	EF014481	6-FAM	86–108
Amil2_010[1]	F-CAGCGATTAATATTTTAGAACAGTTTT R-CGTATAAACAAATTCCATGGTCTG	TA(TG)11	EF014484	VIC	142–172
Amil2_011[2]	F-CACTCCTTACGCTGCTAGAT R-CTCGCTAAAATGAGAGACCA	(CA)2GA(CA)6CT	EF989162	6-FAM	146–177
Amil2_012[1]	F-TTTTAAAATGTGAAATGCATATGACA R-TCACCTGGGTCCCATTTCT	GA(CA)6GA(CA)2	EF014485	VIC	91–105
Amil2_018[2]	F-GCCCTCCTTAGGTGATTTAC R-ATCGTTTTGAGCAATCAGAC	(CA)9	EF989161	VIC	348–384
Amil2_022[1]	F-CTGTGGCCTTGTTAGATAGC R-AGATTTGTGTTGTCCTGCTT	(AC)10	EF014486	NED	138–182
Amil5_028[1]	F-GGTCGAAAAATTGAAAAGTG R-ATCACGAGTCCTTTTGACTG	(TCACA)7TCAC(TCACA)4	EF014488	PET	132–197

[1]van Oppen *et al.* (2007); [2]Underwood *et al.* (2009) Product size (bp): Product sizes found in this study.

DNA extraction and microsatellite genotyping

The fragments, both skeleton and tissue together, were crushed manually with a bone cutter and incubated overnight at 56 °C with lysis buffer and Proteinase K. The NucleoSpin® Tissue DNA extraction kit (Macherey-Nagel, Düren, Germany) was used following the company's animal tissue protocol for 100 µL DNA extract. Samples were genotyped using seven microsatellite primer pairs designed for *Acropora millepora* (Table 2), but cross-amplifications showed that they can be applied to *A. tenuis* from the Great Barrier Reef (GBR) (Underwood *et al.*, 2009) and several other acroporid species from the Pacific Ocean (Richards & van Oppen, 2012). The primers were combined in one multiplex (PCR) with a volume of 12.5 µL containing 2.5 µL template DNA, 1.25 µL (2 µM) primer mix with fluorescently labelled primers 6-FAM, VIC, PET and NED (Applied Biosystems, Foster City, CA, USA), 2.5 µL H_2O and 6.25 µL QIAGEN Multiplex PCR Master Mix (QIAGEN, Hilden, Germany). The PCR cycling parameters were: an activation step for 5 min at 95 °C, followed by 35 cycles of denaturation for 30 s at 95 °C, annealing for 90 s at 60 °C and 30 s at 72 °C. The final extension was done for 30 min at 68 °C. The PCR product was diluted 10 or 100 times and analysed together with a GeneScan™-500 LIZ® size standard (Applied Biosystems) on an ABI 3730 DNA Analyzer (Applied Biosystems). The resulting electropherograms were scored manually with GeneMarker® (2.4.0; SoftGenetics, State College, PA, USA).

Genetic diversity analysis

The software GenAlEx 6.5 (Peakall & Smouse, 2012) was used to identify multilocus genotypes (MLGs) that were likely to be the result of fragmentation of the coral colony. The departure from Hardy–Weinberg equilibrium (HWE) was determined for each locus with FSTAT 2.9.3 (Goudet, 2001) and presented as F_{IS} (calculated as smallF; Weir & Cockerham, 1984), with significance levels based on 77,000 permutations. Populations with heterozygote deficiency were further analysed with INEst 2.0 (Chybicki & Burczyk, 2009) utilizing a Bayesian approach for estimating both null alleles and inbreeding simultaneously (Campagne *et al.*, 2012). The model was run with 50,000 burn-ins and 500,000 cycles. Linkage disequilibrium (LD) was calculated with FSTAT and the *P*-value for genotypic disequilibrium was based on 210,000 permutations. Number of alleles per population, corrected for sample size and expressed as allelic richness, was also calculated with FSTAT. Observed, expected and unbiased heterozygosity (sample size corrected) were calculated with GenAlEx. Bottleneck 1.2.02 (Cornuet & Luikart, 1997) was used to check for recent bottleneck events and run under the two-phased mutation model with 12% variance, 95% stepwise mutation model and 10,000 iterations.

Population structure

To investigate population structure among populations, pairwise F_{ST}-values were estimated using the method of Weir & Cockerham (1984) (θ) with FSTAT and tested for significance with 55,000 permutations. Pairwise F_{ST}-values were utilized in a Mantel test in GenAlEx to test for linear association with geographical distances measured as the shortest distance by sea (isolation by distance, IBD). An analysis of molecular variance (AMOVA) was conducted with GenAlEx, testing population structure within and among populations, estimating overall F_{ST} as well as $F'_{ST,}$ (F_{ST} corrected by the maximum F_{ST} achievable). Significance was tested with 9999 permutations. Principal coordinates analyses (PCoA) were conducted in GenAlEx to examine the spatial variation. The software STRUCTURE 2.3.4 (Pritchard *et al.*, 2000), which uses a Bayesian clustering based on the Markov chain Monte Carlo (MCMC) assignment

method, was run without prior population information and under the admixture model to determine the number of genetic clusters (K). STRUCTURE was run for K = 1–12, using 10 runs with a burn-in length of 100,000 and 1,000,000 MCMC replications. HARVESTER 0.6.94 (Earl & Vonholdt, 2012) was used to visualize and analyse the STRUCTURE output by plotting log probability L (K) and ΔK (Evanno *et al.*, 2005). In addition, INSTRUCT was run for K = 1–12, using 10 runs with a burn-in length of 100,000 and 1,000,000 MCMC replications to infer population structure in case of inbred populations (Gao *et al.*, 2007).

RESULTS

Genotypic diversity

Four clonal MLGs were found: two clones at the sample site Mi, one at St and one at Mo, each of them twice. As these individuals most likely were the result of fragmentation, four duplicated individuals were excluded from the analysis. One MLG was found in two samples, one in La and one in Di.

Genetic diversity

All seven loci used in this study were polymorphic with 2–12 alleles (Na) per locus (see Table S2) and allelic richness (A_r) ranged between 4.7 and 6.1 (Table 1). Observed heterozygosity (H_o) was low, ranging between 0.286 and 0.460, while unbiased expected heterozygosity (uH_e) ranged between 0.627 and 0.789. All sample sites showed positive F_{IS}-values, indicating heterozygote deficits, ranging between 0.314 and 0.629, and significant departure from HWE (Table 1). A significant heterozygote deficit was observed for all seven loci within the sample sites La, Wa, Mo, Di, Ki and DS as well as for six loci in Mi, Ja, Mf, and Mk. In St, high F_{IS}-values were found for all loci, but only two were significantly different from zero (Amil2_018 and Amil2_028) (see Table S2) probably due to a smaller sample size (n = 17). Further analysis with INEst supported a model including inbreeding rather than a null allele model, most likely causing the high inbreeding coefficients in all populations (see Table S3). Significant LD was found for eight of the 21 locus pairs ($P < 0.05$) and locus Amil2_012 was involved five times. Four sample sites showed LD but in few loci (number of loci with LD in parentheses): La (1), Mo (1), DS (2) and Mk (1). None of the populations showed evidence of a recent bottleneck.

Population structure

Significant genetic structuring was found among all sample sites, with an overall F_{ST}-value of 0.057 ($P < 0.0001$) and F'_{ST}-value of 0.224. Significant differentiation was visible in 55% of the total pairwise population comparisons. Sample sites La, Ki and Mi were for 70% of the comparisons significantly differentiated from all other sites and St was significantly different in 90% of the cases from all other sites (Table 3). The highest genetic differentiation was found for the island sites of Mi and St ranging from 0.027 to 0.174 and from 0.035 to 0.174 respectively. The PCoA divided La, St, Mf and Mk from the others along the first axis, and Wa, DS and Mi along the second axis, together explaining 75.11% of the variation (Fig. 2). The Mantel test, using all populations, showed no significant correlation between population differentiation and geographical distance (IBD; $R^2 = 0.0973$, $P = 0.061$). The Bayesian clustering implemented in STRUCTURE revealed a plateau for the log probability between K = 3 and K = 6 and an optimum ΔK at K = 3, which is the likely amount of genetic clusters. All three genetic clusters were found at all sample sites; however, their prevalence differed between sites (Fig. 1b). Based on the proportion of each genetic cluster within each sample site, three groups of sample sites could be identified: (1) Kenya and northern Tanzania (La, Wa, Mo, Di, Ki and Ja), (2) southern Tanzania (Mf, Mk) and (3) sample sites located in the Zanzibar and Pemba channels (Mi, St and DS), which

Table 3 Pairwise F_{ST}-values (Weir & Cockerham, 1984; below diagonal) and level of significance (above diagonal) after 55,000 permutations in *Acropora tenuis* from Kenya and Tanzania.

	La	Wa	Mo	Di	Ki	Mi	St	Ja	DS	Mf	Mk
La		NS	*	***	**	***	*	*	***	NS	NS
Wa	0.013		NS	NS	NS	*	**	NS	NS	NS	NS
Mo	0.035	0.027		NS	*	***	***	NS	*	NS	***
Di	0.050	0.003	0.045		*	**	***	NS	*	NS	**
Ki	0.052	0.035	0.040	0.050		***	***	NS	***	NS	**
Mi	0.067	0.053	0.114	0.078	0.124		***	***	NS	NS	NS
St	0.062	0.111	0.153	0.159	0.143	0.174		**	***	NS	***
Ja	0.035	0.023	0.024	0.037	0.036	0.121	0.103		*	NS	**
DS	0.053	0.028	0.056	0.052	0.083	0.027	0.164	0.060		NS	NS
Mf	0.007	−0.008	0.084	0.051	0.062	0.061	0.035	0.044	0.045		NS
Mk	0.017	0.009	0.085	0.049	0.078	0.038	0.065	0.066	0.040	−0.025	

*Significance at the 5% nominal level; **significance at the 1% nominal level; ***significance at the 0.1% nominal level; NS: non-significant; for abbreviations of sample sites see Table 1; for geographical location of samples sites, see Fig. 1 and Table S1.

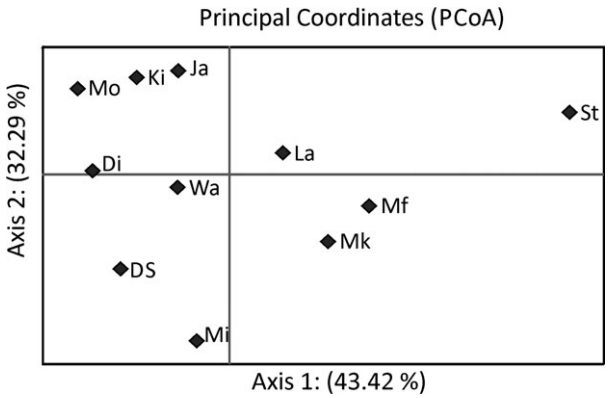

Figure 2 Principal coordinates analysis (PCoA) from the covariance matrix with data standardization using GenAlEx 6.5 (Peakall & Smouse, 2012) for *Acropora tenuis* from East Africa. The first two axes explain 75% of the variation (the first axis explains 43%, the second axis explains 32% of the variation). For sample site codes see Table 1.

display more differentiated signatures. The programme InStruct provided similar results for $K = 3$ (data not shown) as found with STRUCTURE.

DISCUSSION

The two main components of this study are the genetic diversity and structure of *A. tenuis* in Kenya and Tanzania. Key indicators of genetic diversity are the allelic richness and heterozygosity of populations. Genetic structure is determined by the scale of connectivity among populations and is dependent on oceanographic patterns and the life history of the coral species.

Heterozygote deficits and the contribution of clones

Significantly positive F_{IS} -values were observed for all sampled populations. Heterozygote deficits were comparable to other microsatellite studies of *A. tenuis* in the GBR (Underwood, 2009), as well as other scleractinian corals (Mackenzie *et al.*, 2004; Magalon *et al.*, 2005; Maier *et al.*, 2005; Severance & Karl, 2006; Underwood *et al.*, 2007; van Oppen *et al.*, 2008; Ridgway *et al.*, 2008; Souter *et al.*, 2009; Nakajima *et al.*, 2010; Starger *et al.*, 2010; Combosch & Vollmer, 2011; Adjeroud *et al.*, 2014). Such heterozygote deficits may result from several factors, such as null alleles, inbreeding, genetic patchiness at a local scale due to several differentiated cohorts (Wahlund, 1928) and (recent) admixture (van Oppen *et al.*, 2008). However, heterozygote deficits were found for all loci at all sample sites, indicating that the contribution of null alleles is very unlikely. A model including inbreeding, rather than a null allele model, was supported by INEst, indicating that inbreeding caused such high levels of heterozygote deficits. Allelic richness was high compared to *A. tenuis* from the GBR using the same markers (Underwood, 2009) and similar to other acroporids in the Pacific Ocean (Richards & van Oppen, 2012). Heterozygote deficits can be attributed to genetic patchiness caused by biological factors concerning temporal and spatial admixture for *A. tenuis* from the GBR (Underwood, 2009), whereas LD in combination with heterozygote deficits can be attributed to the recent admixture of populations (van Oppen *et al.*, 2008). The significant LD in combination with a strong signal for heterozygote deficits and high allelic richness indicates both sampling of different genetic cohorts and recent admixture of the population with recruits from differentiated sources. This is confirmed by the observation that *A. tenuis* colonies were relatively small (personal observation R.M. van der Ven) and therefore likely new settlers on the reef.

Asexual reproduction caused by coral fragmentation is common in branching acroporids (Baums *et al.*, 2006; Baums, 2008) including *A. tenuis* (Underwood, 2009) and might contribute to deviations from HWE. However, in this study no contribution was found as only five repeated MLGs were identified (2% of total samples), of which four were excluded from analysis. Colonies formed by clonal fragmentation comprise on average 10% of sampled colonies of *A. tenuis* in the GBR, where this appears to be variable per reef (Underwood, 2009). A low contribution of asexual reproduction was also found for *Acropora digitifera* in Japan, where 1% of sampled individuals was formed by clones (Nakajima *et al.*, 2010). As the sampling method in this study was designed to avoid sampling clones, the observed repeated MLGs might underestimate the total contribution of asexual reproduction in *A. tenuis*. We can, however, conclude that the genetic structure found in this study is predominantly caused by sexual recruits. Although severe bleaching events, as have occurred in 1998 in Kenya and Tanzania (Wilkinson, 2002), may lead to coral mortality and can result in a population bottleneck with subsequent loss of genetic diversity, no evidence of a recent bottleneck was detected.

Genetic structure along the East African coast

This is the first study using microsatellite markers on acroporids in East Africa, and the results are complementary to two population genetic studies on the coral species *Platygyra daedalea* and *Pocillopora damicornis* in Kenya and Tanzania (Souter & Grahn, 2008; Souter *et al.*, 2009), as well as studies on corals in South Africa and Mozambique (e.g. Ridgway *et al.*, 2008; Macdonald *et al.*, 2011).

Significant subdivision was found among coral reefs over a large geographical distance (900 km) for the spawning coral *A. tenuis*, however, no clear genetic break was identified. This is in concordance with other genetic studies in Kenya and Tanzania on mangrove crabs (Ragionieri *et al.*, 2010; Silva *et al.*, 2010, 2013; Farhadi *et al.*, 2013) and fish (Minegishi *et al.*, 2008, 2012). There was no clear relation between differentiation and increasing geographical distance, despite the linear arrangement of the sample sites. This is in contrast

with *A. tenuis* in the GBR (Underwood, 2009), where genetic differentiation is positively related with geographical distance, while lower differentiation is found for sites 1000 km apart in *Acropora digitifera* in Japan (Nakajima *et al.*, 2010). This genetic uniformity is congruent with the uniform oceanographic characteristics of this sub-region of the WIO, characterized by continuous linear flow of the EACC from south to north. The EACC potentially transports larvae from the species rich core region in the NMC up to the northern lower diversity reefs (Obura, 2012). Genetic breaks are found near the borders of this sub-region, as described for the reef-associated parrotfish *Scarus ghobban* between La and sites in Tanzania (Visram *et al.*, 2010) and for the gastropod *Cerithidea decollata* between all sites and Mk (Madeira *et al.*, 2012).

Based on the proportion of each genetic cluster within each sample site, the Bayesian cluster analyses revealed three groups of sample sites: (1) Kenya and northern Tanzania (La, Wa, Mo, Di, Ki and Ja), (2) southern of Tanzania (Mf and Mk) and (3) Pemba and Zanzibar channels (Mi, St and DS). The first group is year-round under influence of the northbound EACC (Schott & McCreary, 2001), while the second group in southern Tanzania is located in the transition of the SEC to the EACC and upstream from the sample sites in the first group. Sites in the second group bear a strong resemblance in coral species diversity with sites in the NMC (Obura, 2012). This resemblance suggests that sites in the second group may share the genetic signature of populations in the NMC region as a result of exchange of larvae between NMC and Mk and further transport of larvae from Mk to Mf. The sample sites of the third group are genetically less uniform than the two other groups. This pattern is confirmed by the Pairwise F_{ST}-values, indicating that, despite the lack of strong genetic structure over long distances, variable connectivity occurs with significant pairwise differentiation between populations, especially for the offshore sites Mi and St. A possible explanation could be that these sites in the Pemba and Zanzibar channels are subject to local oceanographic conditions that may cause larval retention. However, detailed ocean current data are not available for this area. Long-distance dispersal combined with differentiation patterns over a smaller geographical scale are comparable with earlier studies on broadcast-spawning corals (Souter & Grahn, 2008) and brooding corals (Maier *et al.*, 2005; Souter *et al.*, 2009). The pattern of isolation found in this study is comparable with the genetic structure of *Pocillopora damicornis* (Souter *et al.*, 2009), which shows high differentiation in the west of Zanzibar (St) and low differentiation in Mikindani (Mk) in comparison to their other sites.

CONCLUSION

This study confirmed that *A. tenuis*, a broadcast-spawning coral with high dispersal capacity, showed high connectivity among sites as far as 900 km apart. This can be explained by the northbound EACC aiding dispersal by effectively spreading larvae along the coast. No clear genetic break was identified, which is coherent with other connectivity studies in the WIO. The Bayesian cluster analysis suggests three groups of sample sites, one in Kenya and northern Tanzania, a second in southern Tanzania and a third in the Pemba and Zanzibar channels. The sites in the first group are under influence of the prevailing northbound EACC and dispersal is likely facilitated through this linear current. The second group is located further south, in the transition of the SEC to the EACC, where they potentially share genetic material with populations in the NMC. However, connectivity is variable and sample sites in the third group showed high differentiation, especially in Misali and Stonetown, potentially due to local oceanographic conditions causing larval retention. Oceanographic characteristics rather than distance appear to be the determining factors for connectivity among populations of *A. tenuis* in Kenya and Tanzania. The information on variable connectivity and genetic structure of this species, combined with population structure of other reef species, can be implemented in current and future management of marine ecosystems in East Africa, such as conservation measures for genetically more isolated sites (Misali and Stonetown).

ACKNOWLEDGEMENTS

We thank the institutions and foundations that have made our work possible: Fonds Wetenschappelijk Onderzoek Vlaanderen (FWO) for funding the project 'Connectivity of Coral Reefs and Mangroves in the Western Indian Ocean' (COCOMA-WIO; grant 1501612N); Vrije Universiteit Brussel (OZR2068BOF) for financial support; Vlaamse Interuniversitaire Raad Universitaire Ontwikkelingssamenwerking (VLIR-UOS) for a travel grant to R.M.V.; F. Huyghe (Vrije Universiteit Brussel) for assistance during fieldwork; the competent authorities for permits; M. Sheikh (State University of Zanzibar) for logistical support. T. Sierens (Vrije Universiteit Brussel) for assistance during laboratory work; N. van Hoytema (Leibniz Zentrum für Marine Tropenökologie, Bremen) for proofreading. Lastly, we thank the three anonymous referees for their suggestions and improvements of the manuscript.

REFERENCES

Adjeroud, M., Guerecheau, A., Vidal-Dupiol, J., Flot, J., Arnaud-Haond, S. & Bonhomme, F. (2014) Genetic diversity, clonality and connectivity in the scleractinian coral *Pocillopora damicornis*: a multi-scale analysis in an insular, fragmented reef system. *Marine Biology*, **161**, 531–541.

Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L. & Williamson, D.H. (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs*, **28**, 339–351.

Ateweberhan, M., McClanahan, T.R., Graham, N.A.J. & Sheppard, C.R.C. (2011) Episodic heterogeneous decline

and recovery of coral cover in the Indian Ocean. *Coral Reefs*, **30**, 739–752.

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

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

Baums, I.B., Miller, M.W. & Hellberg, M.E. (2006) Geographic variation in clonal structure in a reef-building Caribbean coral, *Acropora palmata*. *Ecological Monographs*, **76**, 503–519.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. (2004) Confronting the coral reef crisis. *Nature*, **429**, 827–833.

Campagne, P., Smouse, P.E., Varouchas, G., Silvain, J.F. & Leru, B. (2012) Comparing the van Oosterhout and Chybicki-Burczyk methods of estimating null allele frequencies for inbred populations. *Molecular Ecology Resources*, **12**, 975–982.

Chybicki, I.J. & Burczyk, J. (2009) Simultaneous estimation of null alleles and inbreeding coefficients. *Journal of Heredity*, **100**, 106–113.

Combosch, D.J. & Vollmer, S.V. (2011) Population genetics of an ecosystem-defining reef coral *Pocillopora damicornis* in the tropical eastern Pacific. *PLoS ONE*, **6**, e21200.

Cornuet, J.M. & Luikart, G. (1997) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics*, **144**, 2001–2014.

Cowen, R.K. & Sponaugle, S. (2009) Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, **1**, 443–466.

Earl, D.A. & Vonholdt, B.M. (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, **4**, 359–361.

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.

Farhadi, A., Farhamand, H., Nematollahi, M.A., Jeffs, A. & Lavery, S.D. (2013) Mitochondrial DNA population structure of the scalloped lobster *Panulirus homarus* (Linnaeus 1758) from the West Indian Ocean. *Ices Journal of Marine Science*, **70**, 1491–1498.

Gao, H., Williamson, S. & Bustamante, C.D. (2007) A Markov chain Monte Carlo approach for joint inference of population structure and inbreeding rates from multilocus genotype data. *Genetics*, **176**, 1635–1651.

Goudet, J. (2001) FSTAT 2.9.3.2, a program to estimate and test gene diversities and fixation indices. Available from http://www2.unil.ch/popgen/softwares/fstat.htm

Graham, E.M., Baird, A.H. & Connolly, S.R. (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs*, **27**, 529–539.

Hancke, L., Roberts, M.J. & Ternon, J.F. (2014) Surface drifter trajectories highlight flow pathways in the Mozambique Channel. *Deep-Sea Research Part II: Topical Studies in Oceanography*, **100**, 27–37.

Harvell, D., Aronson, R., Baron, N., Connell, J., Dobson, A., Ellner, S., Gerber, L., Kim, K., Kuris, A., McCallum, H., Lafferty, K., McKay, B., Porter, J., Pascual, M., Smith, G., Sutherland, K. & Ward, J. (2004) The rising tide of ocean diseases: unsolved problems and research priorities. *Frontiers in Ecology and the Environment*, **2**, 375–382.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A. & Hatziolos, M.E. (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Kleypas, J.A. & Yates, K.K. (2009) Coral reefs and ocean acidification. *Oceanography*, **22**, 108–117.

Lutjeharms, J.R.E. & Bornman, T.G. (2010) The importance of the greater Agulhas Current is increasingly being recognised. *South African Journal of Science*, **106**, 1–4.

Macdonald, A.H.H., Schleyer, M.H. & Lamb, J.M. (2011) *Acropora austera* connectivity in the south-western Indian Ocean assessed using nuclear intron sequence data. *Marine Biology*, **158**, 613–621.

Mackenzie, J.B., Munday, P.L., Willis, B.L., Miller, D.J. & van Oppen, M.J.H. (2004) Unexpected patterns of genetic structuring among locations but not colour morphs in *Acropora nasuta* (Cnidaria; Scleractinia). *Molecular Ecology*, **13**, 9–20.

Madeira, C., Alves, M.J., Mesquita, N., Silva, S.E. & Paula, J. (2012) Tracing geographical patterns of population differentiation in a widespread mangrove gastropod: genetic and geometric morphometrics surveys along the eastern African coast. *Biological Journal of the Linnean Society*, **107**, 647–663.

Magalon, H., Adjeroud, M. & Veuille, M. (2005) Patterns of genetic variation do not correlate with geographical distance in the reef-building coral *Pocillopora meandrina* in the South Pacific. *Molecular Ecology*, **14**, 1861–1868.

Maier, E., Tollrian, R., Rinkevich, B. & Nurnberger, B. (2005) Isolation by distance in the scleractinian coral *Seriatopora hystrix* from the Red Sea. *Marine Biology*, **147**, 1109–1120.

Marshall, P.A. & Baird, A.H. (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*, **19**, 155–163.

McClanahan, T.R., Ateweberhan, M., Graham, N.A.J., Wilson, S.K., Sebastian, C.Ruiz, Guillaume, M.M.M. & Bruggemann, J.H. (2007a) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series*, **337**, 1–13.

McClanahan, T.R., Ateweberhan, M., Muhando, C.A., Maina, J. & Mohammed, M.S. (2007b) Effects of climate and seawater temperature variation on coral bleaching and mortality. *Ecological Monographs*, **77**, 503–525.

McClanahan, T.R., Ateweberhan, M., Darling, E.S., Graham, N.A.J. & Muthiga, N.A. (2014) Biogeography and change

among regional coral communities across the western Indian Ocean. *PLoS ONE*, **9**, e93385.

Minegishi, Y., Aoyama, J. & Tsukamoto, K. (2008) Multiple population structure of the giant mottled eel, *Anguilla marmorata*. *Molecular Ecology*, **17**, 3109–3122.

Minegishi, Y., Gagnaire, P., Aoyama, J., Bosc, P., Feunteun, E., Tsukamoto, K. & Berrebi, P. (2012) Present and past genetic connectivity of the Indo-Pacific tropical eel *Anguilla bicolor*. *Journal of Biogeography*, **39**, 408–420.

Moberg, F. & Folke, C. (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics*, **29**, 215–233.

Nakajima, Y., Nishikawa, A., Iguchi, A. & Sakai, K. (2010) Gene flow and genetic diversity of a broadcast-spawning coral in northern peripheral populations. *PLoS ONE*, **5**, e11149.

Nishikawa, A. & Sakai, K. (2005) Settlement-competency period of planulae and genetic differentiation of the scleractinian coral *Acropora digitifera*. *Zoological Science*, **22**, 391–399.

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.

Obura, D.O. (2001) Differential bleaching and mortality of eastern African corals. *Marine science development in Tanzania and Eastern Africa. Proceedings of 20th anniversary conference on advances in marine science in Tanzania* (ed. by M. Richmond and J. Francis), pp. 301–317. IMS/WIOMSA, Zanzibar.

Obura, D.O. (2012) The diversity and biogeography of western Indian Ocean reef-building corals. *PLoS ONE*, **7**, e45013.

van Oppen, M.J.H. & Gates, R.D. (2006) Conservation genetics and the resilience of reef-building corals. *Molecular Ecology*, **15**, 3863–3883.

van Oppen, M.J.H., Underwood, J.N., Muirhead, A.N. & Peplow, L. (2007) Ten microsatellite loci for the reef-building coral *Acropora millepora* (Cnidaria, Scleractinia) from the Great Barrier Reef, Australia. *Molecular Ecology Notes*, **7**, 436–438.

van Oppen, M.J.H., Lutz, A., De'ath, G., Peplow, L. & Kininmonth, S. (2008) Genetic traces of recent long-distance dispersal in a predominantly self-recruiting coral. *PLoS ONE*, **3**, e3401.

Palumbi, S.R. (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications*, **13**, 146–158.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R. & Jackson, J.B.C. (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science*, **301**, 955–958.

Peakall, R. & Smouse, P.E. (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics*, **28**, 2537–2539.

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

Ragionieri, L., Cannicci, S., Schubart, C.D. & Fratini, S. (2010) Gene flow and demographic history of the mangrove crab *Neosarmatium meinerti*: a case study from the western Indian Ocean. *Estuarine Coastal and Shelf Science*, **86**, 179–188.

Richards, Z.T. & van Oppen, M.J.H. (2012) Rarity and genetic diversity in Indo-Pacific *Acropora* corals. *Ecology and Evolution*, **2**, 1867–1888.

Ridderinkhof, H., van der Werf, P.M., Ullgren, J.E., van Aken, H.M., van Leeuwen, P.J. & de Ruijter, W.P.M. (2010) Seasonal and interannual variability in the Mozambique Channel from moored current observations. *Journal of Geophysical Research: Oceans*, **115**, 18.

Ridgway, T., Riginos, C., Davis, J. & Hoegh-Guldberg, O. (2008) Genetic connectivity patterns of *Pocillopora verrucosa* in southern African marine protected areas. *Marine Ecology Progress Series*, **354**, 161–168.

Schott, F.A. & McCreary, J.P. (2001) The monsoon circulation of the Indian Ocean. *Progress in Oceanography*, **51**, 1–123.

Severance, E.G. & Karl, S.A. (2006) Contrasting population genetic structures of sympatric, mass-spawning Caribbean corals. *Marine Biology*, **150**, 57–68.

Silva, I.C., Mesquita, N. & Paula, J. (2010) Lack of population structure in the fiddler crab *Uca annulipes* along an East African latitudinal gradient: genetic and morphometric evidence. *Marine Biology*, **157**, 1113–1126.

Silva, S.E., Silva, I.C., Madeira, C., Sallema, R., Paulo, O.S. & Paula, J. (2013) Genetic and morphological variation in two littorinid gastropods: evidence for recent population expansions along the East African coast. *Biological Journal of the Linnean Society*, **108**, 494–508.

Souter, P. & Grahn, M. (2008) Spatial genetic patterns in lagoonal, reef-slope and island populations of the coral *Platygyra daedalea* in Kenya and Tanzania. *Coral Reefs*, **27**, 433–439.

Souter, P., Henriksson, O., Olsson, N. & Grahn, M. (2009) Patterns of genetic structuring in the coral *Pocillopora damicornis* on reefs in East Africa. *BMC Ecology*, **9**, 19.

Starger, C.J., Barber, P.H., Ambariyanto & Baker, A.C. (2010) The recovery of coral genetic diversity in the Sunda Strait following the 1883 eruption of Krakatau. *Coral Reefs*, **29**, 547–565.

Underwood, J.N. (2009) Genetic diversity and divergence among coastal and offshore reefs in a hard coral depend on geographic discontinuity and oceanic currents. *Evolutionary Applications*, **2**, 222–233.

Underwood, J.N., Smith, L.D., van Oppen, M.J.H. & Gilmour, J.P. (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology*, **16**, 771–784.

Underwood, J.N., Smith, L.D., van Oppen, M.J.H. & Gilmour, J.P. (2009) Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecological Applications*, **19**, 18–29.

Veron, J.E.N. (2000) *Corals of the world*. Australian Institute of Marine Science, Townsville.

Visram, S., Yang, M.C., Pillay, R.M., Said, S., Henriksson, O., Grahn, M. & Chen, C.A. (2010) Genetic connectivity and historical demography of the blue barred parrotfish (*Scarus ghobban*) in the western Indian Ocean. *Marine Biology*, **157**, 1475–1487.

Wahlund, S. (1928) Zusammensetzung von Populationen und Korrelationserscheinungen vom Standpunkt der Vererbungslehre aus betrachtet. *Hereditas*, **11**, 65–106.

Weir, B.S. & Cockerham, C.C. (1984) Estimating F-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

Wilkinson, C. (2002) *Status of coral reefs of the world*. Coral Reef Monitoring Network, Townsville.

Wilkinson, C. (2008) *Status of coral reefs of the world*. Coral Reef Monitoring Network, Townsville.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Location and date of sampling of *Acropora tenuis* in East Africa.

Appendix S2 Genetic diversity in *Acropora tenuis* at sample sites in East Africa for each microsatellite locus.

Appendix S3 Bayesian model comparison, estimates of inbreeding and null allele frequencies as generated by the software INEst 2.0 (Chybicki & Burczyk, 2009) using the individual inbreeding model (IIM).

BIOSKETCH

Rosa Maria van der Ven is a PhD student whose research interests include the population genetics and physiology of corals to understand their ecology and resilience to climate change. The research team has a joint interest in connectivity of marine populations and its implications for evolution, ecology and conservation.

Author contributions: M.K. and R.M.V. conceived the ideas; J.M.M., R.M.V., M.K. and M.S.M. collected the samples; R.M.V. conducted the laboratory work and analysed the data; R.M.V., L.T., D.J.R.D.R. and M.K. interpreted the data; R.M.V. led the writing, with contributions from all authors.

Editor: Jim Provan