The recovery of coral genetic diversity in the Sunda Strait following the 1883 eruption of Krakatau

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Abstract Surveys of microsatellite variation show that genetic diversity has largely recovered in two reef-building corals, *Pocillopora damicornis* and *Seriatopora hystrix* (Scleractinia: Pocilloporidae), on reefs which were decimated by the eruption of the volcano Krakatau in 1883. Assignment methods and gene flow estimates indicate that the recolonization of Krakatau occurred mainly from the closest upstream reef system, Pulau Seribu, but that larval

input from other regions has also occurred. This pattern is clearer in *S. hystrix*, which is traditionally the more dispersal-limited species. Despite these observed patterns of larval dispersal, self-recruitment appears to now be the most important factor in supplying larvae to coral populations in Krakatau. This suggests that the colonization of devastated reefs can occur quickly through larval dispersal; however, their survival requires local sources of larvae for self-recruitment. This research supports the observation that the recovery of genetic diversity in coral reef animals can occur on the order of decades and centuries rather than millennia. Conservation measures aimed at sustaining coral reef populations in Krakatau and elsewhere should include both the protection of upstream source populations for larval replenishment should disaster occur as well as the protection of large adult colonies to serve as local larval sources.

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Introduction

On August 26, 1883, the eruption and near-total destruction of the volcano Krakatau in the Sunda Strait, Indonesia, completely exterminated all marine life in the surrounding area. Pyroclastic flows deposited molten rock and ash at a temperature of 475–550°C to an average thickness of 20 m (Mandeville et al. 1994) on the surrounding sea floor (Sigurdsson et al. 1991). It is the scientific consensus that all life within a 15 km radius was completely extinguished by this eruption (Simkin and Fiske 1983; Thornton 1996). A new volcanic island Anak Krakatau (“the Child of Krakatau”) has been rising in the caldera since August

1930 and is now approximately 450 m high. Fringing coral reefs have subsequently formed on Anak Krakatau, the remnant islands of Krakatau, and the surrounding areas that were affected by the eruption and resulting tsunami, presenting researchers with a unique opportunity to study the assembly and development of a benthic ecosystem following its complete destruction.

The recovery of terrestrial communities on Krakatau is well documented (Simkin and Fiske 1983; Thornton 1996). However, its marine ecosystems have been largely ignored until recent years (review: Barber et al. 2002). Sluiter (1890) observed coral recruitment on Krakatau less than a decade following the eruption. However, this early reef was subsequently smothered by further volcanic activity (Umbgrove 1930). It is unknown at what point contemporary coral reefs took hold in the region or which reefs served as source populations for the colonization of the Krakatau region. The assembly and structure of coral communities in general has been thoroughly studied (review: Karlson 2002). However, their recruitment and ecological succession on volcanoes has only been investigated in a few cases. Grigg and Maragos (1974) observed coral settlers on lava that was less than 2 years old in Hawaii. Tomascik et al. (1996) report an exceptionally diverse coral community on 5-year-old lava following a major eruption of Gunung Api in the Banda Sea, Eastern Indonesia, forming what may be a new refuge and larval source for surrounding areas. However, colonization in these cases may have come from local sources directly adjacent to the lava flows in question. Due to the extent of destruction in Krakatau, all colonization must have come from elsewhere.

With no additional examples of *de novo* reef formation, it is difficult to predict how corals would have first colonized Krakatau; where they would have come from, or how ecological succession would have proceeded. In the only contemporary research done on the coral reefs of Krakatau, Barber et al. (2002) observed the rapid recovery of genetic diversity in the stomatopod crustaceans *Haptosquilla pulchella* and *H. glyptocercus*. Larval sources for Krakatau were restricted to coral reefs south of the Java and Flores Seas, a putative barrier to marine larval dispersal (Barber et al. 2000).

In the study presented here, the genetic consequences of recolonization were examined in two common Indo-Pacific reef-building stony corals, *Pocillopora damicornis* and *Seriatopora hystrix*. These corals occupy similar reef habitats, yet differ notably in their population genetic structures. *P. damicornis* typically displays more genetically open populations with high gene flow, whereas *S. hystrix* populations are often more closed, exhibiting higher levels of genetic subdivision (Ayre and Dufty 1994; Ayre et al. 1997; Ayre and Hughes 2000, 2004). Although

both species brood larvae on a lunar cycle throughout the year in Australia, Japan, the Philippines, and Taiwan (Atoda 1947, 1951; Harrison and Wallace 1990; Fan et al. 2006; Villanueva et al. 2008), *P. damicornis* is known to brood asexual larvae in Western Australia and Hawai'i (Stoddart 1984) whereas *S. hystrix* broods are usually generated sexually (Ayre and Resing 1986; Sherman 2008). However, *P. damicornis* recruits on eastern Australian reefs appear to be predominantly sexually generated, and so may have been derived from broadcast spawning (Ayre and Miller 2004; Miller and Ayre 2008) a phenomenon also observed in *P. damicornis* in Eastern Pacific Panamá (Glynn et al. 1991).

Overall, these differences indicate a complex relationship between reproduction and genetic structure, but generally suggest higher effective dispersal in *P. damicornis* than *S. hystrix*. As such, *P. damicornis* populations from Krakatau are hypothesized to recover genetic diversity more rapidly than *S. hystrix* and larval sources will be more varied. Support for this hypothesis would be evident in the identification of multiple source populations for *P. damicornis*, high gene flow estimates from areas outside of Krakatau, and gene diversity values that are similar to other, older regions in Indonesia. By contrast, source populations for *S. hystrix* in Krakatau would most likely be restricted to those immediately upstream (from reefs in the Java Sea). Gene flow estimates should also be lower in this species, indicative of a slower recovery of genetic diversity on Krakatau.

Methods

Fieldwork

Coral samples were collected by scuba and snorkeling in 2005 and 2006 (Table 1). In total, 682 samples of *P. damicornis* and 823 samples of *S. hystrix* were collected from across the Indonesian Archipelago for comparative analysis to a subset from the Krakatau region, 122 and 197 samples, respectively (Fig. 1). One branch was removed from each adult colony to ensure non-lethal sampling and minimal impact on the individual. Because reproductive maturity depends on colony size rather than age (Hughes 1984; Lirman 2000; Zakai et al. 2000), adults were defined as colonies greater than 7 cm in diameter for *P. damicornis* and 8 cm for *S. hystrix* (Harrison and Wallace 1990). Species identifications followed Veron (2000). Samples were taken from colonies at least 10 m apart to help minimize resampling of genetic clonemates that may have resulted from fragmentation.

Table 1 Sample regions and localities listed in approximate east to west order

Region	Locality	Latitude	Longitude	<i>P. damicornis</i>	<i>S. hystrix</i>
Aceh	Pulau Weh	5° 36.99N	95° 41.980E	22	25
Krakatau	Anak Krakatau	6° 05.43S	105° 25.10E	19	22
	Anyer	6° 04.61S	105° 52.90E	21	0
	Karang Serang	6° 06.57S	105° 26.39E	17	0
	Rakata (Krakatau Besar)	6° 08.83S	105° 27.80E	26	18
	Rakata Kecil	6° 05.86S	105° 27.07E	24	0
	Sangiang	5° 57.80S	105° 51.88E	25	24
	Sebesi	5° 55.80S	105° 30.93E	22	9
	Sebuku 1	5° 52.78S	105° 32.03E	20	24
	Sebuku 2	5° 53.49S	105° 30.13E	23	25
Pulau Seribu	Alam Kotok	5° 41.98S	106° 32.29E	22	20
	Belat	5° 37.70S	106° 34.38E	20	21
	Karang Congkak	5° 42.53S	106° 34.34E	18	21
	Pramuka	5° 44.77S	106° 35.51E	10	23
	Pulau Pari	5° 50.00S	106° 36.00E	13	38
	Semak Daun	5° 44.33S	106° 33.83E	23	21
Bali	Napoleon Reef	8° 07.57S	114° 38.13E	0	21
	Seraya	8° 16.57S	115° 35.72E	21	20
	Pemuteran	8° 07.26S	114° 37.53E	11	41
Lombok	Gili Trawangan	6° 05.52S	120° 24.83E	18	12
Makassar	Bone Batang	5° 02.10S	119° 16.33E	0	24
	Barrang Lompo	5° 02.70S	119° 19.27E	30	0
Selayar	Gusung	6° 05.52S	120° 24.83E	0	23
Flores	Kukusan	8° 32.96S	119° 48.25E	0	1
	Sebayur	8° 30.44S	119° 42.67E	0	17
Northern Sulawesi	Batu Gosok (Bangka)	1° 47.59N	125° 11.18E	0	12
	Murex House Reef (Bangka)	1° 44.15N	125° 08.95E	2	34
	Nudi Retreat (Lembeh)	1° 29.00N	125° 14.41E	26	36
	Pisok (Manado)	1° 34.43N	124° 48.17E	25	5
	Manado Tua	1° 36.99N	124° 41.68E	2	0
Halmahera	Doi	2° 16.60N	127° 46.79E	0	20
	Jerewai	1° 31.23N	128° 42.02E	17	22
	Tidore	0° 45.21N	127° 24.56E	11	28
	Tonuu	1° 47.91N	127° 59.97E	21	20
Raja Ampat	Alyui	0° 10.47S	130° 14.85E	20	19
	Gam	0° 25.88S	130° 33.16E	4	1
	Jefman	0° 55.64S	131° 07.41E	22	22
	Kri Island	0° 33.38S	130° 40.68E	30	9
	Manta Point	0° 33.71S	130° 32.42E	1	0
	Mayalibit	0° 17.85S	130° 48.49E	9	20
Biak	Adoki	1° 08.53S	135° 59.68E	10	12
	Owi	1° 15.26S	136° 10.99E	9	9
	Rasbar	1° 15.28S	136° 19.07E	0	4
Yapen	Ambai	1° 57.64S	136° 19.23E	15	22
	Serui	1° 54.32S	136° 13.65E	6	0
Manokwari	Lemon	0° 53.41S	134° 04.90E	18	20
Teluk Cenderwasih	Rumberpon	1° 44.23S	134° 12.15E	13	19

Table 1 continued

Region	Locality	Latitude	Longitude	<i>P. damicornis</i>	<i>S. hystrix</i>
Kaimana	Mauwara	3° 49.65S	134° 03.51E	23	0
	Namatote	3° 46.73S	133° 52.93E	0	21
Fakfak	Momon	3° 56.38S	132° 48.21E	4	18

Fig. 1 Study localities in Indonesia with close-up view of the localities in the Krakatau region

Genetic analysis

Genomic DNA was extracted using a modified Chelex protocol (Walsh et al. 1991) in which tissue from 1 or 2 polyps was lysed at 95°C for 1 h in 300 µl of 5% Chelex. The resulting solution was briefly vortexed and centrifuged at 13,000 g for 1 min. The supernatant was then used as the template for the polymerase chain reaction (PCR). *P. damicornis* PCR for 6 microsatellite markers, Pd2-001 through Pd2-006, followed the protocol of Starger et al. (2008). PCR conditions for PV2, PV6, and PV7 followed the protocol of Magalon et al. (2004). Previously published markers Sh2-005, Sh2-006, Sh3-003, Sh3-004, Sh3-008, Sh4-001, and Sh4-010 were amplified in *S. hystrix* samples following the PCR procedure of Underwood et al. (2006). Size fragment analysis for both species was performed with fluorescent-labeled primers on an ABI 3730xl running GeneMapper 3.5 software. Alleles were coded as the number of microsatellite repeats.

Genetic diversity

Clonal diversity could not be statistically assessed due to the need for an explicit, transect-based sampling strategy (Arnaud-Haond et al. 2007) that was not possible in this case due to time constraints in the field. However, in order to avoid any spurious results that might come from sampling genetic clones, all but one representative of each multilocus genotype was removed from the dataset before further analysis. Hardy–Weinberg equilibrium (HWE) was assessed by estimating F_{IS} for each locus in each population in GenoDive 2.0b16 (Meirmans and Van Tienderen 2004). Significantly positive F_{IS} values indicate heterozygote excess whereas negative values indicate heterozygote deficit. Statistical significance was tested with 100,000 permutations at $p = 0.05$ and the false discovery rate (FDR) correction for multiple test (Benjamini and Hochberg 1995). Observed and expected heterozygosities (H_o and H_e) were calculated in GenAlEx 6.3 (Peakall and

Smouse 2006). The possible presence of null alleles was investigated in Genepop on the Web (Raymond and Rousset 1995). Deviations from linkage equilibrium were assessed with likelihood ratio tests with a significance level of $p = 0.05$ (Slatkin and Excoffier 1996) as implemented in Arlequin 3.11 (Excoffier et al. 2005).

In order to compare the genetic diversity found in Krakatau to older reefs throughout Indonesia, Nei's unbiased genetic diversity (Hz) (Nei 1987) was calculated for each locality using the Excel Microsatellite Toolkit (Park 2001). Diversity comparisons between species were made using the Wilcoxon Signed Rank Test. The mean ratio of the number of alleles to the range in allele size (M) was calculated for each locality in Arlequin 3.11 to detect recent reductions in population size (Garza and Williamson 2001) that might be associated with the decimation and recolonization of the islands of Krakatau.

Assignment methods

To examine the potential source populations for recolonization of Krakatau spatial and non-spatial assignment methods were implemented in BAPS 5.3 (Corander and Marttinen 2006; Corander et al. 2008). Populations with fewer than fifteen genetically distinct individuals were excluded from this analysis. BAPS implements a stochastic optimization procedure rather than a Markov chain Monte Carlo (MCMC), and therefore generally performs more quickly than the program Structure (Falush et al. 2003) with similar results (Latch et al. 2006). Individuals were grouped into the localities from which they were sampled using the 'cluster by groups' option, and structure was inferred as clusters of groups. This method was employed because the distance between individuals within localities is trivial relative to the scale of the entire study. The 'cluster by groups' option was therefore most appropriate (see Corander et al. 2008 for a detailed description). In each analysis, maximum K (the number of genetic clusters) was input at intervals of 5 from 5 to 50 (program input: 5, 10, 15, 20, 25, 30, 35, 40, 45, 50). The K value with the lowest log likelihood, "log(ml)", was then called K' and a more focused search was run a further 5 times with maximum K set to K' , $K' - 1$ and $K' + 1$ (example input for $K' = 15$: 14, 14, 14, 14, 14, 15, 15, 15, 15, 15, 16, 16, 16, 16, 16). From these results, the K value with the lowest log (ml), called K , was used to chart the genetic clustering of localities. The spatial method incorporates the geographic proximity of samples into the assignment algorithm when the genetic data are insufficient to resolve cluster membership. Likelihood scores between the spatial and non-spatial methods are directly comparable within each species and are informative as to which analysis produces the more likely structure (J. Corander, *pers. comm.*). The

conditional posterior probability, or 'local uncertainty,' in the assignment of a locality to a specific cluster was also calculated by BAPS (equation 11 in Corander et al. 2008). Admixture inferences were not used because of a strong need for a biologically meaningful number of ancestral populations which is used as prior information (Corander and Marttinen 2006) and which was not available in this case.

Genetic structure and migration

In order to infer genetic differentiation among regions, with the aim of identifying source populations for the recolonization of the Sunda Strait, pairwise F_{ST} values were calculated in Arlequin 3.11 and tested for significance at $p = 0.05$ with the FDR correction for multiple test (Benjamini and Hochberg 1995).

A matrix of pairwise immigration was also estimated among regions using the Bayesian assignment method implemented in BayesAss+ 1.2 (Wilson and Rannala 2003). Default settings for burn-in (200,000), number of MCMC iterations (3 million), and sampling frequency (2,000) were appropriate to reach convergence based on visual inspection of likelihood scores. Regions with fewer than fifteen genetically distinct individuals were excluded from this analysis.

Results

Heterozygosity, clonality, and genetic diversity

For *P. damicornis*, 682 individuals were genotyped and analyzed at 9 microsatellite loci. The number of alleles per locus ranged from 8 at locus Pd2-006 to 28 at locus PV2 (mean = 14.00). Twelve multilocus genotypes were observed in more than one individual; however, only four of these were observed in more than two individuals (Table 4). In total, 14 *P. damicornis* individuals were removed from subsequent analyses.

For *S. hystrix*, 823 individuals were genotyped and analyzed at 7 microsatellite loci. The number of alleles per locus ranged from 8 at locus Sh3-003 and Sh3-008 to 24 at locus Sh2-006 (mean = 14.43). Forty-nine multilocus genotypes were observed in more than one individual; however, only 12 of these were observed in more than two individuals (Table 5). In total, 74 *S. hystrix* individuals were removed from subsequent analyses.

Departures from Hardy-Weinberg equilibrium were evident in many cases based on significantly positive and negative F_{IS} values (Tables 2 and 3) and, as a result, Genepop detected the possibility of null alleles in many populations (data not shown). Similarly, linkage

Table 2 Allele data for *P. damicornis* for populations where $N_g \geq 15$

		Pd2-001	Pd3-002	Pd2-003	Pd3-004	Pd3-005	Pd2-006	Pv2	Pv6	Pv7
Pulau Weh	Na	5	6	2	3	6	5	2	1	1
	Ho	0.278	0.421	0.643	0.524	0.545	0.182	0.400	0.000	0.000
	He	0.489	0.576	0.436	0.482	0.706	0.636	0.320	0.000	0.000
	F_{IS}	0.432	0.269	-0.474	-0.087	0.227	0.714	-0.250	—	—
Anak Krakatau	Na	7	6	3	2	8	4	6	4	5
	Ho	0.647	0.286	0.429	0.118	0.556	0.176	0.563	0.455	0.143
	He	0.740	0.696	0.401	0.484	0.756	0.265	0.711	0.640	0.370
	F_{IS}	0.126	0.590	-0.070	0.757	0.265	0.333	0.209	0.290	0.614
Anyer	Na	3	2	3	1	3	5	7	4	3
	Ho	0.429	0.000	0.941	0.000	0.900	0.158	0.944	0.333	0.350
	He	0.659	0.298	0.602	0.000	0.620	0.428	0.806	0.295	0.296
	F_{IS}	0.349	1.000	-0.563	—	-0.452	0.631	-0.172	-0.129	-0.181
Karang Serang	Na	5	4	2	2	7	5	4	6	6
	Ho	0.563	0.467	0.667	0.118	0.529	0.471	0.462	0.300	0.083
	He	0.764	0.429	0.444	0.484	0.740	0.578	0.689	0.795	0.684
	F_{IS}	0.263	-0.088	-0.500	0.757	0.285	0.186	0.330	0.623	0.878
Rakata	Na	3	6	2	2	8	5	4	6	5
	Ho	0.105	0.450	0.773	0.053	0.478	0.273	0.200	0.500	0.125
	He	0.410	0.571	0.474	0.051	0.596	0.543	0.682	0.746	0.281
	F_{IS}	0.743	0.212	-0.630	-0.027	0.198	0.498	0.707	0.330	0.556
Rakata Kecil	Na	5	6	2	5	10	5	5	6	5
	Ho	0.842	0.350	0.105	0.800	0.952	0.150	0.538	0.438	0.353
	He	0.620	0.628	0.100	0.680	0.745	0.349	0.544	0.785	0.545
	F_{IS}	-0.357	0.442	-0.056	-0.176	-0.279	0.570	0.011	0.443	0.352
Sangiang	Na	6	4	3	4	6	4	7	6	5
	Ho	0.375	0.158	0.250	0.400	0.800	0.136	0.391	0.810	0.208
	He	0.689	0.506	0.223	0.490	0.742	0.685	0.590	0.680	0.359
	F_{IS}	0.456	0.688	-0.121	0.183	-0.079	0.801	0.337	-0.190	0.419
Sebuku 1	Na	3	6	2	2	6	3	6	5	1
	Ho	0.400	0.550	0.400	0.350	0.579	0.211	0.529	0.750	0.000
	He	0.591	0.729	0.320	0.439	0.769	0.436	0.690	0.734	0.000
	F_{IS}	0.323	0.245	-0.250	0.202	0.247	0.517	0.233	-0.021	—
Sebuku 2	Na	3	5	2	2	8	4	7	0	2
	Ho	0.571	0.409	0.529	0.476	0.696	0.476	0.526	0.000	0.063
	He	0.625	0.616	0.389	0.490	0.836	0.670	0.687	0.000	0.061
	F_{IS}	0.086	0.336	-0.360	0.028	0.168	0.289	0.234	NA	-0.032
Alam Kotok	Na	3	4	2	2	6	5	5	2	1
	Ho	0.167	0.294	0.412	0.300	0.682	0.318	0.706	0.000	0.000
	He	0.542	0.621	0.327	0.480	0.657	0.596	0.713	0.500	0.000
	F_{IS}	0.692	0.526	-0.259	0.375	-0.038	0.466	0.010	1.000	—
Belat	Na	4	4	3	2	6	5	6	7	4
	Ho	0.529	0.111	0.118	0.316	0.941	0.111	0.375	0.286	0.375
	He	0.625	0.205	0.112	0.266	0.723	0.512	0.781	0.758	0.631
	F_{IS}	0.152	0.459	-0.046	-0.187	-0.301	0.783	0.520	0.623	0.406
Karang Congkak	Na	6	4	2	2	9	7	4	3	5
	Ho	0.533	0.357	0.500	0.250	0.867	0.353	0.000	0.000	0.250
	He	0.564	0.474	0.375	0.430	0.847	0.709	0.735	0.449	0.615
	F_{IS}	0.055	0.247	-0.333	0.418	-0.024	0.502	1.000	1.000	0.594

Table 2 continued

		Pd2-001	Pd3-002	Pd2-003	Pd3-004	Pd3-005	Pd2-006	Pv2	Pv6	Pv7
Semak Daun	Na	4	5	2	4	11	6	4	6	3
	Ho	0.526	0.647	0.200	0.500	0.857	0.263	0.476	0.438	0.111
	He	0.654	0.663	0.255	0.583	0.746	0.593	0.638	0.689	0.204
	F_{IS}	0.195	0.023	0.216	0.143	−0.149	0.556	0.254	0.365	0.455
Seraya	Na	5	4	3	3	11	5	9	5	5
	Ho	0.133	0.632	0.538	0.333	0.500	0.350	0.333	0.611	0.095
	He	0.689	0.632	0.411	0.497	0.761	0.636	0.802	0.691	0.334
	F_{IS}	0.806	0.000	−0.309	0.329	0.343	0.450	0.584	0.116	0.715
Gili Trawangan	Na	4	4	4	2	5	3	10	6	3
	Ho	0.444	0.556	0.765	0.471	0.417	0.000	0.722	0.500	0.091
	He	0.406	0.691	0.528	0.360	0.694	0.639	0.634	0.727	0.244
	F_{IS}	−0.095	0.196	−0.449	−0.308	0.400	1.000	−0.139	0.312	0.627
Barrang Lompo	Na	6	5	4	6	9	3	6	8	5
	Ho	0.458	0.652	0.667	0.684	0.966	0.533	0.273	0.615	0.233
	He	0.678	0.758	0.517	0.615	0.780	0.516	0.712	0.808	0.598
	F_{IS}	0.324	0.140	−0.289	−0.113	−0.238	−0.033	0.617	0.239	0.610
Nudi Retreat	Na	4	4	2	4	8	6	7	6	2
	Ho	0.174	0.640	0.520	0.200	0.640	0.240	0.542	0.684	0.269
	He	0.518	0.556	0.385	0.284	0.677	0.713	0.765	0.729	0.233
	F_{IS}	0.664	−0.151	−0.351	0.296	0.054	0.663	0.292	0.061	−0.156
Jerewai	Na	4	6	4	3	7	4	4	5	4
	Ho	0.533	0.438	0.438	0.143	0.467	0.500	0.500	0.182	0.222
	He	0.629	0.578	0.363	0.255	0.533	0.619	0.695	0.740	0.617
	F_{IS}	0.152	0.243	−0.204	0.440	0.125	0.192	0.281	0.754	0.640
Tonuu	Na	3	6	2	4	8	3	5	4	4
	Ho	0.143	0.842	0.222	0.700	0.850	0.250	0.231	0.250	0.273
	He	0.253	0.665	0.198	0.536	0.785	0.656	0.642	0.719	0.616
	F_{IS}	0.434	−0.267	−0.125	−0.305	−0.083	0.619	0.641	0.652	0.557
Alyui	Na	2	4	2	3	5	2	3	4	2
	Ho	0.200	0.947	0.105	0.944	0.842	0.158	1.000	1.000	0.111
	He	0.180	0.569	0.100	0.523	0.727	0.145	0.569	0.652	0.105
	F_{IS}	−0.111	−0.664	−0.056	−0.805	−0.158	−0.086	−0.756	−0.533	−0.059
Jefman	Na	5	4	4	5	8	6	5	8	5
	Ho	0.467	0.182	0.500	0.318	0.667	0.250	0.556	0.474	0.238
	He	0.698	0.591	0.409	0.527	0.709	0.500	0.715	0.823	0.747
	F_{IS}	0.331	0.692	−0.223	0.396	0.059	0.500	0.222	0.424	0.681
Kri	Na	3	7	3	6	10	4	9	8	2
	Ho	0.227	0.655	0.571	0.690	0.833	0.462	0.654	0.538	0.036
	He	0.334	0.691	0.426	0.566	0.834	0.675	0.805	0.814	0.270
	F_{IS}	0.319	0.052	−0.341	−0.218	0.001	0.316	0.188	0.338	0.868
Ambai	Na	3	4	3	5	8	3	4	7	5
	Ho	0.214	0.308	0.267	0.357	0.867	0.375	0.273	0.357	0.143
	He	0.548	0.559	0.238	0.651	0.742	0.320	0.657	0.786	0.768
	F_{IS}	0.609	0.450	−0.121	0.451	−0.168	−0.171	0.585	0.545	0.814
Lemon	Na	6	2	3	2	5	3	3	7	7
	Ho	0.235	0.091	0.800	0.625	0.167	0.059	0.941	0.889	0.250
	He	0.360	0.087	0.504	0.430	0.340	0.299	0.628	0.718	0.508
	F_{IS}	0.346	−0.048	−0.586	−0.455	0.509	0.803	−0.499	−0.239	0.508

Table 2 continued

		Pd2-001	Pd3-002	Pd2-003	Pd3-004	Pd3-005	Pd2-006	Pv2	Pv6	Pv7
Mauwara	Na	7	4	4	3	5	4	7	6	6
	Ho	0.522	0.278	0.476	0.409	0.706	0.071	0.909	0.429	0.316
	He	0.629	0.514	0.500	0.334	0.715	0.671	0.767	0.731	0.500
	F_{IS}	0.170	0.459	0.048	−0.226	0.012	0.894	−0.186	0.414	0.368

Shown for each locus and locality are the number of alleles observed (A), observed heterozygosity (Ho), and expected heterozygosity (He). F_{IS} is the inbreeding coefficient. Values in italics indicate significant departures from Hardy–Weinberg equilibrium after FDR correction

disequilibrium was detected in some cases, but was not consistent across loci and study localities and no two loci were linked in all localities (data not shown). Underwood et al. (2007) and van Oppen et al. (2008) attribute inconsistent Hardy–Weinberg and linkage disequilibrium in *S. hystrix* from Western Australia and the Great Barrier Reef to genetic subdivision at the local scale, combined with admixture of populations, and concluded that null alleles were not a cause of the heterozygote deficits. High levels of genetic subdivision at the local scale in both *P. damicornis* and *S. hystrix* in Krakatau and throughout Indonesia (see results from BAPS 5.3) lead to the same conclusion here and therefore did not preclude further analyses with these data.

The number of unique genotypes observed, Nei's unbiased gene diversity (Hz), M value, and BAPS cluster for each population are given in Tables 4 and 5. Nearly all localities in Krakatau display M statistics below 7 indicating recent reductions in population size (Garza and Williamson 2001). Average M in localities across Indonesia was 0.67 for *P. damicornis* (Table 4) and 0.83 for *S. hystrix* (Table 5).

When comparing the two species to each other at the 4 localities within Krakatau where both species were sampled, Nei's unbiased gene diversity (Hz) was greater for *P. damicornis* (Table 4) than in *S. hystrix* (Table 5) in all comparisons (Wilcoxon signed rank test, $p = 0.05$). When comparing localities across all of Indonesia where both species were sampled, gene diversity is also significantly higher in *P. damicornis* (mean Hz = 0.57) than in *S. hystrix* (mean Hz = 0.45) (Wilcoxon signed rank test, $p = 0.00$).

When comparing localities within Krakatau to the remaining localities throughout Indonesia for *P. damicornis*, genetic diversity localities in Krakatau (mean Hz = 0.55) was marginally higher than the mean Hz for the remaining localities throughout Indonesia (mean Hz = 0.53) (Table 4). The mean genetic diversity of *S. hystrix* localities in Krakatau (mean Hz = 0.41) was lower than the mean of the remaining localities throughout Indonesia (mean Hz = 0.48) (Table 5).

Assignment methods

For both species, there was strong agreement between the spatial and non-spatial assignment methods implemented in BAPS. Likelihood was higher in the non-spatial analysis for *P. damicornis* (−11,587.93 vs. −11,743.45) and *S. hystrix* (−11,098.75 vs. −11,345.53) indicating that the molecular data alone were adequate to resolve genetic structure and that departures from HWE did not spuriously affect the results. Each locality was assigned to a genetic cluster, given in Fig. 2a, b and Tables 4 and 5. The conditional posterior probabilities of assignment were all greater than or equal to 0.99 indicating the highest probability of membership.

The Bayesian assignment method implemented in BAPS indicated the presence of $K = 16$ genetic clusters from 26 localities of *P. damicornis* in Indonesia (Table 4), 5 of which occur in Krakatau. Three of these clusters are found in one locality each and are private to the Sunda Strait: Rakata, Sangiang, and Anyer. Three localities in Krakatau (Krakata Kecil, Sebuku 1 and Sebuku 2) cluster with 2 localities in Pulau Seribu (Alam Kotok and Semak Daun) to form Cluster #1 (Table 4). Anak Krakatau and Karang Serang together form Cluster #6, which is found nowhere else in Indonesia.

The Bayesian assignment method implemented in BAPS indicated the presence of $K = 20$ genetic clusters from 31 localities of *S. hystrix* in Indonesia (Table 5), only one of which occurs in Krakatau. *S. hystrix* from Sangiang, Anak Krakatau, Sebuku 1, Sebuku 2 form Cluster #2 with all localities from Pulau Seribu: Alam Kotok, Pramuka, Semak Daun, Karang Kongka, Belat, Pulau Pari. This cluster occurs nowhere else in Indonesia.

Genetic structure and migration

In *P. damicornis*, pairwise F_{st} was significant between Krakatau and 11 out of 13 other regions (Table 6). The smallest pairwise F_{st} values were between Krakatau and Pulau Seribu ($F_{st} = 0.03$) and Krakatau and Bali ($F_{st} = 0.03$). In *S. hystrix*, pairwise F_{st} estimates were

Table 3 Allele data for *S. hystrix* for populations where $N_g \geq 15$

		Sh2-005	Sh2-006	Sh3-003	Sh3-004	Sh3-008	Sh4-001	Sh4-010
Pulau Weh	Na	5	3	2	3	2	2	2
	Ho	0.720	0.320	0.000	0.360	0.000	0.200	0.467
	He	0.608	0.594	0.493	0.627	0.497	0.241	0.420
	F_{IS}	-0.184	0.462	1.000	0.426	1.000	0.169	-0.111
Anak Krakatau	Na	4	6	1	6	1	5	5
	Ho	0.682	0.636	0.000	0.476	0.000	0.238	0.500
	He	0.561	0.667	0.000	0.520	0.000	0.298	0.477
	F_{IS}	-0.215	0.046	–	0.085	–	0.202	-0.048
Rakata	Na	3	4	1	4	1	2	5
	Ho	1.000	0.167	0.000	0.556	0.000	0.389	0.611
	He	0.549	0.157	0.000	0.545	0.000	0.375	0.600
	F_{IS}	-0.820	-0.059	–	-0.020	–	-0.037	-0.018
Sangiang	Na	5	6	1	4	2	3	4
	Ho	0.708	0.542	0.000	0.696	0.000	0.261	0.542
	He	0.734	0.752	0.000	0.665	0.080	0.235	0.489
	F_{IS}	0.034	0.279	–	-0.045	1.000	-0.108	-0.108
Sebuku 1	Na	6	5	3	7	1	4	6
	Ho	0.870	0.583	0.000	0.478	0.000	0.238	0.458
	He	0.698	0.497	0.156	0.682	0.000	0.330	0.635
	F_{IS}	-0.245	-0.175	1.000	0.299	–	0.278	0.278
Sebuku 2	Na	7	5	2	2	2	2	4
	Ho	0.957	0.560	0.000	0.476	0.080	0.727	0.625
	He	0.730	0.567	0.077	0.444	0.077	0.463	0.470
	F_{IS}	-0.311	0.013	1.000	-0.071	-0.042	-0.571	-0.328
Alam Kotok	Na	7	4	2	4	2	2	4
	Ho	0.850	0.450	0.050	0.650	0.000	0.368	0.400
	He	0.694	0.558	0.049	0.548	0.198	0.301	0.475
	F_{IS}	-0.225	0.193	-0.026	-0.187	1.000	-0.226	0.158
Belat	Na	6	6	1	2	3	3	7
	Ho	0.842	0.684	0.000	0.524	0.053	0.100	0.526
	He	0.755	0.668	0.000	0.482	0.483	0.096	0.634
	F_{IS}	-0.116	-0.025	–	-0.087	0.891	-0.039	0.170
Karang Congkak	Na	7	5	1	5	1	2	6
	Ho	1.000	0.667	0.000	0.714	0.000	0.048	0.571
	He	0.752	0.745	0.000	0.622	0.000	0.046	0.635
	F_{IS}	-0.330	0.105	–	-0.148	–	-0.024	0.100
Pramuka	Na	6	7	1	3	1	3	4
	Ho	0.913	0.739	0.000	0.391	0.000	0.348	0.609
	He	0.665	0.582	0.000	0.519	0.000	0.360	0.691
	F_{IS}	-0.372	-0.269	–	0.246	–	0.034	0.119
Pulau Pari	Na	7	6	3	8	3	3	6
	Ho	0.692	0.667	0.024	0.711	0.024	0.514	0.550
	He	0.795	0.713	0.156	0.817	0.116	0.480	0.614
	F_{IS}	0.129	0.065	0.848	0.131	0.789	-0.069	0.104
Semak Daun	Na	7	6	1	5	3	4	4
	Ho	1.000	0.667	0.000	0.810	0.048	0.350	0.619
	He	0.766	0.681	0.000	0.668	0.441	0.303	0.586
	F_{IS}	-0.305	0.022	–	-0.212	0.892	-0.157	-0.056

Table 3 continued

		Sh2-005	Sh2-006	Sh3-003	Sh3-004	Sh3-008	Sh4-001	Sh4-010
Napoleon Reef	Na	6	7	1	6	2	2	5
	Ho	0.900	0.722	0.000	0.524	0.050	0.476	0.632
	He	0.785	0.728	0.000	0.624	0.049	0.444	0.507
	F_{IS}	−0.146	0.008	–	0.160	−0.026	−0.071	−0.246
Pemuteran	Na	6	4	1	4	3	4	5
	Ho	0.810	0.575	0.000	0.564	0.026	0.314	0.711
	He	0.622	0.514	0.000	0.645	0.075	0.278	0.678
	F_{IS}	−0.301	−0.118	–	0.126	0.656	−0.132	−0.049
Seraya	Na	6	5	1	4	2	3	4
	Ho	0.450	0.526	0.000	0.588	0.105	0.364	0.800
	He	0.488	0.472	0.000	0.618	0.332	0.310	0.603
	F_{IS}	0.077	−0.114	–	0.048	0.683	−0.173	−0.328
Bone Batang	Na	5	6	2	9	4	5	3
	Ho	0.636	0.682	0.000	0.750	0.095	0.167	0.174
	He	0.718	0.769	0.100	0.853	0.531	0.622	0.162
	F_{IS}	0.114	0.113	1.000	0.120	0.821	0.732	−0.076
Selayar	Na	6	4	1	4	2	4	3
	Ho	0.500	0.267	0.000	0.778	0.333	0.063	0.733
	He	0.762	0.691	0.000	0.616	0.491	0.561	0.540
	F_{IS}	0.344	0.614	–	−0.263	0.321	0.889	−0.358
Sebayur	Na	9	5	1	6	4	3	7
	Ho	0.938	0.500	0.000	0.588	0.308	0.533	0.529
	He	0.760	0.635	0.000	0.737	0.648	0.531	0.554
	F_{IS}	−0.234	0.213	–	0.202	0.525	−0.004	0.044
Bangka (Murex)	Na	8	6	6	9	3	4	7
	Ho	0.676	0.382	0.259	0.682	0.000	0.360	0.667
	He	0.812	0.760	0.460	0.819	0.362	0.682	0.786
	F_{IS}	0.167	0.497	0.436	0.168	1.000	0.472	0.152
Nudi Retreat	Na	10	8	3	8	3	9	9
	Ho	0.829	0.686	0.229	0.829	0.094	0.529	0.697
	He	0.822	0.836	0.295	0.820	0.090	0.749	0.803
	F_{IS}	−0.007	0.180	0.225	−0.010	−0.038	0.293	0.132
Doi	Na	11	6	3	7	3	4	3
	Ho	0.550	0.737	0.100	0.632	0.150	0.368	0.300
	He	0.711	0.778	0.184	0.809	0.141	0.464	0.516
	F_{IS}	0.227	0.053	0.456	0.219	−0.062	0.206	0.419
Jerewai	Na	6	3	2	5	1	5	5
	Ho	0.636	0.400	0.227	0.409	0.000	0.182	0.864
	He	0.614	0.580	0.201	0.594	0.000	0.319	0.670
	F_{IS}	−0.037	0.310	−0.128	0.311	–	0.430	−0.288
Tidore	Na	4	4	1	4	1	4	3
	Ho	0.107	1.000	0.000	0.444	0.000	0.143	0.571
	He	0.136	0.549	0.000	0.568	0.000	0.136	0.433
	F_{IS}	0.211	−0.821	–	0.217	–	−0.052	−0.320
Tonuu	Na	6	5	2	8	2	2	3
	Ho	0.526	0.632	0.050	0.947	0.526	0.158	0.526
	He	0.565	0.547	0.049	0.780	0.465	0.145	0.497
	F_{IS}	0.069	−0.154	−0.026	−0.215	−0.131	−0.086	−0.058

Table 3 continued

		Sh2-005	Sh2-006	Sh3-003	Sh3-004	Sh3-008	Sh4-001	Sh4-010
Alyui	Na	6	7	1	5	3	4	3
	Ho	0.588	0.375	0.000	0.684	0.167	0.474	0.632
	He	0.685	0.791	0.000	0.532	0.403	0.537	0.644
	F_{IS}	0.141	0.526	–	–0.286	0.586	0.119	0.019
Jefman	Na	7	5	1	4	1	4	5
	Ho	1.000	0.364	0.000	0.727	0.000	0.190	0.773
	He	0.716	0.543	0.000	0.691	0.000	0.178	0.675
	F_{IS}	–0.397	0.331	–	–0.052	–	–0.070	–0.145
Mayalibit	Na	4	8	1	2	3	2	2
	Ho	0.650	0.375	0.000	0.400	0.278	0.500	0.400
	He	0.499	0.729	0.000	0.320	0.356	0.375	0.320
	F_{IS}	–0.303	0.485	–	–0.250	0.221	–0.333	–0.250
Ambai	Na	8	6	2	6	3	3	2
	Ho	0.773	0.286	0.045	0.545	0.182	0.214	0.045
	He	0.798	0.707	0.044	0.694	0.549	0.253	0.044
	F_{IS}	0.031	0.596	–0.023	0.214	0.669	0.152	–0.023
Lemon	Na	10	10	1	4	3	2	5
	Ho	0.900	0.500	0.000	0.550	0.105	0.350	0.350
	He	0.788	0.838	0.000	0.571	0.400	0.489	0.348
	F_{IS}	–0.143	0.403	–	0.037	0.737	0.284	–0.007
Rumberpon	Na	5	2	1	4	4	3	3
	Ho	0.706	0.500	0.000	0.417	0.278	0.063	0.250
	He	0.739	0.375	0.000	0.462	0.622	0.432	0.227
	F_{IS}	0.044	–0.333	–	0.098	0.553	0.855	–0.103
Namatote	Na	8	7	1	3	3	2	3
	Ho	0.762	0.650	0.000	0.524	0.050	0.235	0.381
	He	0.785	0.711	0.000	0.475	0.141	0.291	0.390
	F_{IS}	0.029	0.086	–	–0.103	0.646	0.190	0.023
Mommon	Na	7	6	1	5	3	4	3
	Ho	0.500	0.533	0.000	0.500	0.333	0.267	0.500
	He	0.653	0.596	0.000	0.750	0.549	0.673	0.565
	F_{IS}	0.234	0.104	–	0.333	0.393	0.604	0.115

Shown for each locus and locality are the number of alleles observed (A), observed heterozygosity (Ho), and expected heterozygosity (He). F_{IS} is the inbreeding coefficient. Values in italics indicate significant departures from Hardy–Weinberg equilibrium after FDR correction

significant between Krakatau and all other regions (Table 7). The lowest pairwise F_{st} values were observed between Krakatau and Pulau Seribu ($F_{st} = 0.02$). The second lowest F_{st} value was between Krakatau and Bali ($F_{st} = 0.04$).

Immigration rates inferred from BayesAss+ (Tables 8 and 9) indicate that *P. damicornis* populations in Krakatau are 96% self-seeding with the remaining larval input from distant sources. In addition, Krakatau is identified as a larval source for *P. damicornis* populations in Aceh, Pulau Seribu, and Lombok. *S. hystrix* in Krakatau is 75% self-seeding with 23% of its larvae immigrating from Pulau Seribu. Krakatau is identified as a possible larval source for *S. hystrix* populations in Biak.

Discussion

Comparing levels of genetic diversity between Krakatau and other regions

Following the complete destruction of Krakatau in 1883 and the extermination of all marine life on the surrounding islands, genetic diversity has largely recovered for two species of reef-building corals through larval migration from the nearby upstream reefs of Pulau Seribu, and to a lesser extent from Bali and more distant sites in Indonesia. However, many populations in Krakatau do fall below the mean diversity values for Indonesia indicating either that recovery is not complete, or that diversity has declined

Table 4 *P. damicornis* locality statistics

Locality	N	Ng	Hz	Hz SD	<i>M</i>	<i>M</i> SD	BAPS cluster
Pulau Weh	22	22	0.42	0.09	0.81	0.27	15
Anak Krakatau	19	19	0.58	0.06	0.74	0.31	6
Anyer	21	20	0.46	0.08	0.69	0.28	9
Karang Serang	17	17	0.65	0.05	0.66	0.27	6
Rakata (Krakatau Besar)	26	26	0.50	0.07	0.68	0.29	2
Rakata Kecil	24	24	0.57	0.07	0.67	0.28	1
Sangiang	25	24	0.56	0.06	0.62	0.22	10
Sebesi	11	11	NA	NA	NA	NA	NA
Sebuku 1	20	20	0.54	0.09	0.67	0.30	1
Sebuku 2	23	23	0.56	0.09	0.62	0.35	1
Alam Kotok	22	22	0.52	0.08	0.75	0.28	1
Belat	20	20	0.53	0.09	0.68	0.26	11
Karang Congkak	18	18	0.60	0.06	0.74	0.28	11
Pramuka	10	10	NA	NA	NA	NA	NA
Pulau Pari	13	13	NA	NA	NA	NA	NA
Semak Daun	23	23	0.57	0.07	0.65	0.23	1
Seraya	21	21	0.62	0.05	0.71	0.26	13
Pemuteran	11	11	0.06	1.94	0.67	0.2	NA
Gili Trawangan	18	18	0.57	0.06	0.71	0.24	14
Barrang Lompo	30	30	0.68	0.04	0.75	0.23	12
Murex House Reef (Bangka)	2	2	NA	NA	NA	NA	NA
Nudi Retreat	26	26	0.55	0.07	0.60	0.24	8
Tanjung Pisok	25	21	0.50	0.07	0.71	0.29	8
Manado Tua	2	2	NA	NA	NA	NA	NA
Jerewai	17	17	0.58	0.05	0.71	0.26	3
Tidore	11	11	NA	NA	NA	NA	NA
Tonuu	21	21	0.60	0.07	0.64	0.28	7
Alyui	20	16	0.41	0.09	0.61	0.27	16
Gam	4	4	NA	NA	NA	NA	NA
Jefman	22	22	0.65	0.05	0.72	0.25	3
Kri	30	30	0.60	0.09	0.68	0.30	7
Manta Point	1	1	NA	NA	NA	NA	NA
Mayalibit	9	9	NA	NA	NA	NA	NA
Adoki	10	8	NA	NA	NA	NA	NA
Owi	9	9	NA	NA	NA	NA	NA
Ambai	15	15	0.61	0.07	0.62	0.22	3
Serui	6	6	NA	NA	NA	NA	NA
Lemon	18	18	0.44	0.06	0.64	0.28	4
Rumberpon	13	13	NA	NA	NA	NA	NA
Mauwara	23	21	0.61	0.05	0.59	0.23	5
Mommon	4	4	NA	NA	NA	NA	NA

Shown for each locality are the number of samples taken (N), the number of unique genotypes observed (Ng), Nei's unbiased gene diversity (Hz) and standard deviation, Garza-Williams statistic value (*M*) and standard deviation, and the cluster to which each population was assigned by BAPS. Conditional posterior probabilities of assignments were all ≥ 0.99 . Results are presented for localities with Ng ≥ 15 only

since the initial colonization. In many cases, reduced genetic diversity may persist for thousand of generations following a founder event (Hewitt 2000). Such reductions are of particular concern, especially in threatened and

endangered species, because reductions in genetic diversity may limit the ability of populations to respond to environmental change (Willi and Hoffmann 2009). For example, clonal populations of reef corals may be more

Table 5 *S. hystrix* locality statistics

Locality	N	Ng	Hz	Hz SD	<i>M</i>	<i>M</i> SD	BAPS cluster
Pulau Weh	25	23	0.51	0.05	0.81	0.28	18
Anak Krakatau	22	19	0.37	0.1	0.64	0.26	2
Rakata (Krakatau Besar)	18	14	NA	NA	NA	NA	NA
Sangiang	24	23	0.43	0.12	0.66	0.28	2
Sebesi	9	4	NA	NA	NA	NA	NA
Sebuku 1	24	23	0.44	0.11	0.58	0.23	2
Sebuku 2	25	15	0.41	0.09	0.71	0.32	2
Alam Kotok	20	20	0.41	0.09	0.67	0.34	2
Belat	21	20	0.46	0.11	0.73	0.30	2
Karang Congkak	21	20	0.41	0.14	0.67	0.31	2
Pramuka	23	21	0.41	0.11	0.72	0.30	2
Pulau Pari	38	38	0.53	0.11	0.5	0.18	2
Semak Daun	21	20	0.5	0.1	0.58	0.23	2
Pemuteran	41	41	0.41	0.11	0.63	0.3	1
Napoleon Reef	21	21	0.46	0.12	0.59	0.32	1
Seraya	20	18	0.42	0.08	0.64	0.36	8
Gili Trawangan	12	12	NA	NA	NA	NA	NA
Kukusan	1	1	NA	NA	NA	NA	NA
Bone Batang	24	21	0.55	0.11	0.38	0.16	6
Gusung, Selayar	23	21	0.54	0.1	0.70	0.31	9
Sebayur	17	17	0.57	0.1	0.61	0.31	12
Batu Gosok	12	12	NA	NA	NA	NA	NA
Murex House Reef (Bangka)	34	34	0.68	0.07	0.70	0.29	10
Nudi Retreat	36	28	0.64	0.12	0.82	0.16	3
Tanjung Pisok	5	5	NA	NA	NA	NA	NA
Pulau Doi	20	19	0.53	0.11	0.78	0.30	3
Jerewai	22	21	0.44	0.1	0.79	0.25	14
Tidore	28	15	0.27	0.1	0.58	0.33	7
Tonuu	20	17	0.45	0.1	0.64	0.34	15
Alyui	19	17	0.53	0.1	0.61	0.24	16
Gam	1	1	NA	NA	NA	NA	NA
Jefman	22	17	0.41	0.13	0.66	0.27	17
Kri	9	9	NA	NA	NA	NA	NA
Mayalibit	20	20	0.38	0.09	0.49	0.30	19
Adoki	12	12	NA	NA	NA	NA	NA
Owi	9	8	NA	NA	NA	NA	NA
Rasbar	4	4	NA	NA	NA	NA	NA
Ambai	22	20	0.45	0.13	0.72	0.28	4
Lemon	20	20	0.5	0.11	0.67	0.31	13
Rumberpon	19	19	0.42	0.1	0.79	0.31	5
Namatote	21	21	0.41	0.11	0.81	0.28	20
Mommon	18	18	0.56	0.1	0.70	0.32	11

Shown for each locality are the number of samples taken (N), the number of unique genotypes observed (Ng), Nei's unbiased gene diversity (Hz) and standard deviation, Garza-Williams statistic value (*M*) and standard deviation, and the cluster to which each population was assigned by BAPS. Conditional posterior probabilities of assignments were all ≥ 0.99 . Results are presented for localities with $Ng \geq 15$ only

susceptible to bleaching if the most common clone is thermally sensitive (Edmunds 1994). However, this is probably not the pattern observed in Krakatau. Coral

genetic diversity in this very new habitat is comparable and, in the case of *P. damicornis*, higher than other localities in Indonesia. These observations show that it is

Fig. 2 a *P. damicornis* BAPS cluster assignments with close-up view of the Krakatau region. Numbers indicate the cluster to which each study site was assigned, given in Table 4.
b *S. hystrix* BAPS cluster assignments with close-up view of the Krakatau region. Numbers indicate the cluster to which each study site was assigned, given in Table 5

Table 6 *P. damicornis*: Pairwise F_{st} among regions

	#	1	2	3	4	5	6	7	8	9	10	11	12
Aceh	1												
Krakatau	2	0.00											
Pulau Seribu	3	0.00	0.03										
Bali	4	0.00	0.03	0.04									
Lombok	5	0.00	0.04	0.05	0.00								
Makassar	6	0.00	0.10	0.11	0.05	0.06							
Northern Sulawesi	7	0.00	0.04	0.03	0.03	0.06	0.13						
Halmahera	8	0.04	0.06	0.05	0.01	0.05	0.03	0.02					
Raja Ampat	9	0.00	0.05	0.02	0.02	0.09	0.10	0.05	0.00				
Biak	10	0.00	0.01	0.00	0.00	0.07	0.07	0.04	0.00	0.00			
Yapen	11	0.00	0.16	0.13	0.06	0.18	0.08	0.13	0.00	0.06	0.03		
Manokwari	12	0.00	0.10	0.08	0.12	0.21	0.21	0.10	0.09	0.11	0.08	0.21	
Kaimana	13	0.00	0.04	0.02	0.00	0.11	0.10	0.03	0.00	0.02	0.01	0.11	0.09

Bold values indicate significance at $p = 0.05$ level after FDR correction

Table 7 *S. hystrix*: Pairwise F_{st} among sub-regions

	#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Aceh	1															
Krakatau	2	0.22														
Pulau Seribu	3	0.22	0.02													
Bali	4	0.22	0.04	0.04												
Flores	5	0.24	0.22	0.19	0.13											
Selayar	6	0.28	0.13	0.09	0.12	0.12										
Makassar	7	0.26	0.22	0.19	0.13	0.10	0.14									
Northern Sulawesi	8	0.14	0.10	0.10	0.05	0.10	0.08	0.13								
Halmahera	9	0.13	0.12	0.11	0.07	0.11	0.11	0.15	0.07							
Raja Ampat	10	0.17	0.21	0.18	0.15	0.11	0.09	0.15	0.08	0.10						
Biak	11	0.20	0.20	0.18	0.15	0.11	0.09	0.16	0.07	0.12	0.09					
Yapen	12	0.32	0.35	0.32	0.33	0.28	0.32	0.35	0.23	0.21	0.19	0.21				
Manokwari	13	0.31	0.36	0.33	0.31	0.25	0.28	0.31	0.23	0.21	0.17	0.19	0.14			
Teluk Cenderawasih	14	0.3	0.29	0.27	0.25	0.27	0.32	0.29	0.18	0.19	0.15	0.18	0.13	0.14		
Kaimana	15	0.37	0.34	0.33	0.27	0.27	0.35	0.22	0.20	0.26	0.24	0.26	0.46	0.42	0.43	
Fakfak	16	0.18	0.13	0.13	0.06	0.13	0.16	0.15	0.06	0.06	0.12	0.11	0.28	0.27	0.29	0.19

Bold values indicate significance at $p = 0.05$ level after FDR correction (All values were significant)

possible for coral reef animals to re-establish and recover genetic diversity in a matter of decades and centuries rather than millennia.

Comparison between the two species

Previous research into the population genetic patterns of corals (Ayre and Hughes 2004) leads one to expect faster recovery and higher genetic diversity in *P. damicornis* relative to *S. hystrix*. This hypothesis was also based on an unusually long larval life span in *P. damicornis* (Richmond 1987), possibly leading to dispersal from varied and distant

sources. Although a direct comparison to larval life span in *S. hystrix* is not available, these genetic patterns support previous genetic studies, that larval dispersal may be more limited in *S. hystrix*.

A difference in genetic diversity in Krakatau between the two species is clear, but probably does not indicate a difference in the degree of recovery. In Krakatau the genetic diversity (Hz) of *P. damicornis* (mean Hz = 0.55) is significantly higher than that of *S. hystrix* (mean Hz = 0.41). While this might be taken to indicate more rapid recovery in *P. damicornis* due to higher gene flow, genetic diversity is typically higher in *P. damicornis* than

Table 8 *P. damicornis* immigration matrix

		1	2	3	4	5	6	7	8	9	10	11	12	13
Aceh	1	0.69	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Krakatau	2	<u>0.07</u>	0.96	<u>0.07</u>	0.01	<u>0.09</u>	0.00	0.00	0.01	0.01	0.01	0.00	0.01	0.01
Pulau Seribu	3	0.04	0.01	0.89	0.01	0.01	0.00	0.00	0.02	0.00	0.01	0.00	0.01	0.01
Bali	4	0.01	0.01	0.00	0.81	<u>0.05</u>	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.02
Lombok	5	0.01	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Makassar	6	0.01	0.00	0.00	0.01	<u>0.08</u>	0.99	0.00	0.01	0.00	<u>0.05</u>	0.00	0.00	0.02
Northern Sulawesi	7	0.02	0.01	0.01	<u>0.05</u>	0.04	0.00	0.99	0.01	<u>0.06</u>	<u>0.02</u>	0.00	0.00	<u>0.02</u>
Halmahera	8	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.67	0.00	0.01	0.00	0.01	0.00
Raja Ampat	9	<u>0.07</u>	0.00	0.00	0.01	0.01	0.00	0.00	<u>0.11</u>	0.82	<u>0.07</u>	0.01	0.00	0.01
Biak	10	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.68	0.00	0.00	0.00
Yapen	11	0.02	0.01	0.01	<u>0.08</u>	0.01	0.00	0.00	<u>0.14</u>	<u>0.09</u>	<u>0.07</u>	0.96	0.01	0.00
Manokwari	12	<u>0.07</u>	0.00	0.01	0.02	0.01	0.00	0.00	0.01	0.00	<u>0.06</u>	0.00	0.95	<u>0.22</u>
Kaimana	13	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.68

All standard deviation values are ≤ 0.05 . Bold values indicate self-recruitment rates for each region. Underlined values highlight immigration rates of $\geq 5\%$

Table 9 *S. hystrix* immigration matrix

	#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Aceh	1	0.99	0.00	0.00	0.00	0.00	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Krakatau	2	0.00	0.75	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.00	<u>0.12</u>	0.00	0.01	0.00	0.00	0.01
Pulau Seribu	3	0.00	<u>0.23</u>	0.99	0.00	0.00	<u>0.07</u>	0.00	0.00	<u>0.18</u>	0.00	0.00	0.00	0.01	0.00	0.00	0.01
Bali	4	0.00	0.00	0.00	0.85	0.01	0.01	<u>0.05</u>	0.00	0.00	0.00	0.01	0.00	0.03	0.00	0.00	0.01
Flores	5	0.00	0.00	0.00	0.00	0.98	0.01	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.01
Selayar	6	0.00	0.00	0.00	0.00	0.00	0.68	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Makassar	7	0.00	0.00	0.00	0.00	0.01	<u>0.15</u>	0.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Northern Sulawesi	8	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Halmahera	9	0.00	0.00	0.00	<u>0.12</u>	0.00	0.01	0.01	<u>0.06</u>	0.73	0.00	0.00	0.00	0.00	0.00	0.00	<u>0.10</u>
Raja Ampat	10	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	<u>0.07</u>	0.99	0.00	0.00	0.00	0.00	0.00	0.01
Biak	11	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.01
Yapen	12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.01
Manokwari	13	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.92	0.00	0.00	0.01
Teluk Cenderawasih	14	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.01
Kaimana	15	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	<u>0.11</u>
Fakfak	16	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68

All standard deviation values are ≤ 0.05 . Bold values indicate self-recruitment rates for each region. Underlined values highlight immigration rates of $\geq 5\%$

in *S. hystrix* throughout Indonesia suggesting that the differences observed in Krakatau are typical for Indonesian reefs. Considering this, recovery relative to the rest of Indonesia has largely occurred for both species.

Identifying larval sources for the colonization of Krakatau

The observed settlement and growth of reef corals less than 10 years following Krakatau's destruction (Sluiter 1890)

indicates that dispersal to the Krakatau region from outside regions occurred almost immediately following the complete destruction of the coral reef biota. Coral larvae typically settle shortly after release meaning that, regardless of dispersal potentials, actual mean dispersal distance is very low (Sammarco and Andrews 1989; Isomura and Nishihira 2001). Results from pairwise gene flow estimates and the Bayesian assignment method implemented in BAPS indicate that *P. damicornis* populations in Krakatau have been colonized primarily by immigration from the closest reef

system in Pulau Seribu, but supplemented from larval sources throughout the Indonesian Archipelago and possibly unsampled regions elsewhere. The rapid recovery of genetic diversity on Krakatau has also been observed for the mantis shrimp, *Haptosquilla pulchella* where larval sources were largely dominated by localities in the Java Sea (Barber et al. 2002). Similarly for *P. damicornis*, Rakata Kecil, Sebuku 1 and Sebuku 2 from Krakatau form one genetic cluster (Cluster #1) that also includes two sites from Pulau Seribu (Alam Kotok and Semak Daun), suggesting that Pulau Seribu is the most likely source population for these reefs. This inference is supported most strikingly by pairwise F_{st} estimates which are lower between Krakatau and Pulau Seribu than between Krakatau and any other region with only two exceptions. First, there was no significant F_{st} between Krakatau and Pulau Weh in Aceh indicating that northern Sumatra may serve as an additional source population. Second, pairwise F_{st} was not significant between Krakatau and Biak; however, this is not likely due to connectivity given the geographic distance between the two regions. Pairwise F_{st} estimates also identify Bali as a possible source for the initial colonization of *P. damicornis* populations in Krakatau, supporting the hypothesis that the Java Sea was a major larval source for the recovery of Krakatau. In addition, Anak Krakatau and Karang Serang cluster only with each other in Cluster #6 while, Sangiang, Anyer, and Rakata each clusters alone suggesting that not all larval sources have been sampled.

Similarly, larval sources for *S. hystrix* populations in Krakatau are dominated by nearby, upstream Java Sea populations in Pulau Seribu and Bali. Sangiang, Sebuku 1, Sebuku 2, and Anak Krakatau cluster with all populations in Pulau Seribu to form one genetic cluster that occurs nowhere else in Indonesia (Table 5). In addition, the lowest pairwise F_{st} values observed anywhere in Indonesia in this species are between Krakatau and Pulau Seribu ($F_{st} = 0.02$), between Krakatau and Bali ($F_{st} = 0.04$), and between Bali and Pulau Seribu ($F_{st} = 0.04$). These results are further supported by the migration estimates from BayesAss+, which identifies 23% of the corals in Krakatau as migrants from Pulau Seribu. Taken together, these data suggest that these *S. hystrix* populations most likely originated via the immigration of coral larvae from the Java Sea. This is reasonable considering that surface currents in the Sunda Strait flow in a southwesterly direction from the Java Sea toward the Indian Ocean throughout the year (Wyrki 1961). This also reinforces previous observations that populations of this extremely philopatric species typically depend on nearby sources of larvae for recovery (Underwood et al. 2007).

Long distance dispersal serves as a means by which coral populations can be founded and maintained over evolutionary time. Because the islands of Krakatau are

geographically isolated from adjacent source populations, dispersal is likely to have initially occurred from nearby, unaffected reefs. Pairwise F_{st} estimates indicate connectivity between Krakatau and Pulau Seribu support the original hypothesis. The assignment test implemented by BayesAss+, however, indicates not only that the Krakatau region is now predominantly self-seeding, but may also be serving as a larval source. Immigration estimates that identify Krakatau as connected to more distant sites upstream, including its function as a larval source, seem unlikely because of sea surface currents which flow from the Java Sea toward the Indian Ocean via the Sunda Strait. Nevertheless, immigration estimates indicating dispersal from Krakatau to Pulau Seribu and Biak, for example, may indicate unusual dispersal events mediated by pumice—which is very common in the Krakatau region (*personal observation*)—or another rafting material (Jokiel 1984) during periods of atypical sea surface circulation. Connectivity over great distances has also been observed among East African *P. damicornis* populations while adjacent sites were also found to be genetically distinct (Souter et al. 2009). Coupled genetic, demographic, and physical oceanographic models may help resolve some of the apparent discontinuities between genetics and geography in coral population genetic studies (Galindo et al. 2006).

Conservation implications

The volcanic eruption and virtually instantaneous destruction of the coral reef ecosystems of Krakatau was a highly unusual event. However, many coral reef ecosystems throughout the world are now experiencing rapid and near-complete degradation. Mass mortalities of coral populations are projected to become increasingly common in the near future (McClanahan 2002; Gardner et al. 2003). Threats to coral reef ecosystems are well documented (Burke et al. 1997; Wilkinson 2004; reefsatrisk.wri.org); however, additional scientific data are still needed for their effective conservation. Connectivity has been listed as one of the most critical gaps in scientific knowledge needed for marine conservation (Sale et al. 2005). This is due largely to our need to accurately predict how recovery can occur following extreme (or even chronic) disturbance events. It is important to identify those populations that will serve as sources to areas that are likely to experience drastic population decline in the near future such as climate change-induced coral bleaching and mortality (Underwood et al. 2007) and understand how remote coral reefs and MPAs may serve as larval sources and sinks (McClanahan et al. 2005; Miller and Ayre 2008). In the case study presented here, it was the availability of larvae in Pulau Seribu and Bali, and the dispersal corridor in the Java Sea, that served to repopulate coral reefs in the Krakatau region.

The protection of potential source populations may prove critical in the recovery of degraded coral populations. However, the notion that protected areas can serve as sources of larvae and adults to surrounding areas, called the “spillover effect” has only been demonstrated in a limited number of cases, and typically only apply to adult fish and not their larvae (Palumbi 2004; Alcalá et al. 2005; Ashworth and Ormond 2005; Sanchirico et al. 2006). Due to the highly self-seeding nature of coral populations and many marine ecosystems, external sources of larvae may not sustain downstream populations of coral reef animals over significant periods of time (Cowen et al. 2006). More likely, larval sources will serve to repopulate surrounding areas should disaster occur, and then only initially. This is highly dependent on the existence of healthy source populations. A complete recovery will depend on local sources of larvae in the form of healthy adult corals.

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