

Rapid recovery of genetic diversity of stomatopod populations on Krakatau: temporal and spatial scales of marine larval dispersal

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Although the recovery of terrestrial communities shattered by the massive eruption of Krakatau in 1883 has been well chronicled, the fate of marine populations has been largely ignored. We examined patterns of genetic diversity in populations of two coral reef-dwelling mantis shrimp, *Haptosquilla pulchella* and *Haptosquilla glyptocercus* (Stomatopoda: Protosquillidae), on the islands of Anak Krakatau and Rakata. Genetic surveys of mitochondrial cytochrome oxidase *c* (subunit 1) in these populations revealed remarkably high levels of haplotypic and nucleotide diversity that were comparable with undisturbed populations throughout the Indo-Pacific. Recolonization and rapid recovery of genetic diversity in the Krakatau populations indicates that larval dispersal from multiple and diverse source populations contributes substantially to the demographics of local populations over intermediate temporal (tens to hundreds of years) and spatial scales (tens to hundreds of kilometres). Natural experiments such as Krakatau provide an excellent mechanism to investigate marine larval dispersal and connectivity. Results from stomatopods indicate that marine reserves should be spaced no more than 50–100 km apart to facilitate ecological connectivity via larval dispersal.

Keywords: larval dispersal; recruitment; population genetics; marine reserve; Krakatau; stomatopod

1. INTRODUCTION

Prior to 1883, the island of Krakatau, located in the Sunda Strait west of Java (figure 1), consisted of three volcanoes, Rakata, Danan and Perbuwatan. On 26 August 1883, after three months of minor activity, a catastrophic eruption destroyed over two thirds of Krakatau, leaving only a fraction of Rakata remaining (Simkin & Fiske 1983). Within 18 h, the eruption deposited *ca.* 14 km³ of volcanic material subaqueously within a 15 km radius (figure 1*b*) of the island (Mandeville *et al.* 1996). Submarine pyroclastic flows (an unsorted mixture of hot gases, ash, pumice and other volcanic materials) averaging 20 m in thickness (Sigurdsson *et al.* 1991) blanketed the sea floor at temperatures of 475–550 °C (Mandeville *et al.* 1994), effectively sterilizing the entire Krakatau island group above and below water; neighbouring islands Sebesi, Sebuku and Lagoendi were similarly buried (Verbeek 1885).

Researchers quickly realized the potential of Krakatau for understanding the colonization and organization of a tropical ecosystem. Following the initial observations of Verbeek (1885), a succession of authors (Trueb 1888; Penzig 1902; Ernst 1908) documented the early stages of recovery of the terrestrial fauna and several volumes have been written on the subject (Dammerman 1929; Docters van Leeuwen 1929; Flenley & Richards 1982; Thornton 1996). However, with a few minor exceptions, the recovery of nearshore marine ecosystems of Krakatau has been overlooked. Five years after the eruption, Sluiter (1890) documented coral recruits on basaltic boulders and, in

1889, Strubell (as cited in Dammerman 1929) noted the presence of several marine gastropods. Umbgrove (1930) found no trace of Sluiter's nascent coral reefs; severe erosion of the Rakata's pumice cliffs apparently had completely buried the community.

Previous studies of coral reefs impacted by volcanic activity have documented the rapid recolonization of corals onto volcanic substrates (Tomascik *et al.* 1996) and the gradual succession of coral species over time (Grigg & Maragos 1974) where portions of existing reef communities have been inundated by lava flows. By contrast, the complete destruction of the coral reef communities surrounding the islands of Krakatau allows the observation of the reassembly, *de novo*, of an entire coral reef ecosystem. Unfortunately, the opportunity to observe much of this process on Krakatau has largely passed in the 118 years since the eruption. However, the natural experiment afforded by Krakatau and the emergence in the 1930s of Anak Krakatau, a new volcanic island born in the caldera of Krakatau (Simkin & Fiske 1983), still provide an excellent opportunity for studying marine colonization processes such as dispersal and recruitment.

Many vertebrate and invertebrate coral reef species disperse via larval developmental stages that enter the plankton and travel on ocean currents (Thresher & Brothers 1989; Wellington & Victor 1989, 1992; McEdward 1995). For the few species where data are available, there is a positive relationship between length of larval period and dispersal distance (Shanks *et al.* 2002), resulting in the presumed ecological and genetic connectivity among disjunct marine populations (see Roberts 1997). This notion is supported by studies reporting genetic homogeneity among populations of many marine species with high dispersal potential (for reviews and exceptions, see Palumbi

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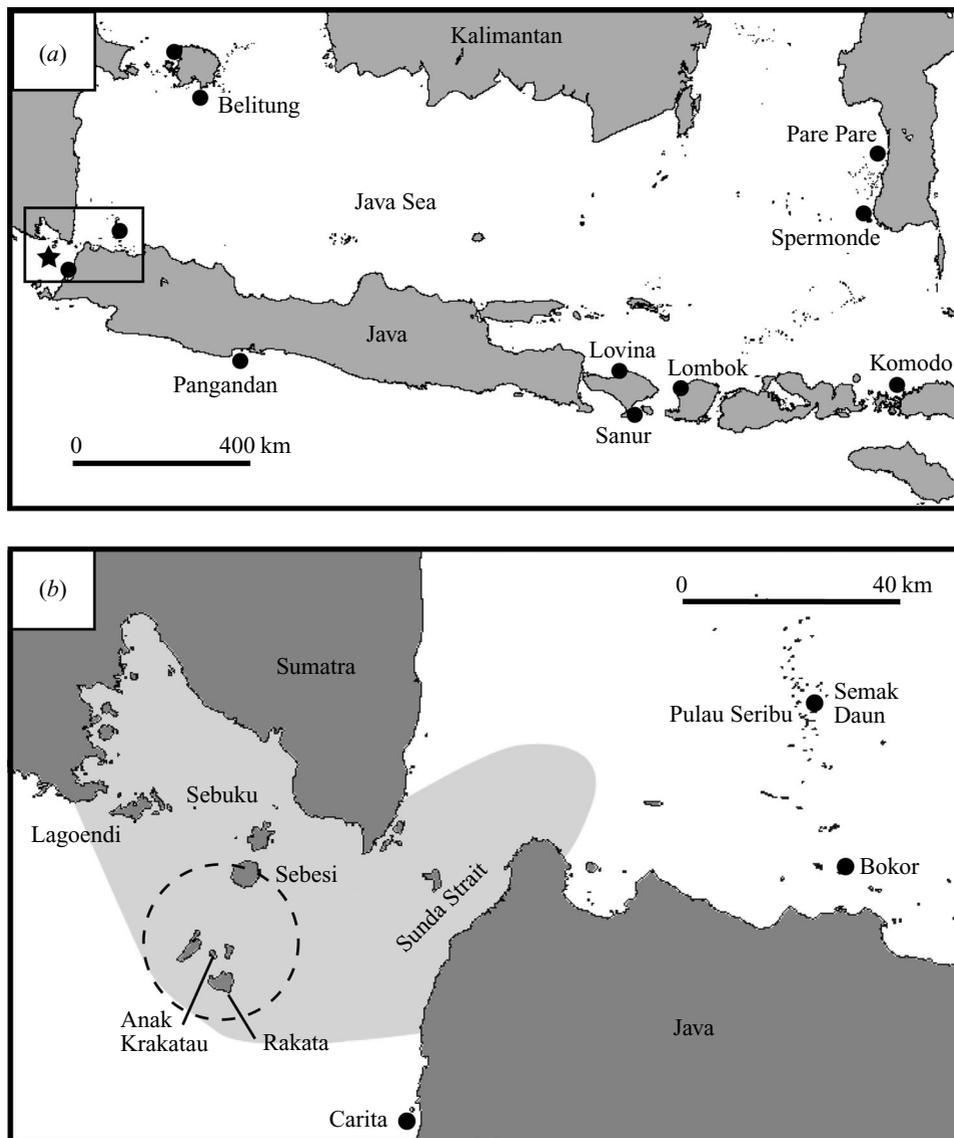


Figure 1. (a) Map of southern Indonesia including collecting localities (filled circles) from Belitung, Java, southern Sulawesi, and Bali (Lovina, Sanur), Lombok and Komodo of the Lesser Sunda Islands. The Krakatau island group in the Sunda Strait is marked by a star. (b) A detailed view of the islands of Krakatau and neighbouring islands including nearby collecting localities (filled circles). Dashed circle marks a 15 km radius surrounding the islands of Krakatau. Light grey shading represents the extent of the pyroclastic deposits from the 1883 eruption of Krakatau (after Carey *et al.* 1996).

1992, 1995, 2002). However, crustacean larvae have various behaviours to facilitate local larval retention (Lambert & Epifanio 1982; Cronin & Forward 1986; Young 1995) and have been shown to fall short of their dispersal potential (Knowlton & Keller 1986; Burton & Lee 1994). Similarly, recent research on two families of coral reef fishes (damselfishes and wrasses) has shown that dispersive larvae that spend four weeks in the plankton often stay close to their point of origin and that up to 50–60% may settle back on their natal reefs (Jones *et al.* 1999; Swearer *et al.* 1999). These results clearly demonstrate that larval dispersal may often be more limited than believed, based on larval period alone, and that some larvae may successfully recruit after only short dispersal distances. However, the extent to which larval dispersal results in successful recruitment of larvae into the breeding stock of distant populations remains largely unknown.

Although high larval retention and high gene flow may seem paradoxical, it is possible that self-seeding over eco-

logical time-scales due to frequent short dispersal, and genetic mixing over evolutionary time-scales due to less frequent long-distance gene flow, are completely compatible. Genetic and ecological studies address larval dispersal on extremely different spatial and temporal scales. Ecological studies follow the fate of individuals or groups of larvae over very short time-scales (a single generation) and distances of the order of kilometres. By contrast, genetic studies of marine populations typically focus on broader processes that act over evolutionary time-scales and thousands of kilometres (Palumbi 1994). Few studies bridge the gap between these extremes, yet understanding dispersal over 10–100 generations or 10–100 kilometres is crucial to an understanding of the ecological function of marine populations, as well as the management of marine resources, the design of marine reserves, the dynamics of invasive species and the impact of environmental change. The recovering reefs of Krakatau offer a unique opportunity to study the dynamics of marine dispersal at inter-

mediate scales of time (tens to hundreds of years) and space (tens to hundreds of kilometres)—at most 50–100 generations have passed since the Krakatau reefs were destroyed and these reefs are separated from mainland source populations by at least 40 km, requiring moderate dispersal.

Indo-Pacific populations of the stomatopod *Haptosquilla pulchella* Miers (a benthic marine crustacean associated with coral reefs) display striking patterns of regional genetic differentiation over scales of hundreds of kilometres, suggesting limited pelagic dispersal (Barber *et al.* 2000), yet populations along continuous shorelines can be genetically homogeneous over thousands of kilometres (Barber *et al.* 2002a). Similar patterns have been observed in a congener, *Haptosquilla glyptocercus* Wood-Mason (Barber *et al.* 2002b).

In this paper, we investigate patterns of genetic diversity in populations of *H. pulchella* (Protosquillidae) and *H. glyptocercus* on the islands of Rakata and Anak Krakatau to understand better the process of larval dispersal over intermediate temporal and spatial scales. If dispersal in these taxa is rare over moderate geographical distances and is followed by local self-seeding, a founder effect (Mayr 1942), evidenced by a signal of reduced genetic variation, is expected in populations from Krakatau. By contrast, if moderate dispersal is common on ecological time-scales, genetic variation will accumulate rapidly during the recovery of Krakatau populations and the resulting populations will reflect regional genetic diversity. The regional genetic differentiation in both taxa, and especially the geographical placement of Krakatau near a pronounced genetic break between *H. pulchella* populations (Barber *et al.* 2000, 2002a), provide an excellent signal to pinpoint potential source populations of the larval colonists.

2. METHODS

The islands of Rakata and Anak Krakatau were visited on an exploratory trip in October 2000 and specimens were collected and preserved in ethanol for genetic analysis. Mitochondrial cytochrome oxidase *c* subunit 1 (CO1) sequences were obtained for 11 *H. pulchella* from Anak Krakatau and 11 *H. glyptocercus* from Rakata following the methods of Barber *et al.* (2002a). These sequences were then compared with data from 382 individuals from a total of 23 additional populations of *H. pulchella* and with 236 individuals from an additional 23 populations of *H. glyptocercus*. These populations span the Indo-Pacific, including Papua New Guinea, the Philippines and Indonesia.

Molecular diversity indices for all populations of both species were calculated using ARLEQUIN (Schneider *et al.* 2000). For all populations, haplotype diversity (h) and variance were calculated following Nei (1987) and nucleotide diversity (π) and variance were calculated following Tajima (1983) and Nei (1987). Estimations of θ_s ($\theta = 2N\mu$ estimated from the number of segregating sites) were calculated following Watterson (1975) with variance estimates calculated following Tajima (1989).

3. RESULTS

Although *H. glyptocercus* is commonly observed on reefs inhabited by *H. pulchella* (P. H. Barber, personal observation), only the latter were observed on the Anak Krakatau. Along the northern shore of the island, the

water had a milky appearance and the benthic environment consisted of unconsolidated volcanic materials mixed with volcanic conglomerates and was sparsely covered with an unidentified macro alga. Reef development on the steep slopes of this nearly barren volcanic cone was restricted to a small outcrop of basaltic boulders and consisted of spats and juvenile corals with no more than a few small branches. Rather than inhabiting cavities in coral or coral rubble, as is typical of protosquillids, individual stomatopods occupied cavities in welded volcanic deposits.

On the southeastern shore of Rataka, both *H. pulchella* and *H. glyptocercus* were observed, but the latter was the most common and was the only species collected. Reef development was moderate and appeared more typical of low-diversity Sunda Shelf coral reef environments. The very narrow fringing reef bordered only a few hundred metres of coastline and the remaining observed coastline consisted of unconsolidated volcanic deposits.

A total of 625 base pairs of CO1 data were obtained from 11 individuals each of *H. pulchella* and *H. glyptocercus* from populations on Anak Krakatau and Rakata, respectively. Among *H. pulchella*, 9 out of 11 individuals had unique mitochondrial haplotypes. Genetic diversity measures ($h = 0.964$, $\pi = 0.00617$, $\theta_s = 4.438$) were similar to *H. pulchella* populations throughout the Indo-Pacific, where h ranged from 1.0 to 0.667 (mean = 0.894), π ranged from 0.0442 to 0.00234 (mean = 0.00893) and θ_s ranged from 21.002 to 2.121 (mean = 6.773). On Rakata, 10 out of 11 *H. glyptocercus* were genetically distinct ($h = 0.982$), but π and θ_s were relatively low (0.00582 and 4.780, respectively). Across the Indo-Pacific, h ranged from 1.0 to 0.933 (mean = 0.981), π ranged from 0.0376 to 0.00382 (mean = 0.0126) and θ_s ranged from 28.34 to 2.94 (mean = 9.877). All values and variances are reported in tables 1 and 2.

The 11 *H. pulchella* haplotypes from Anak Krakatau were compared with haplotypes from 382 individuals representing 23 Indonesian and the West Pacific localities. Five of these haplotypes were shared with one or more localities, but only from populations on Java, Bali, Komodo and Lombok (table 3). Three of these haplotypes were widely distributed among five or six populations, including both nearby Java populations from Carita and Pulau Seribu (50 km southeast and 140 km to the east, respectively), as well as distant populations from Bali, Lombok and Komodo (up to 1600 km eastward). The fourth haplotype was shared with both Pulau Seribu and Lombok (1600 km) and a fifth was shared only with the Lombok population. Surprisingly, although haplotypes were shared over distances up to 1600 km, none was characteristic of the genetically distinct populations of Belitung located only 400 km north and directly upstream of the islands of Krakatau (Wyrteki 1961) and none was characteristic of any populations north of the Java Sea.

Similarly, 11 *H. glyptocercus* haplotypes from Rakata were compared with 247 CO1 sequences obtained from 24 Indonesian and West Pacific populations and only two haplotypes were shared with other localities. Again, haplotypes were shared only with Java or the Lesser Sunda Island populations (Bali, Lombok, Komodo) and none was shared with populations north of the Java Sea (table 3); one haplotype was shared with Pulau Seribu (140 km

Table 1. Molecular diversity indices for *Haptosquilla pulchella*.

(Calculated by ARLEQUIN v. 2.0 (Schneider *et al.* 2000). Values of haplotype diversity (h), nucleotide diversity (π) and θ_s are reported with variance. Values are in descending order by haplotype diversity. Anak Krakatau data are highlighted in bold and median values are at the foot. All collection localities are from Indonesia with the exception of the Philippines and Papua New Guinea.)

location	n	h	var(h)	π	var(π)	θ_s	var(θ_s)
Santa Cruz, Philippines	10	1	0.05	0.01	0.006	10	19
Toli Toli, Sulawesi	13	0.99	0.04	0.003	0.002	4	3.2
Carita, Java	16	0.98	0.03	0.008	0.005	8	11
Pare Pare, Sulawesi	10	0.98	0.05	0.004	0.003	5	4.8
Sengigi, Lombok	10	0.98	0.05	0.039	0.021	18	58
Tanjung Pandang, Belitung	10	0.98	0.05	0.005	0.003	4	4.2
Sangihe, Talaud	20	0.97	0.03	0.009	0.005	7	7.9
Lovina, Bali	48	0.97	0.01	0.021	0.011	16	22
Anak Krakatau	11	0.96	0.05	0.006	0.004	4	4.3
Madang, Papua New Guinea	8	0.96	0.08	0.005	0.004	5	5.4
Bokor, Pulau Seribu, Java	14	0.96	0.05	0.015	0.008	9	15
Labun Bajo, Komodo	6	0.93	0.12	0.044	0.026	21	104
Batu Hitam, Belitung	10	0.93	0.07	0.004	0.003	4	3.8
Nogsa, Riau	21	0.92	0.04	0.005	0.049	7	6.6
Long Island, Papua New Guinea	10	0.91	0.08	0.003	0.002	2	1.4
Obi	9	0.89	0.09	0.007	0.004	6	8.6
Sanur, Bali	16	0.87	0.08	0.007	0.004	8	9.1
Pulau Tiga, Sulawesi	14	0.81	0.09	0.002	0.002	2	1.3
Kuandang, Sulawesi	10	0.8	0.1	0.002	0.002	2	1.4
Lembah, Sulawesi	10	0.78	0.14	0.003	0.002	3	2.1
Pantaloan, Sulawesi	10	0.78	0.14	0.003	0.002	3	2.1
Una Una, Togian Islands	21	0.74	0.08	0.003	0.002	3	2
Spermonde, Sulawesi	76	0.71	0.06	0.002	0.002	7	4.8
Malalayan, Sulawesi	10	0.67	0.16	0.004	0.003	4	3.1
median		0.930		0.0052		4.61	

to the east) and the second was shared with both Pulau Seribu and Sanur, Bali (1200 km to the east).

In both species, haplotypes from Krakatau were more likely to be shared with nearby than distant populations. For *H. pulchella*, 18.2% (4 out of 22) of the haplotypes from nearby populations Carita and Pulau Seribu were shared with the Anak Krakatau population. By comparison, only 10% (5 out of 50) of haplotypes from the distant Lesser Sunda Island populations (Bali, Lombok, Komodo) were shared with Anak Krakatau. Similarly for *H. glyptocercus*, 18.9% (2 out of 11) of the haplotypes from the Pulau Seribu population were shared with the Rakata populations, whereas only 4% (1 out of 25) of the Sunda Islands haplotypes were shared.

4. DISCUSSION

Genetic diversity measures in two stomatopod species from the recovering reefs of Krakatau were as high as values from populations presumed to be long-established throughout Indonesia and the West Pacific, demonstrating both substantial recolonization and a remarkable gain of genetic variability over historical time periods. In both species, haplotypes were identical to those found in nearby populations on Java as well as distant populations such as Bali, Lombok and Komodo, up to 1600 km away. Although haplotypes were shared over scales of hundreds of kilometres, surprisingly none of the shared haplotypes was characteristic of the genetically distinct populations

observed on Belitung, 400 km directly upstream of the islands of Krakatau. That all shared haplotypes from Anak Krakatau have origins in Java or the Lesser Sunda Islands suggests that dispersal over distances of 400 km may be extremely rare and/or that there are physical or ecological limits to dispersal across the Java Sea (Barber *et al.* 2000). Because haplotypes were more than twice as likely to be shared with nearby than distant populations, dispersal appears to be limited, favouring recruitment from more proximal localities (e.g. Carita and Pulau Seribu) on ecological time-scales.

The establishment of a new population from a small number of colonists may result in a founder effect, where genetic variability of the new population is reduced compared with founding populations (Mayr 1942). This pattern has been most commonly observed in terrestrial populations recolonized following the last glacial epoch (Hewitt 1996, 2000) and can lead to the fixation (Phillips 1994; Luikart & Allendorf 1996; Wilson *et al.* 1996; Barber 1999) or near fixation (Danzmann & Ihssen 1995; Luikart & Allendorf 1996) of presumably neutral markers over wide geographical ranges or at individual localities (Fedorov *et al.* 1996). If newly founded populations increase in size more from local reproduction than from immigration (i.e. self-seeding), the genetic contribution of future migrants to genetic diversity will be reduced in comparison with the original colonists, resulting in decreased genetic variability that can persist for thousands of generations (Berry 1996; Hewitt 2000).

Table 2. Molecular diversity indices for *Haptosquilla glyptocercus*.

(Calculated by ARLEQUIN v. 2.0 (Schneider *et al.* 2000). Values of haplotype diversity (h), nucleotide diversity (π) and θ_s are reported with variances. Values are in descending order by haplotype diversity. Values from Rakata are highlighted in bold and median values are at the foot. All collection localities are from Indonesia with the exception of the Philippines and Papua New Guinea.)

locality	n	h	var(h)	π	var(π)	θ_s	var(θ_s)
Dodepo, Sulawesi	10	1	0.045	0.0074	0.0045	6.01	7.62
Gorontalo, Sulawesi	10	1	0.045	0.0106	0.0062	10.25	19.98
Komodo	9	1	0.052	0.0105	0.0062	9.2	17.31
Kwandang, Sulawesi	11	1	0.039	0.0105	0.0061	9.9	17.89
Lombok	10	1	0.045	0.0116	0.0067	9.54	17.56
Lovina, Bali	5	1	0.127	0.0067	0.0047	4.8	7.4
Malalayan, Sulawesi	11	1	0.039	0.0094	0.0055	8.88	14.59
Pangandan, Java	11	1	0.039	0.0085	0.0050	6.83	9.12
Pantaloan, Sulawesi	11	1	0.039	0.0088	0.0051	7.51	10.82
Sanur, Bali	11	1	0.039	0.0376	0.0202	28.34	131.1
Spermonde, Sulawesi	11	1	0.039	0.01	0.0058	8.54	13.62
Banda	11	0.982	0.046	0.0146	0.0082	14.68	37.21
Biak, Iryan Jaya	11	0.982	0.046	0.0228	0.0125	15.36	40.58
Rakata	11	0.982	0.046	0.0058	0.0036	4.78	4.88
Una Una, Togian Islands	11	0.982	0.046	0.0214	0.0118	15.36	40.58
Derawan, Kalimantan	10	0.978	0.054	0.0089	0.0053	7.78	12.04
Postijons	10	0.978	0.054	0.0107	0.0062	9.9	18.75
Tuken Besi	10	0.978	0.054	0.008	0.0048	6.72	9.24
One Tree Island, Australia	9	0.972	0.064	0.0038	0.0026	2.94	2.37
Halmahera	11	0.964	0.051	0.0257	0.014	14.68	37.21
Sengihi, Talaud	11	0.964	0.051	0.0336	0.0181	19.12	61.47
Papua New Guinea	11	0.946	0.066	0.0073	0.0044	7.17	9.92
Semak Daun, Pulau Seribu, Java	11	0.946	0.066	0.0049	0.0031	5.46	6.15
Davao, Philippines	10	0.933	0.077	0.0079	0.0048	5.66	6.81
median		0.981		0.0094		8.54	

Table 3. Frequency and geographical distribution of haplotypes shared between **Anak Krakatau** and other populations. (First row is haplotype number, first column is locality. Populations from Anak Krakatau and Rakata are highlighted in bold.)

(a) <i>Haptosquilla pulchella</i>	1	2	3	4	5
Anak Krakatau	1	2	1	1	1
Carita, Java	2	2	—	1	—
Komodo	—	—	—	1	—
Lombok	1	2	—	1	—
Lovina, Bali	6	4	1	1	2
Pulau Seribu, Java	1	—	—	1	—
Sanur, Bali	2	6	—	—	—

(b) <i>Haptosquilla glyptocercus</i>	1	2	3	total
Rakata	2	1	1	4
Anyer, Java	—	—	—	0
Komodo	—	—	—	0
Lombok	—	—	—	0
Lovina, Bali	—	—	—	0
Pulau Seribu, Java	3	1	—	4
Sanur, Bali	—	1	1	2

Rather than showing reduced genetic diversity, stomatopod populations from the islands of Krakatau showed remarkably high levels of genetic diversity that were equiv-

alent to or greater than the levels of other Indo-Pacific populations presumed to have existed since the end of the last ice age. For *H. pulchella*, diversity measures were largely similar across all localities (table 1), with the exception of populations in the Lesser Sunda Islands where values of π and θ_s were increased by an order of magnitude due to admixture of haplotypes from highly divergent clades (Barber *et al.* 2000, 2002a). Similarly, haplotypic diversity was reduced in populations along the shores of Sulawesi due to the predominance of a single haplotype (Barber *et al.* 2002a).

Populations of *H. glyptocercus* from Rakata also showed high levels of genetic diversity, although both π and θ_s fell below the median values (table 2). Admixture of highly divergent lineages in a single population led to inflated estimates of π and θ_s in several localities (Barber *et al.* 2002b). However, the values observed on Rakata were more typical. The similar values for diversity measures across all populations of both species imply the action of similar demographic processes across localities.

Because no data are directly available, the possibility that the coral reef ecosystems survived the eruptions even partially intact must be addressed. Coral mortality may exceed 50% from the deposition of only 10 cm of sediments (Nowlis *et al.* 1997). Prior to the paroxysmal eruption of 26 August 1883, three months of relatively minor activity had already completely destroyed the forests on Krakatau and deposited 50 cm of ash on the shores (Simmons 1888), suggesting that coral reef ecosystems

were severely impacted prior to the paroxysmal eruption. Ecologically, both *H. pulchella* and *H. glyptocercus* live in cavities in coral or coral rubble and occur subtidally to 20 m and intertidally to 2 m, respectively (Erdmann 1997). Because the temperature of the pyroclastic deposits was 475–550 °C even 40 m below the sea surface (Mandeville *et al.* 1996), survival of either of these species proximal to Krakatau is extremely unlikely.

That populations have been re-established at all on the islands of Krakatau requires dispersal over moderate distances of open ocean. It is clear that no stomatopods could have survived within the 15 km radius from the caldera (figure 1b). Because of unsuitably deep water in the Sunda Strait, the nearest potential source populations of either species are on Sebesi, 20 km to the north. However, Sebesi, as well as nearby Sebuk and Lagoendi, were devastated and smothered in a layer of ash 1–1.5 m thick (Verbeek 1885) and even South Sumatra, which is about 40 km away, was heavily impacted with 50 cm of ash (Carey *et al.* 1996). These data suggest that benthic marine populations throughout the region may have been severely impacted or destroyed, indicating that colonization of the islands of Krakatau required dispersal of at least 20 km, but probably 40 km or further.

The genetic variation observed in populations on the islands of Krakatau (up to 1.3% for *H. pulchella* and 1.1% for *H. glyptocercus*) is too great to have evolved *in situ* because CO1 evolves at a rate of *ca.* 1–2% per million years (Palumbi 1996; Bermingham *et al.* 1997; Knowlton & Weigt 1998). Thus, the diversity present in these populations requires multiple recruitment events. Because reduced genetic diversity is expected if early colonists contribute substantially to population growth, the observed high genetic diversity downplays the role of self-seeding by early founders, favouring instead frequent recruitment events from one or more source populations (40 km or more distant).

The results presented here provide strong evidence that the dispersal and recruitment of pelagic larvae in two species of stomatopod are common over spatial scales of tens and perhaps hundreds of kilometres and are processes that occur over ecological time-scales. Such information is critical to understanding the ecological function of marine populations and for the design and implementation of effective marine management policy (Roberts 1997; Botsford *et al.* 2002; Palumbi 2002). For example, this study of stomatopods shows successful recruitment and connectivity over intermediate temporal and spatial scales, but previous work on the same taxa shows sharp regional genetic breaks over 300–400 km on evolutionary time-scales (Barber *et al.* 2000, 2002a). Combining these results provides a context in which to frame conservation strategies and suggests that several regional reserve systems may be necessary to protect distinct biogeographical regions and that, within each reserve system, reserves should be spaced *ca.* 50–100 km apart to facilitate connectivity via larval dispersal.

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