

Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences

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Abstract

To help stem the precipitous decline of coral reef ecosystems world-wide, conservation efforts are focused on establishing interconnected reserve networks to protect threatened populations. Because many coral reef organisms have a planktonic or pelagic larval dispersal phase, it is critical to understand the patterns of ecological connectivity between reserve populations that result from larval dispersal. We used genetics to infer dispersal patterns among 24 Indo-West Pacific populations of the mantis shrimp, *Haptosquilla pulchella*. Contrary to predictions of high dispersal facilitated by the strong currents of the Indonesian throughflow, mitochondrial DNA sequences from 393 individuals displayed striking patterns of regional genetic differentiation concordant with ocean basins isolated during periods of lowered sea level. Patterns of genetic structuring indicate that although dispersal within geographical regions with semicontiguous coastlines spanning thousands of kilometres may be common, ecologically meaningful connections can be rare among populations separated by as little as 300 km of open ocean. Strong genetic mosaics in a species with high dispersal potential highlight the utility of genetics for identifying regional patterns of genetic connectivity between marine populations and show that the assumption that ocean currents will provide ecological connectivity among marine populations must be empirically tested in the design of marine reserve networks.

Keywords: dispersal, genetics, larvae, marine, reserves, Stomatopod

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Introduction

Obtaining a detailed understanding of the dispersal patterns of pelagic marine larvae is challenging because they are minute travellers on vast seas. With the exception of species with very limited dispersal capabilities (e.g. Olsen 1985; Davis & Butler 1989), most information on larval dispersal comes from indirect estimates based on a variety of sources, including oceanography (Lee *et al.* 1994; Limouzy-Paris *et al.* 1997), species invasions (Carlton & Scanlon 1985; Hicks &

Tunnell 1995) and genetics (Palumbi 2001a). For the limited number of species where data are available there is a strong positive correlation between duration of larval dispersal and the realized dispersal distance (Shanks *et al.* 2001) and it is generally believed that species with long larval periods disperse widely on ocean currents. This belief has been reinforced by the capture of coastal marine larvae far out to sea (Scheltema 1988) and by low genetic structuring in many marine populations (Palumbi 1994). Studies challenging this paradigm, however, are mounting. Increasingly evidence shows larvae fail to fully achieve their dispersal potential (e.g. Burton & Feldman 1982; Knowlton & Keller 1986; Burton & Lee 1994) and recent studies by Swearer *et al.* (1999) and Jones *et al.* (1999) indicate that levels of local larval retention may be

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high. Furthermore, genetic results that indicate high dispersal over evolutionary time scales may often be consistent with very low dispersal over ecological time (Waples 1998; Palumbi 2001b).

Understanding the ecological connections provided by dispersing larvae has become a high priority in marine conservation biology. Globally, marine habitats are in decline (Bryant *et al.* 1998; UNFAO 2000; NMFS 2001): of particular concern are coral reefs where 10% of reef environments have been permanently lost, and this figure is predicted to climb as high as 70% by 2020 (Wilkinson 1992). To combat this trend, governments and management agencies are turning to marine reserves. Studies have shown that marine reserves can enhance the biomass and diversity of over-exploited communities (Roberts & Polunin 1991; Russ & Alcala 1996; Roberts 1997a; Johannes 1998). However, reserves can only be self-sustaining if recruitment exceeds mortality and emigration, and with the exception of migratory species, larvae often represent the major source of recruitment. For a population of a species to be self-replenishing, it has been suggested that the reserve size must equal or exceed the average dispersal distance (Botsford *et al.* 2001). For species with dispersal distances of hundreds of kilometres, sufficiently large reserves are impractical, suggesting an alternative strategy consisting of networks of reserve populations connected through larval dispersal (Hastings and Botsford 2001; Palumbi 2001b). Because sustainability of such networked populations will require demographically meaningful levels of larval exchange (i.e. enough recruits to ensure population persistence), it is paramount to understand the demographic connections between populations.

Building on the premise of current-mediated larval dispersal, Roberts (1997b) predicted patterns of connectivity between Caribbean reef populations by superimposing larval duration on oceanographic current data, and genetic studies do indicate high connectivity among many populations in this region (Mitton *et al.* 1989; Silberman *et al.* 1994; Shulman & Bermingham 1995). Barber *et al.* (2000), used genetic techniques to infer dispersal history among populations of *Haptosquilla pulchella* Miers 1880 (a benthic coral reef stomatopod) where dispersal was expected to be high because of the strong currents of the Indonesian throughflow. Contrary to predictions of genetic homogeneity, striking patterns of regional genetic differentiation concordant with ancient ocean basins were observed across the Indo-West Pacific, suggesting a history of limited dispersal between oceanographic regions. In this paper, we expand on our previous work on *Haptosquilla pulchella* to explore more thoroughly (i) the geographical scale of larval dispersal; (ii) the processes responsible for maintaining old genetic boundaries; and (iii) the implications of these results in the context of larval ecology and marine reserve design.

Oceanography and dispersal potential

Indonesia straddles Wallace's Line and bisects the Pacific and Indian Oceans. A net transport of nearly 20 million m³/s (Godfrey 1996) called the Indonesian Throughflow moves water from the Pacific into the Indian Ocean through the Indonesian Archipelago. Originating from the Pacific, Indonesian Throughflow waters enter the Celebes Sea, move southward at velocities up to 1 m/sec (Wyrтки 1961) through the Makassar Strait, spread south and east into the Flores and Banda Seas, and ultimately exit between the Lesser Sunda Islands (Gordon & Fine 1996). Seasonally reversing east–west currents up to 75 cm/s in the Java and Flores Seas (Wyrтки 1961) further mix the surface waters (Fig. 1).

As with most stomatopod species in the superfamily Gonodactyloidea, the larval behaviour and duration of the mantis shrimp *Haptosquilla pulchella* are not fully known. Attempts to raise these larvae in laboratory conditions have succeeded only to the fourth stadial molt when they emerge from the brooding female's burrow (Erdmann, unpublished data). Planktonic larvae have been recorded in three of eight families in Gonodactyloidea by the capture of larvae in deep-water plankton (Gurney 1946; Michel 1968) and in plankton tows taken hundreds of miles offshore (Michel 1968; Michel 1970). Ecologically and behaviourally similar species of *Neogonodactylus* have pelagic larval durations of 3.5–4.5 weeks (after passing the fourth stadial molt and entering the first pelagic larval stage) and recruit at 6.5–7.5 mm (Provenzano & Manning 1978; Morgan & Goy 1987). Larvae from *H. pulchella* hatch from similarly sized eggs and have nearly identical early development up to the fourth stadial molt as *Neogonodactylus* but recruit at a larger size of 9.5–11 mm (Erdmann 1997). Given that Hamano *et al.* (1995) have shown that stomatopod larval development is isochronal and regular, the larger size at settlement and slow larval growth of other *Haptosquilla* species (Sèrene 1954) suggest that the larval period of *H. pulchella* may be reasonably estimated at 4–6 weeks. Assuming passive planktonic dispersal and an average current of 25 cm/s, a dispersal potential of 600–900 km is estimated. Drogues have drifted more than 1200 km on surface currents through the Celebes Sea and Makassar Strait in only 4 weeks (Lukas *et al.* 1991) suggesting that this may represent an underestimate. Assuming that *H. pulchella* larvae travel on these ocean currents, the combination of Indo-Pacific current patterns (Wyrтки 1961) and dispersal potential with empirical transport data (Lukas *et al.* 1991) indicate no clear barriers to dispersal among Philippine and Indonesian populations. It is therefore predicted that connectivity should be high within this region (as evidenced by limited genetic structure). However westward transport from Papua New Guinea/Irian Jaya is predicted to be limited by the retroflexion of the

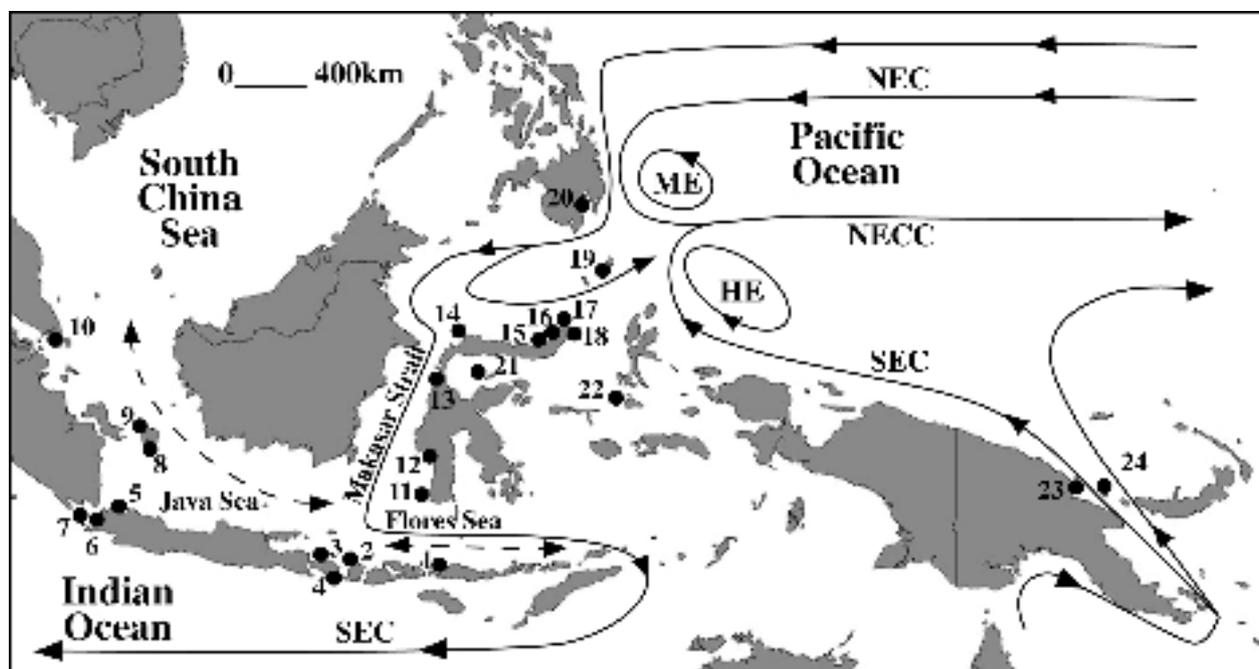


Fig. 1 Map of the Indo-West Pacific depicting sampled populations and currents (Wyrтки 1961; Godfrey 1996; Lukas *et al.* 1996). Populations are marked by numbers that correspond to Table 1. Dominant currents of the Indonesian Throughflow are marked with solid lines, seasonally reversing monsoon-generated currents are dashed. NEC (North Equatorial Current), NECC (North Equatorial Counter Current), SEC (South Equatorial Current), HE (Halmahera Eddy), ME (Mindano Eddy).

South Equatorial Current (SEC) waters in the region of Halmahera and should be evidenced by a genetic break.

Materials and methods

Sampling and sequencing

Juvenile and adult *Haptosquilla pulchella* ($n = 393$) were collected from 24 Indo-West Pacific reef systems from the Lesser and Greater Sunda Islands, South China Sea, Makassar Strait, Celebes Sea, Bay of Tomini, Maluku Sea and Papua New Guinea (Fig. 1, Table 1), and were preserved in 70–95% ethanol. DNA extractions were performed with a 10% Chelex® (BioRad) solution (Walsh *et al.* 1991). Amplifications of mitochondrial CO-1 were performed using published protocols (Barber & Erdmann 2000). Double-stranded polymerase chain reaction fragments were directly sequenced on an ABI 377 using BigDye® (Perkin Elmer) terminator chemistry. Forward and reverse sequences were proofread in Sequencher™ and all resulting 625 base-pair (bp) fragments were aligned by eye.

Phylogenetics, population structuring and dispersal

A minimum-spanning tree was created via the MINSPNET algorithm as employed in ARLEQUIN (Schneider *et al.*

2000) and drawn by hand in Adobe ILLUSTRATOR™. For consistency, the network from Barber *et al.* (2000) was used as a backbone. All alternative connections were examined to determine if they resulted in fundamental changes in the topology. Unique clusters of three or more haplotypes found primarily or exclusively in a single geographical region were colour-coded. Molecular diversity indices and levels of population subdivision were estimated using the AMOVA algorithm as implemented in ARLEQUIN (Schneider *et al.* 2000). Analyses were run based on haplotype frequencies with regional subdivisions defined following the results of the minimum-spanning tree. Additionally, AMOVA analyses were run separately for each of the major phylogeographic provinces as well as the five reef systems sampled in the Spermonde Archipelago to determine levels of genetic structuring within geographical regions as well as estimate pair-wise Φ_{ST} values. Estimates of Φ_{ST} were plotted against geographical distance to test for isolation by distance. Geographic distances were calculated in ARCVIEW™ 3.0 (ESRI), and distance estimates consisted of the shortest path, by sea, between any two populations. Significance of the resulting relationship was determined using a Mantel test as implemented in the program MANTEL written by A. J. Bohanek (available at <http://www.bio.sdsu.edu/pub/andy/MANTEL.html>)

The geographical scale of larval dispersal was explored using several methods. The first examines the similarity of

Table 1 Sampling localities, sample size and genetic diversity measures

Locality	<i>n</i>	Latitude, longitude	<i>h</i>	π	θ_s
1 Labun Bajo, Komodo	6	S 8°29.2', E 119°52.6' E	0.933	0.0442	21.02
2 Sengigi, Lombok	10	S 8°30.6', E 116°03.0'	0.978	0.0394	18.03
3 Lovina, Bali	48	S 8°09.5', E 115°01.7'	0.972	0.0211	15.77
4 Sanur, Bali	16	S 8°40.0', E 115°15.7'	0.867	0.0068	7.53
5 Bokor, Pulau Seribu	14	S 5°56.6', E 106°37.9'	0.956	0.0153	9.43
6 Carita, Java	16	S 6°5.9', E 105°26.0'	0.983	0.0078	8.44
7 Anak Krakatau	11	S 8°09.5', E 115°25.9'	0.964	0.0062	4.44
8 Tanjung Pandang, Belitung	10	S 3°49.8', E 107°40.7'	0.927	0.0043	4.24
9 Batu Hitam, Belitung	10	S 3°14.4', E 107°59.6'	0.978	0.0054	4.10
10 Nogs Point, Riau	21	N 1°12.0', E 104°10.0' E	0.919	0.0049	6.67
11 Spermonde, S. Sulawesi	76	S 5°7.40', E 119°20.6'	0.708	0.0024	7.34
12 Pare Pare, S. Sulawesi	10	S 4°02.5', E 119°35.0'	0.978	0.0042	4.60
13 Pantaloan, S. Sulawesi	10	S 0°42.7', E 119°51.6'	0.778	0.0028	2.83
14 Toli Toli, N. Sulawesi	13	N 1°19.3', E 120°51.5'	0.987	0.0030	3.87
15 Pulau Tiga, N. Sulawesi	14	N 0°49.8', E 123°47.5'	0.813	0.0023	2.20
16 Kuandang, N. Sulawesi	10	N 0°55.1', E 124°03.9'	0.800	0.0024	2.12
17 Malalayan, N. Sulawesi	10	N 1°27.3', E 124°48.7'	0.667	0.0039	3.53
18 Lembbeh, H. Sulawesi	10	N 1°28.2', E 125°14.0'	0.778	0.0026	2.83
19 Sangihe, Talaud	20	N 3°59.6', E 126°39.7'	0.974	0.0085	7.33
20 Santa Cruz, Philippines	10	S 6°50.0', E 125°25.1'	1.000	0.0095	9.90
21 Una Una, Togian Islands	21	S 0°08.0', E 121°34.9'	0.738	0.0029	3.34
22 Obi	9	S 1°40.1', E 127°24.5'	0.889	0.0068	6.25
23 Long Island, PNG	10		0.911	0.0025	2.12
24 Madang, PNG	8		0.964	0.0054	4.63

Bold numbers in first column correspond to numbers on Fig. 1. 'Southern' populations are 1–7, 'northern' 8–22, and Papua New Guinea 23–24. Haplotype (*h*) and nucleotide (π) diversity and θ_s were calculated in ARLEQUIN (Schneider *et al.* 2000).

populations based on shared haplotypes. A matrix consisting of all nonsingleton haplotypes scored as presence or absence data was used to construct an area cladogram via neighbour-joining with Papua New Guinea populations defined as the outgroup. Assuming that shared haplotypes result from dispersal, the topology should reflect regions connected through larval dispersal. The second approach was a hierarchical analysis of nucleotide diversity as implemented in the program NUCLEODI (Holsinger & Mason-Gamer 1996). This method uses coalescence to partition nucleotide diversity into hierarchical levels. Populations with the closest mean coalescence times cluster together and are inferred to have the most recent connections, presumably through gene flow or past association. The final approach compared mean geographical distances separating population pairs sharing haplotypes to the mean geographical distance between populations to test for departures from random. Only haplotypes shared between two populations were analysed because haplotypes that are shared between many populations may indicate ancestral polymorphism. Although ancestral haplotypes may also occur in population pairs, the geographical distribution of these associations should be random; departure from this expectation favours the interpretation of recent (but perhaps still not contemporary) dispersal.

Results

Mitochondrial CO-1 data collected from 393 individuals from 24 populations yielded 189 unique mitochondrial haplotypes of 625 bp. Of 174 variable sites 15.5% were first positions, 4.6% were second positions, and 79.9% were third positions. Haplotypic diversity was high in all populations (0.67–1.0, Table 1). The majority of haplotypes (76%) were singletons and 37–100% (mean 71%) of the haplotypes in any population were found only in a single individual. Of the remaining 45 haplotypes, 32 were shared among populations. The bulk of these shared haplotypes (*n* = 25) were shared between two or three populations, although one haplotype occurred in 20% of the total sample and was found in 12 populations (Table 2). Thirteen haplotypes were private (found in more than one individual, but in only one population). The minimum-spanning tree shows three distinct clades separated by large genetic and geographical breaks (Fig. 2). The first group, Clade 1, consists of the two populations (23, 24) from Papua New Guinea. Clade 2 is separated from Clade 1 by 34 mutational steps (5.4% sequence divergence) and is found only in the southern most Indonesian populations (populations 1–7), hereafter referred to as 'southern populations'. Clade 3 is separated from Clade 2 by 36

Table 2 Distribution of nonsingleton haplotypes

Hap.*	Population																								Tot. n*	Tot. pop.*	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24			
1		1					1		2	41	2	5	2	6	4	6	5	3								78	12
2		2	4	6	1	2	2																			17	6
3		1	6	2		2	1																			12	5
4								3	1	4	3								1							12	5
5													1								10					11	2
6											1	1		2	3							1				8	5
7			5		1	1																				7	3
8											1		1	2	1			1								6	5
9	1	1	1			1	1																			5	5
10			2		1		1																			4	3
11					3	1																				4	2
12																			1			3				4	2
13											3						1									4	2
14	1		1	1																						3	3
15																			1			2				3	2
16											1	1	1													3	3
17								1	1				1													3	3
18								2		1																3	2
19			1	1		1																				3	3
20																							1	2		3	2
21			1				1																			2	2
22															1				1							2	2
23	1											1														2	2
24							1		1																	2	2
25			1										1													2	2
26							1						1													2	2
27								1					1													2	2
28																			1			1				2	2
29														1					1							2	2
30														1	1											2	2
31														1	1											2	2
32																						1	1			2	2
33																					5					5	1
34										5																5	1
35											3															3	1
36																						3				3	1
37																						2				2	1
38							2																			2	1
39											2															2	1
40											2															2	1
41																					2					2	1
42								2																		2	1
43																					2					2	1
44					2																					2	1
45	2																									2	1

*Hap., Haplotype; Tot. n, total n; Tot. pop., total populations. Bold numbers in the first column refer to individual haplotypes. Bold numbers in the first row refer to populations described in Table 1 and Fig. 1. Haplotypes 1–32 are shared between multiple populations and 33–45 are private haplotypes. Total observations of a given haplotype and the number of population in which a given haplotype was found are summarized in the final two columns.

mutational steps (5.8% sequence divergence) and dominates Indonesian and Philippine populations ('northern populations') found north of the Flores and Java Seas (populations 8–22), although a few Clade 3 haplotypes were found in Komodo, Lombok and northern Bali (populations 1–3). Alternative connections between haplotypes do not affect the results or conclusions.

The most common haplotype (~20%) in Clade 3 forms the centre of a star phylogeny (Fig. 2a). This haplotype dominated Sulawesi populations (Fig. 2b) where frequencies averaged 46% (15–60%) but diminished quickly beyond the Sulawesi coastline. Many clades radiating from this central haplotype have strong regional affinities (Fig. 2b). The largest clade (green) consisted of 17 haplotypes, 14 of which dominated the populations in or bordering the South China Sea. A clade of eight haplotypes (blue) was found primarily in the Philippines and the eastern most Indonesian populations, and a clade of seven haplotypes (red) was only found in the Flores Sea. Yellow clade haplotypes dominated in the Bay of Tomini and were only encountered once outside of this region. Additional smaller clades were limited to South Sulawesi (grey), and the Philippines/Eastern Indonesia (pink and orange). All of these clades with the exception of the orange clade had one or more diagnostic characters that unite them, although low levels of homoplasy (0.8–2.5%) were often observed. AMOVA showed high levels of genetic structuring ($\Phi_{ST} = 0.87$, probability of observing an equal or greater value at random = 0) with 85% of the observed variance being a result of differences between Papua New Guinea, 'southern', and 'northern' populations. Variance among populations within groups and variance within populations accounted for 2% and 13%, respectively. Among 'southern' populations, there was genetic structure ($\Phi_{ST} = 0.14$, $P = 0$). The presence of genetic structure as well as higher haplotype and nucleotide diversity in these populations (Table 1) was due to the presence of a few Clade 3 haplotypes in three populations otherwise dominated by Clade 2 haplotypes as evidenced by the reduction of Φ_{ST} (0.027, not significant) if Clade 3 haplotypes are omitted. Among 'northern' populations, $\Phi_{ST} = 0.12$ ($P = 0$) indicating significant structuring of genetic variation. Within all Sulawesi populations $\Phi_{ST} = 0.014$ ($P = 0.02$) but within the Spermonde Archipelago $\Phi_{ST} = -0.03$ (not significant). Isolation by distance plots revealed no significant patterns. In 'southern' populations, there was no relationship

between Φ_{ST} and geographical distance with (Mantel statistic = 0.324, not significant) or without (Mantel statistic = -0.078, not significant) clade 3 haplotypes. Among 'northern' populations the relationship between Φ_{ST} and geographical distance was slightly positive (Mantel statistic = 0.222, not significant) but along the Sulawesi coastline it was negative (Mantel statistic = -0.065, not significant). Despite this pattern, widespread haplotypes shared clear geographical restrictions (Table 2). For example, each of the four most common haplotypes occurs over a relatively small range. The most common is virtually restricted to Sulawesi, being found only four times off this coast. The second and third most common haplotypes are found only on Java and the islands to the east, and the fourth haplotype only occurs in the South China Sea, except for three individuals found on Sulawesi. Scoring all nonsingleton haplotypes as presence-absence data yielded a matrix of 45 characters. The resulting neighbour-joining tree (Fig. 3) shows a separation between 'southern' and 'northern' populations paralleling the divisions in the minimum-spanning tree. Within the 'northern' group, the South China Sea populations form a clade that includes one population from Sulawesi, and the remaining Sulawesi populations form a separate clade. Eastern Indonesian populations (populations 19 and 22) form a final clade. Hierarchical analysis of nucleotide diversity produced a well-defined area cladogram (Fig. 4) with three highly significant divisions paralleling the minimum-spanning tree. Clade 1 consists of Papua New Guinea populations and is sister to Clade 2, consisting of 'southern' populations ($g = 0.697$, $P = 0$). Clade 3 consists of 'northern' populations ($g = 0.810$, $P = 0$) and contains three primary clusters. The first consists of all but one Sulawesi populations, and includes a single population (population 8) from the South China Sea ($g = 0.151$, $P = 0$). The second group consists of two South China Sea populations, and one population each from Sulawesi and the Philippines ($g = 0.031$, $P = 0.001$). The final group is an eastern Indonesian group and includes the Bay of Tomini ($g = 0.031$, $P = 0.001$). Table 3 reports all pairs of 'southern' and 'northern' populations that share haplotypes. The mean distance between these population pairs was 784 km (standard error (SE) = 51) and was significantly different ($P = 0.002$, t -test) from the average distance between all 'southern' and 'northern' populations (1391 km, SE = 111). The median value of distance between populations sharing haplotypes was 630 km.

Fig. 2 (*opposite*) (A) Unrooted minimum-spanning tree depicting genetic relationship of 189 unique mitochondrial haplotypes from 393 individuals sampled from 24 regions throughout the Indo-West Pacific. Clade 1 consists of populations from Papua New Guinea, Clade 2 is populations only from the Sunda Islands, and Clade 3 are populations north of the Flores and Java Seas. The size of the circles is proportional to the haplotype frequencies. All haplotypes are separated by a single mutational step unless otherwise noted by hatch marks or numerals. Groups of three or more haplotypes found primarily or exclusively in a single geographic region are coloured. (B) Map of Indonesia and the Philippines 18 000–20 000 years before the present when sea levels were lowered by 130 m (Porter 1989) exposing the Sunda and Sahul continental shelves (grey shading). The relative frequencies in each population of haplotypes from the coloured clades in (A) as well as of the black central haplotype in Clade 3 are shown by pie diagrams.

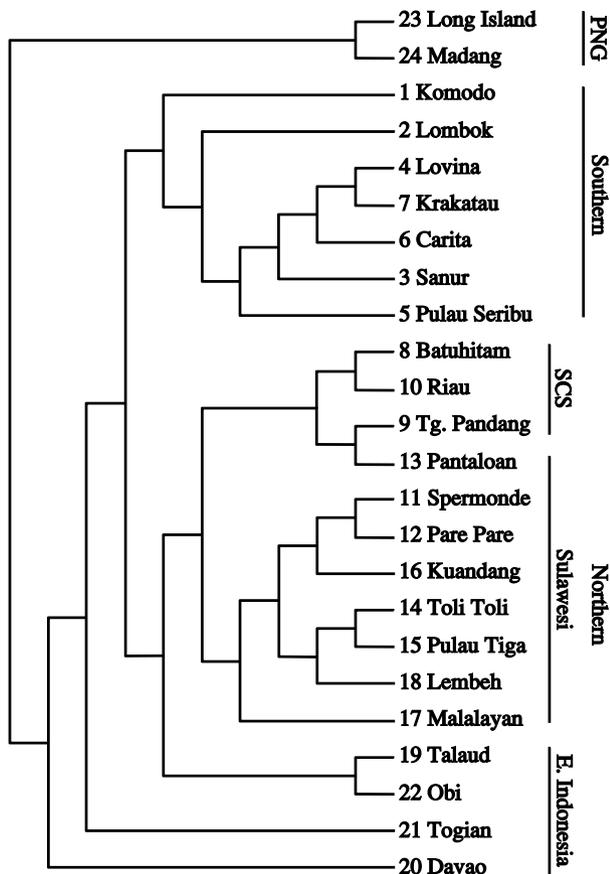


Fig. 3 Neighbour-joining area cladogram created using shared haplotypes scored as presence-absence characters showing the relationship among 'southern' and 'northern' populations including populations from the South China Sea (SCS), Sulawesi and Eastern Indonesia. Papua New Guinea samples were defined as the outgroup. Distance measure used was mean character difference and ties were broken randomly.

Discussion

Genetic and geographical structuring of populations

In contrast to the prediction of genetic homogeneity among Indonesian and Philippine populations, results show populations north and south of the Flores and Java Seas 300–400 km apart are separated by a large genetic break corresponding to Clades 2 and 3 (Fig. 2) which Barber *et al.* (2000) suggested results from isolation during Pleistocene low sea level stands. Only Clade 2 haplotypes were found in Indian Ocean population (populations 4, 6 and 7) and only Clade 3 haplotypes were found north of the Flores and Java Seas, suggesting that these two clades may represent Indian and Pacific Ocean lineages. Similar results and conclusions have been reported in fish (Lacson & Clark 1995), crabs (Lavery *et al.* 1996), prawns (Duda & Palumbi 1999), sea stars (Williams & Benzie 1997; Benzie

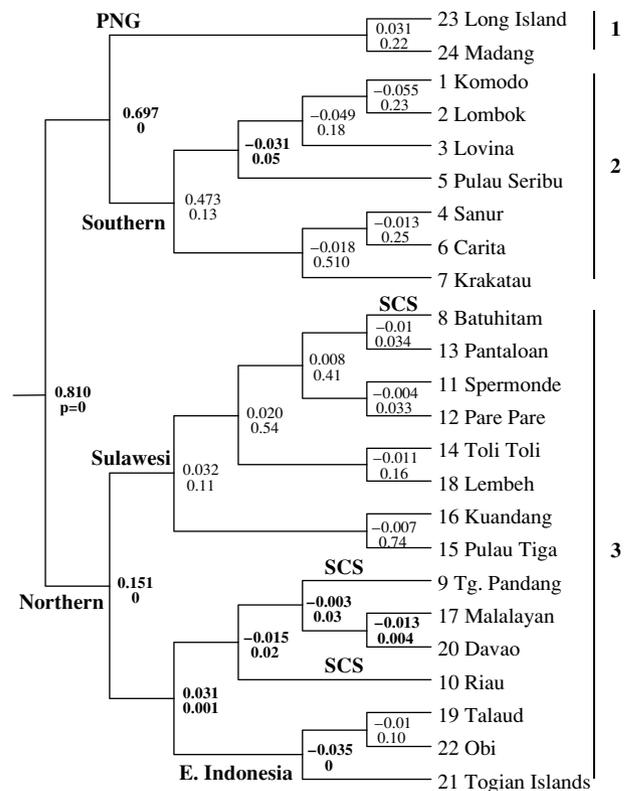


Fig. 4 Results of a hierarchical analysis of nucleotide variation following the method of Holsinger and Mason-Gamer (Holsinger & Mason-Gamer 1996) showing the relationship among 'southern' and 'northern' populations including populations from the South China Sea (SCS), Sulawesi and Eastern Indonesia. Numbers at nodes (above) indicate distance between daughter nodes. Numbers below indicate the probability of a random value (based on 10 000 random replicates) equal to or greater than the observed value based on the hypothesis of no differentiation. Significant values ($P < 0.05$) are shown in bold.

1999) and mangroves (Duke *et al.* 1998), but only on very broad spatial scales (> 1000 km).

An equally large genetic break (34 steps) was discovered between Indonesian/Philippine and Papua New Guinea populations (Clade 1, Fig. 2) that mirrors a substantially shallower genetic break across the same region in nautilus (Wray *et al.* 1995), giant clams (Benzie & Williams 1997), sea stars (Williams & Benzie 1998; Benzie 1999) and sea urchins (S. Palumbi and L. Geyer, unpublished data). This result is consistent with the prediction that the retro-reflection of South Equatorial Current waters in the region of Halmahera (Lukas *et al.* 1991; Lukas *et al.* 1996; Nof 1996) would limit westward larval dispersal from Papua New Guinea to Indonesia and the Philippines, resulting in a genetic break. This hypothesis should be further tested by comparative studies utilizing other taxa with similar dispersal characteristics.

Table 3 Geographic distance between population pairs from 'southern' and 'northern' populations that share haplotypes

Haplotype	Population 1	Population 2	Distance (km)
11	5	6	125
30	14	15	340
31	14	15	340
22	16	19	450
23	1	12	500
29	14	18	520
12	19	22	630
15	19	22	630
28	19	22	630
24	9	10	660
5	14	21	1000
21	4	7	1150
13	11	17	1240
25	4	14	1250
18	8	11	1340
27	8	13	1540
26	9	14	1720

Haplotypes are listed in the first column. Population numbers refer to populations in Table 1 and Fig. 1. Distances are in kilometres. Mean distance between random 'southern' and 'northern' populations is 1391 km.

In addition to deep genetic breaks, there are fine-scale patterns of regional differentiation in 'northern' populations that correspond to distinct ocean basins that were more isolated during the Pleistocene (Fig. 2). Similarly fine-scale regional differentiation is reported among Indonesian populations east and west of the Makassar Strait in scad mackerel (Perrin and Borsa 2001) and limpets (L. Kirkendale, unpublished data), and Nelson *et al.* (2000) report small genetic breaks among populations of clownfish from the Andaman Sea/S. Sumatra and populations to the east.

Within 'northern' populations, most variation is within one or two mutational steps of a common central haplotype (mean nucleotide diversity 0.0045). This haplotype was the only haplotype shared by a majority of 'northern' populations, suggesting that this pattern results from ancestral polymorphism (Templeton *et al.* 1995), a conclusion supported by its position at the centre of the star phylogeny. This common haplotype dominated populations from Sulawesi (Fig. 2b), resulting in a significantly lower mean haplotypic diversity ($P < 0.01$, t -test) in these populations. Although this pattern could result from a population bottleneck followed by a recent range expansion, two observations make this conclusion unlikely. First, values of θ_s ($2N\mu$ calculated from the number of segregating sites) are similar among all populations (except Bali, Lombok and Komodo where amixis of Clades 2 and 3 results in inflated diversity measures) indicating equivalent popula-

tion sizes. Secondly, similarly high haplotype frequency is only observed in populations along the shores of Sulawesi, a surprising result given that lowered sea levels had an impact on populations throughout the Indo-Pacific. Instead, the similarly high frequency of one haplotype throughout Sulawesi can be interpreted as frequent dispersal and gene flow between these populations. However the slight but significant Φ_{ST} value among Sulawesi populations indicates that these coastal populations are not panmictic.

Green clade haplotypes dominate in South China and western Java Sea populations. This pattern probably results from recolonization, following postglacial rise in sea level, from populations further north in the South China Sea that persisted in isolation during the last glacial maxima (Fig. 2b). This hypothesis is supported by sea-level reconstructions (Voris 2000) which show that the last land bridge separating the South China and Java Sea populations connected Borneo to the island of Belitung, by the fact that the southern and easternmost populations (populations 8 and 9) are dominated by green clade haplotypes as well as by the results of Yu *et al.* (2000), which show genetic isolation of giant clams in the South China Sea. Although green haplotypes could have invaded from the east, the substantially lower numbers of green clade haplotype in eastern Indonesia despite a 213 : 41 sampling bias favouring the latter make this alternative explanation unlikely.

Philippine and eastern Indonesian populations share several regional clades (blue, orange, pink clades) and this is concordant with increased isolation of the Celebes Sea during periods of low sea level when land bridges restricted water flow between the Celebes and Sulu Sea and the Makassar Strait was constricted (Fig. 2b) (Voris 2000) and cool upwellings further isolated this region (Fleminger 1986). Present day currents (Fig. 1) (Lukas *et al.* 1996) may facilitate retention of larvae in this region, maintaining distinct populations (Sinclair & Iles 1989) and a signal of regional genetic identity. Genetic isolation of the Togian Islands populations (population 21) in the Bay of Tomini, a region with numerous endemics (Wallace *et al.*, 2002), parallels patterns in corals (C. Wallace and A. Chen, unpublished data) and limpets (Kirkendale, unpublished data). The Togian Islands are dominated by yellow clade haplotypes, yet these haplotypes are not observed in Maluku Sea populations (populations 18 and 22), suggesting that dispersal in or out of the Bay of Tomini is extremely rare in this species. However, the single yellow clade individual found in Toli Toli (population 14) indicates that such dispersal is possible.

The geographical scale of dispersal

Levels of genetic structuring in *Haptosquilla pulchella* are substantially higher than those reported for other marine

species with pelagic larval dispersal (Planes 1993; Palumbi *et al.* 1997; Williams & Benzie 1998; Rocha-Olivares *et al.* 1999; Aubert & Lightner 2000; Nelson *et al.* 2000; Weber *et al.* 2000) and are more similar to values reported for species with extremely limited or no dispersal (Hellberg 1994; Doherty *et al.* 1995; Allcock *et al.* 1997; Wright *et al.* 2000). Limited dispersal is strongly suggested by regional genetic differentiation in Clade 3 populations. Although the origins of regional genetic structure probably resulted from increased isolation during the Pleistocene (Barber *et al.* 2000), the retention of historical geographical affinities through at least 10 000 years of modern ocean conditions is not consistent with high dispersal. Instead, this result suggests that either limited dispersal or recruitment maintain historical differences.

However, the patterns of regional genetic similarity (especially the high degree of similarity of Sulawesi populations spread over 1300 km) are inconsistent with extremely limited dispersal. The haplotype-based area cladogram shows that Sunda Island populations share haplotypes to the exclusion of populations from the north where regional associations are seen between populations in the South China Sea, Sulawesi and the Western Pacific (Fig. 3). If shared haplotypes are assumed to result from dispersal (as random retention of ancestral polymorphisms should not have a geographical signal), these results indicate that dispersal is common within, but is limited between, geographical regions. Similar conclusions are drawn from hierarchical analysis of nucleotide variation (Fig. 4) in which nodes with negative or nonsignificant values indicate populations of mixed origin (Holsinger, personal communication), indicating a regional mixing of the haplotype pool (i.e. dispersal). This result is remarkable in that geographically proximal populations may be more genetically similar to distant populations than to each other despite no obvious barriers to dispersal between them.

Limited dispersal is often accompanied by a pattern of isolation by distance (e.g. Hellberg 1994; Chenoweth *et al.* 1998a; Todd *et al.* 1998; Wilke & Davis 2000; Palumbi 2001b), yet none of the regional isolation by distance analyses were significant, suggesting that dispersal within geographical regions is not severely limited. However, isolation by distance is not always observed even in low dispersal species (Wright *et al.* 2000) or may only be observed on limited spatial scales (Planes *et al.* 1996; Johnson & Black 1998; Todd *et al.* 1998). Alternatively, *H. pulchella* populations may not have achieved equilibrium following postglacial rise in sea level, a requirement for the development of isolation by distance (Slatkin 1993). Furthermore, multiple independent loci may be required to detect a statistically significant pattern of isolation by distance over small spatial scales in marine populations (Palumbi 2001b).

The mean distance between population pairs sharing haplotypes was 784 km and was significantly lower than random predictions, suggesting that this pattern does not result from ancestral polymorphism. This dispersal estimate is high in comparison to the geographical scale of genetic breaks and may be inflated due to undersampling. Perhaps a better estimate of dispersal range can be obtained by looking at two unique events. The first is the colonization of Anak Krakatau, an island formed following the 1883 eruption of Krakatau that extinguished all life near Krakatau and neighbouring islands (Simkin & Fiske 1984; Sigurdsson *et al.* 1991). Because *H. pulchella* do not occur below 20 m and require close proximity to fresh-water sources (Erdmann 1997), colonization of this population would require pelagic dispersal across the unsuitable habitat of the Sunda Strait from mainland sources about 50 km distant. The lack of a signal of a founder effect as evidenced by the high haplotypic diversity in this population (0.964, similar or greater than all other populations) would require multiple such events. Second, the presence of Clade 3 haplotypes in 'southern' populations dominated by Clade 2 haplotypes indicates that dispersal must occasionally occur across 400 km of deep water of the Flores Sea. However, because limited gene flow (i.e. $Nm = 1$) will tend to limit genetic differentiation between populations (Slatkin 1987), the strong genetic break among 'northern' and 'southern' Indonesian populations indicates that such long distance pelagic dispersal must occur infrequently on evolutionary time scales.

Causes of dispersal limits

The failure of Holocene ocean currents to disrupt geographical genetic distinctions of Pleistocene origin indicates that there must be limits to dispersal in *H. pulchella*. Because the larval biology of *H. pulchella* is not fully known, it is possible that, unlike other stomatopods, it does not have pelagic larvae. However, recolonization of populations on Anak Krakatau combined with the absence of any signal of a founder effect in this population provided clear evidence for pelagic dispersal.

If long distance dispersal by *H. pulchella* larvae is relatively rare, connectivity between distant localities may require stepping-stones (Parsons 1996; Williams & Benzie 1997; Shulman 1998). Because *H. pulchella* is ecologically limited to reefs near to fresh-water inputs (Erdmann 1997), the distribution of such stepping-stones may profoundly affect dispersal patterns. For example, in 'southern' or Sulawesi populations, where such habitats are numerous, genetic structure is rare. However, the absence of useable habitats on the small oceanic reefs and islands scattered across the Java and Flores Seas may contribute to the genetic break across these waters. Extensive collections in the Postiljon Islands, equidistant between the Spermonde

(population 11) and Bali (populations 3, 4), failed to capture *H. pulchella*, suggesting that this may be the case. Lack of suitable stepping-stones may also explain the strong genetic break between Belitung and Pulau Seribu populations, a region characterized by extremely limited reef development (personal observation). If the lack of stepping-stones results in the failure of *H. pulchella* larvae to disperse across broad reaches of open oceans, coastlines not currents are paramount in understanding the observed genetic patterns. Performing similar genetic analyses on ecologically similar stomatopod species common to both coastal and oceanic reefs could test this hypothesis.

Another alternative is that although some broad-scale oceanographic data may provide reasonable dispersal predictions (i.e. the retroflexion of the SEC), other data may oversimplify the currents experienced by larvae that originate in near-shore environments. Eddies, stagnation zones, and local reversals of long shore currents are common in coral-reef systems, as are seasonal, tidal and weather-driven changes in current flow (Frith *et al.* 1986; Wolanski & Hamner 1988; Wolanski 1994; Bradbury and Snelgrove 2001). These mesoscale coastal current patterns may greatly influence larval movements (Sammarco & Andrews 1988; Black 1993; Sponaugle & Cowen 1996; Sponaugle & Cowen 1997; Wing *et al.* 1998; Huntley *et al.* 2000) and local retention (Lobel & Robinson 1986; Boehlert *et al.* 1992; Lee *et al.* 1992; Lee *et al.* 1994; Archambault *et al.* 1998), and are implicated in the formation of discrete population units (Sinclair & Iles 1989) as well as in genetic structuring (Aubert & Lightner 2000).

Behaviourally, marine larvae, including those of *H. pulchella*, may not disperse as passive particles (see Levin 1990). Stomatopod larvae are strong swimmers (personal observation), which can be an important component of dispersal profiles in larger marine invertebrates (Katz *et al.* 1994; Yoshimura *et al.* 1999) and fishes (Stobutzki & Bellwood 1994; Leis *et al.* 1996; Leis & Carson-Ewart 1997). Crustacean larvae respond behaviourally to oceanographic conditions (Young 1995) and can limit their exposure to currents through vertical migrations (Cronin & Forward 1986; Tankersley *et al.* 1995; Dame & Allen 1996; Forward *et al.* 1997). Such behaviour has been suggested for stomatopods (Reaka & Manning 1987), potentially limiting dispersal.

Regional genetic differentiation could also result through differential recruitment from a mixed larval pool (Staton & Rice 1999) if larvae lack the necessary settlement cues (Zimmer-Faust & Tamburri 1994) or if resident adults interfere with settling larvae (Woodin 1976; Morgan 1995). Such mechanisms could generate or maintain population structure if they discriminated between local and immigrant larvae and are testable by comparing genetic patterns in local adult and larval populations.

Natural selection could also create or maintain genetic boundaries (Williams *et al.* 1973; Koehn *et al.* 1976; Johnson & Black 1984; Ayre 1990; McMillen-Jackson *et al.* 1994; Hilbish 1996) but would require differential selective regimes in similar water bodies over relatively short distances and is considered unlikely. Perhaps more likely, recent evidence suggests that there is high larval mortality during open-ocean transport (Swearer *et al.* 1999; Cowen *et al.* 2000) and that larvae that do survive may be more physiologically stressed and thereby less able to recruit successfully (Morgan 1995). Thus, larvae dispersing long distances are selected against, providing a mechanism to limit genetic exchange over broad reaches of open ocean.

Inter- and intraspecific competition could also limit larval recruitment. Although described as a single species, the levels of divergence between Clades 1, 2 and 3 (5.4% and 5.8% in CO-1 sequence, respectively) are similar to cryptic species of Alpheid shrimp (Knowlton & Weigt 1998) suggesting that they may be distinct taxa. If the major genetic divisions do represent distinct species, inter-specific agonistic behaviours common in Gonodactylid stomatopods (Dingle *et al.* 1973; Reaka & Manning 1981; Caldwell 1982) could limit sympatric distributions. Stomatopods can distinguish between individual intraspecific members (Caldwell 1985) and agonistic behaviour can vary significantly between conspecific populations (Caldwell & Dingle 1977), suggesting a potential mechanism for maintaining even minor historic subdivisions.

Although the species status of this taxon merits careful morphological study, whether *H. pulchella* represent one or three species does not impact the conclusions of this study. Patterns of fine-scale genetic structuring indicating limited dispersal or recruitment are independent of the taxonomic status of the three deeply divergent lineages. Inability to disperse or recruit across the Halmahera Eddy or the open ocean environments may well have resulted in speciation. The sympatry of Clade 3 haplotypes in 'southern' populations clearly indicates that these 'species' can co-occur. However, their limited presence in 'southern' localities (and absence in others) indicates limitations to recruitment or dispersal.

Consequences for conservation

The results of this study clearly indicate limited connectivity among regional *H. pulchella* populations. Although this taxon represents only one example from a wide variety of species, each with unique dispersal profiles (e.g. Thresher & Brothers 1989; Wellington & Victor 1992; Palumbi and Hedgecock 2001), these data have broader conservation implications. The recovery of three deeply divergent clades in *H. pulchella* and concordant genetic patterns in other taxa indicates that Indo-Pacific

waters probably harbour a wealth of undescribed marine biodiversity, as suggested by Knowlton (1993) for marine species in general. More importantly, this biodiversity is organized into discrete geographical units, providing a critically important regional context to frame marine management efforts.

The levels of gene flow required to generate the low Φ_{ST} values observed within geographical regions may be significant in an evolutionary context by limiting differentiation among populations. However, they are far below the demographically significant amount required for persistence of reserve populations (Palumbi 2001b; Thorrold *et al.* 2001). This result is underscored by the results of Thorrold *et al.* (2001) that documented pronounced geographical structuring in weakfish populations based on biochemical assays despite genetic homogeneity. Therefore, the recovery of even slight genetic spatial patterning is inconsistent with demographically meaningful levels of larval dispersal. Although occasional long distance dispersal events may increase local genetic diversity, management strategies cannot assume that dispersal between distant populations, even in the same geographical regions, will provide sufficient recruitment for sustainable populations.

Perhaps intuitively obvious in importance, the availability of stepping-stones has rarely been explicitly discussed in the context of connectivity of marine populations (e.g. Parsons 1996; Williams & Benzie 1997; Shulman 1998) in favour of ocean currents or effects of Pleistocene sea-level changes. The high genetic similarity among populations spread over 1300 km of Sulawesi coastline in contrast to the sharp genetic breaks across the Flores and Java Seas stresses how important coastlines and stepping-stones may be in maintaining high levels of connectivity. Stepping-stones may be a function of both marine environments (e.g. coral reefs) and terrestrial environments (e.g. rivers) and must be accounted for in the design of reserve networks.

Although the short-term success of marine reserves is largely a function of the degree to which management plans are enforced and accepted by local communities (e.g. Russ & Alcala 1999; McClanahan 1999), long-term persistence of nonself-seeding reserved populations will require demographic connectivity. Average, broad-scale current patterns are a reasonable starting place for predictions about connectivity between marine populations (Roberts 1997b). However, initial oceanographic predictions should be treated as testable hypotheses, and conditioned by biogeographic and historical information. Testing such hypotheses through ecological, biochemical (e.g. DiBacco & Levin 2000), genetic, or oceanographic means should be a high priority task associated with understanding the connections and management options in complex marine ecosystems.

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