

Workplan Activity Title (#): Tracking reef coral movements across the Pacific

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Summary:

The suite of global problems facing corals range from wholesale problems such as global climate change to local issues such as dynamite fishing and pollution. Human reaction to these problems are major issues in global conservation, but are held up by deep gaps in our knowledge about coral dispersal.

Dispersal of organisms plays a fundamental role in how species respond to climate change. Many terrestrial plants and animals have been moving poleward, up to 100s of km, as climates have shifted. For plants, recent reports suggest that there is a race in some areas between the speed of change and the speed of range expansion. Nearly all these studies have focused on continental species with great scope for movement. There is no information about the movement potential for important species such as reef building corals that live in fragmented habitats. We conducted genetic surveys of reef building corals from 20 populations from seven archipelagoes in the central Pacific in order to assess the ability of larval dispersal to serve as a mechanism of range response during climate change. Our samples spanned 30° of latitude and 6000 km. We find very high levels of genetic difference among all archipelagoes, implying extremely limited ability of corals to disperse among island groups. These results are probably driven by the predominately east-west movement of ocean currents in the central Pacific. Lack of north-south ocean currents in this area may largely prohibit the kind of response to climate change seen in many continental species.

Dispersal also plays a strong role in strategies to mitigate anthropogenic damage to corals through the creation of marine managed areas. The value of a single managed area depends strongly on its size relative to dispersal. The value of a network of managed areas depends on the spacing of replicate areas compared to dispersal. In both cases, information about short and long term dispersal is needed.

Our data from 20 populations allows us to examine the scales of genetic differentiation, and infer scales of dispersal, especially within archipelagoes. We find variable levels of differentiation at scales from 5 to 170 km. In 4 of 5 archipelagoes, there is at least one population that is highly divergent from other populations, even those as close as 5 km distant. Overall, populations over 50 km apart tend to have higher probability of genetic differentiation than populations closer than 50 km. The scale of buildup of genetic differentiation with distance is highly variable, but suggest average coral dispersal of about 1-10 km.

These data make two suggestions about marine managed areas. First, managed areas in different archipelagoes will not substantially support one another ecologically. Using the Hastings-Botsford limit as a criterion for when different populations will form an effective network, we find that managed areas in different archipelagoes have too low a rate of gene flow to form effective networks. This means that coral reef conservation in one region of the Pacific will not help other regions. The ocean areas managed by central Pacific nations are each so large that coral conservation efforts need to focus on local networks built over smaller spatial scales rather than rely on coral movement across national boundaries.

At smaller spatial scales, dispersal of 1 -10 km suggests that the small managed areas typical of coral reef areas are in general too small to support stable coral populations within their boundaries by themselves. Networks of managed areas can help stabilize populations even if individual areas are too small. The scale of dispersal suggested here would demand a network with spacing between areas of 10 km or less.

This report is divided into two sections – the first concentrates on the implications of coral dispersal for climate change adaptation. The second concentrates on dispersal over long and short scales and the implications to marine managed area design. The sections are written in a complimentary but stand-alone fashion in order to allow them to be submitted as separate paper

Non academic products and deliverables:

In country training: mapping and coral genetic identifications training sessions for in-country students in Pohnpei, Palau, Tuvalu.

Reports to in-country natural resource management agencies: Tuvalu, Tonga.

Microdocumentaries on coral reef conservation, global warming and dispersal:

Delivered to <http://Microdocumentary.org> and
<http://dsc.discovery.com/videos/short-attention-span-science-tracking-coral-across-the.html>

Sustainability: The coral reef notebook. 2 DVD set from Short Attention Span Science Videos

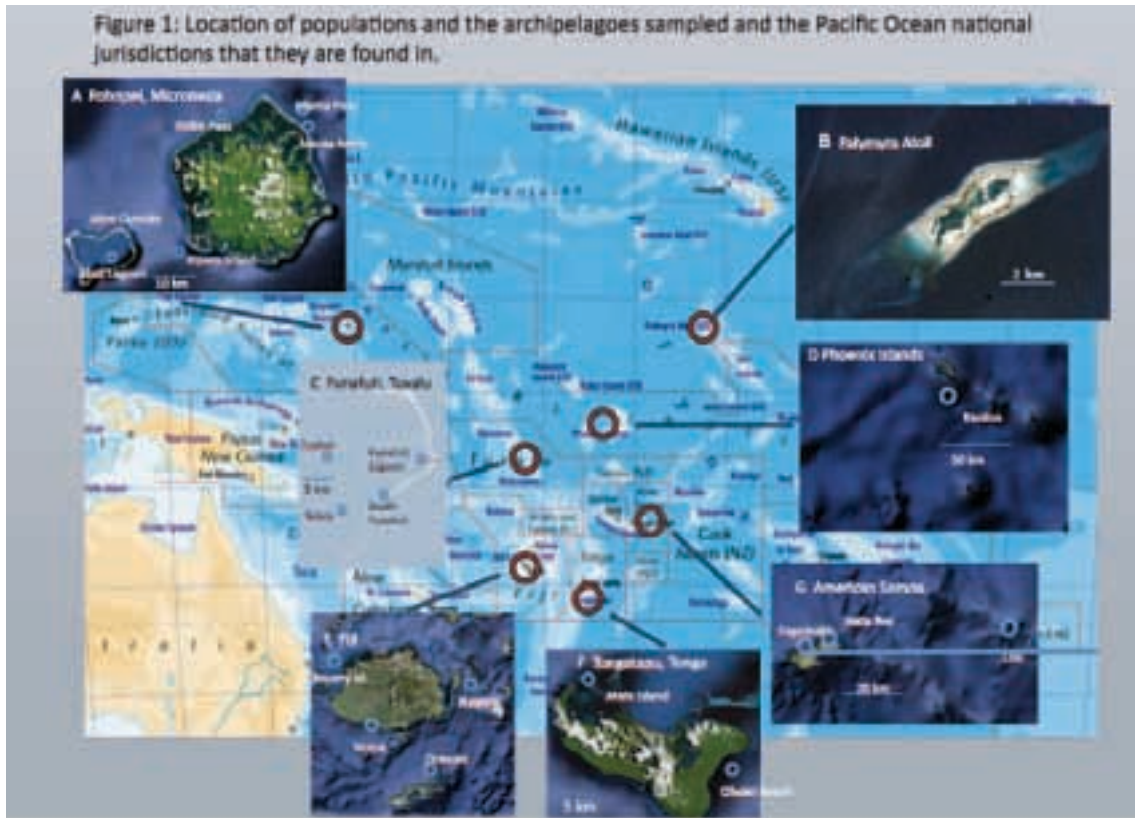
Section I:

Mismatch between climate change and coral dispersal rates in the south Pacific

Ecological communities of plants and animals respond to climate change through many mechanisms, but a common response is a shift in species distributions towards the poles (Walther *et al.* 2002). In association with altered climates, terrestrial species such as forest trees, butterflies, birds and mammals and coastal marine species have shifted distributions poleward by tens to hundred of kilometers over the past 20 – 100 years (Parmesan *et al.* 1999; Sagarin *et al.* 1999; Walther *et al.* 2002; Parmesan 2006). By moving populations out of environments that have grown less hospitable, or by moving genes that are adapted to warmer climates into previously cooler areas, migration and dispersal represent some of the chief natural adaptations of ecosystems to climate shifts (Iverson *et al.* 2004; Parmesan 2006).

Among reef building coral on Pacific archipelagoes, the wide distribution of many species with planktonic eggs and larvae (Veron 1986) suggests that dispersal among islands is common. If so, adaptation to climate change through range shifts may be possible. However, coral genetic structure sometimes suggests that dispersal may be low (Ayre & Hughes 2000; Vollmer & Palumbi 2007) especially when oceanic currents forestall easy movement among localities (Galindo *et al.* 2006). The dominance of east-west moving ocean currents in the central Pacific (Trembl *et al.* 2008) suggests that the north-south dispersal required for climate adaptation might be limited. However, there are no data comparing spawning coral populations across a broad span of the Pacific from the equator to the poleward limit of a species' distribution with which to test this idea.

Here we analyze the genetics of coral populations from seven different archipelagoes in the central Pacific, from the equator to the southern limit of abundant coral growth, in order to test their ability to adapt to climate change through dispersal. We obtained DNA sequence data for four highly polymorphic loci (the mitochondrial control region, a nuclear intron and two nuclear exons) in the common tabletop coral, *Acropora hyacinthus* for 497 individual colonies from 20 populations in seven island archipelagoes across the central Pacific (Figure 1, Table S1). *Acropora hyacinthus* spawn eggs into the water and is one of the most common corals from Africa to French Polynesia (Veron 1993) making it a good model for a coral with a wide range and potentially high dispersal.



The majority of pairwise population comparisons across archipelagoes and loci exhibit high values of genetic differentiation measured by F_{ST} showing clearly that coral populations over 1000–6000 km were dramatically different (representative histograms in Figure S1). Mean F_{ST} for mitochondrial control region sequences was 0.22. The three nuclear genes had average F_{ST} s of 0.07, 0.08, and 0.15. AMOVAs performed by Arelquin 3.0 (Schneider *et al.* 2000) on the four loci estimated that between 3 and 11% of the genetic variance was distributed among archipelagoes (all p values < 0.03).

Recent theory suggests that these values are severe underestimates. Hedrick (Hedrick 2005) showed that estimates of genetic variance for loci with high heterozygosity and many alleles were low by a factor of approximately $(1-H_s)/(1+H_s)$ where H_s is the average heterozygosity within populations. Such corrections seem appropriate for these coral data where H_s ranges from 0.4 to 0.75 (Table 1). For example, Palmyra and Fiji share no mtDNA haplotypes, but the large number of haplotypes in the analysis creates high within-population variance, and a traditional calculation of F_{ST} yields a low value of only 0.30 for these two populations. A recalculation of this F_{ST} using Hedrick's F'_{ST} suggests that geographically-based genetic differentiation is much higher (0.81). Correcting F_{ST} values as in Hedrick (Hedrick 2005) suggests that genetic differentiation among archipelagoes ranges from 0.28 to 0.44 for the nuclear loci and 0.72 for mtDNA (Figure 3).

Figure 2: Average genetic differentiation across archipelago boundaries for table top corals in the central Pacific. Values are Hedrick's F'_{ST} averaged among populations and loci.



High genetic diversity among archipelagoes shows that these coral populations are effectively isolated both ecologically and evolutionarily. Populations in an island model with F_{ST} values as high the ones we report generally are considered to have gene flow between them of less than 2-4 larvae per generation. Using F'_{ST} values instead as the basis of this projection suggests gene flow of one migrant or less each generation. Because corals are long lived, generation times may be 10-25 years or higher (Babcock 1991), and so the annual rate of long distance coral dispersal may be substantially less than one larva per year.

Movement of less than a single coral larva per year between archipelagoes will slow dispersal-based responses of coral populations to climate change. The large expanse of open ocean between habitats and the low dispersal potential of these coral larvae may thus combine to trap coral populations on islands or island groups, limiting the potential of central Pacific corals to escape climate change by migrating poleward.

Also slowed will be the dispersal of genes that adapt corals to warmer temperatures. If corals growing in currently warm, equatorial conditions harbor genes or symbionts that favor growth in these conditions, then spread of these warm-adapted traits might help increase fitness of corals as global temperatures increase. For example, average sea

surface temperatures in Palmyra or the Phoenix Islands (27-29° C, <http://coralreefwatch.noaa.gov>) are significantly warmer and spend much more time close to the 31°C threshold of coral bleaching than Tongatapu, Tonga (24-28° C). The next most southerly coral habitat, the Kermadec Islands are even cooler and harbor few coral genera (Brook 1999). Even if Palmyra populations were adapted to warmer temperatures, and the Tongan population came under temperature stress due to global climate change, flow of adapted genes between the two would be rare. The two locations share no haplotypes for control region sequences, only two of three common haplotypes at the exon 3684, and only two of five for the intron PaxC. With such very low gene flow, cool populations may need to evolve high temperature adaptation *in situ* without benefit of adaptive mechanisms that may have evolved previously in equatorial habitats.

In the central Pacific, low capacity for range shifts among corals suggests that this primary mechanism of population response to climate may be limited. If coral populations are effectively trapped on islands, then the ability of coral populations to sustain themselves through other responses to climate change, such as local adaptive evolution or individual colony acclimation, may become paramount.

Methods:

Coral DNA was isolated and amplified as previous described (Oliver & Palumbi 2009) using control region and PaxC primers from ref (Vollmer & Palumbi 2007), and primers for the protein coding loci 3684 and 5491 courtesy of J. Ladner (sequences...). Diploid sequences were analyzed with PHASE to determine the most likely allele content for each individual. Common alleles (occurring at least ten times in the data set) ranged from five in locus 5491 to 22 in the PaxC intron (Table 2). Haplotypes are defined by variation at 9 to 22 Single Nucleotide Polymorphisms (Table 2). Haplotype data for each individuals were used in all subsequent analyses. Structure was determined using Arlequin 3.0 (Schneider *et al.* 2000). Geographic separation was determined from straight line distances based on Google Earth.

Table 1: Variability in the four loci sequenced.

	CR	PaxC	3684	5491
<i>bp sequenced</i>	417	247	289	348
<i># haplotypes</i>	17	22	10	5
<i># SNPs</i>	12	20	9	11

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Supplemental results:

Sample sizes and locations are presented in Table S1. Representative histograms of F_{ST} values among archipelagoes are in Figure S1.

Figure S1; Genetic differences (F_{ST}) for *A. hyacinthus* populations in inter-archipelago comparisons. Histograms show the number of pairwise comparisons across archipelagoes and across loci that fall within 0.1 F_{ST} intervals.

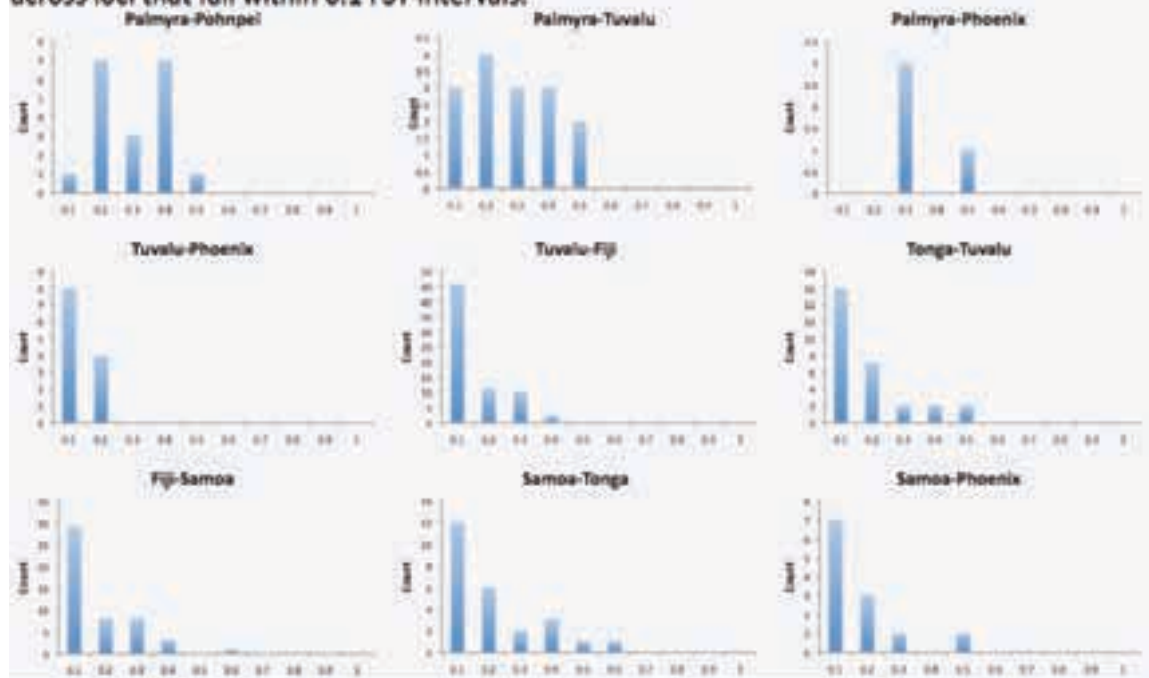


Table S1: Sample sizes (number of alleles or haplotypes sequenced) and populations sampled for *A. hyacinthus*.

		Samples size (number of haplotypes)			
Population		CR	PaxC	3684	5491
American Samoa					
	<i>Ofu</i>	60	79	68	104
	<i>Vatia Bay</i>	28	87	84	68
	<i>Fagemalo</i>	14	33		92
Fiji					
	<i>Bounty Isl.</i>	17	31	32	26
	<i>Dravuni</i>	37	73	69	20
	<i>Votua-Maui Bay</i>	27	34	27	42
	<i>Naigani-Makogai</i>	21	33	44	32
Tuvalu					
	<i>Fuafuti</i>	23	48	16	42
	<i>Funafuti Lagoon</i>	29	59	26	52
	<i>S. Funafuti</i>	29	46	46	28
	<i>Tefala</i>	7	22	22	
Tonga					
	<i>Atata Isl</i>	14	45	18	12
	<i>Oholei Beach</i>	6	42	36	10
Pohnpei					144
	<i>Manta Pass</i>	20	36	32	
	<i>Manta Reef</i>	27	40	50	
	<i>Kipara Isl</i>	65	124	200	
	<i>Palikir Pass</i>	9	18		
	<i>Ahnt Outside</i>	15	24	26	
	<i>Ahnt Lagoon</i>	24	33		
Phoenix		10	12	12	16
Palmyra		15	32	34	16
Total		497	951	842	688

Section 2:

Short and long scale population structure in central Pacific reef corals: Implications for population survival and marine managed areas

Species in discontinuous habitats typically exist in metapopulations in which dispersal and local population dynamics play a strong role in stabilizing populations (James *et al.* 2002). When human use of ecosystems has strong ecological impact (Palmer *et al.* 2004), managed areas such as marine or terrestrial parks can create or enhance population fragmentation. Dispersal among these managed areas plays a strong role in whether protection stabilizes threatened populations. Particularly in marine systems where managed areas are often too small to be individually stable (Lubchenco *et al.* 2003), creating networks of protected habitats can help stabilize populations if they can disperse among them at a high enough rate (Hastings & Botsford 2006). As a result, the correct match of dispersal to the scale of habitat protection is needed for managed area networks to succeed (Gaines *et al.* 2010).

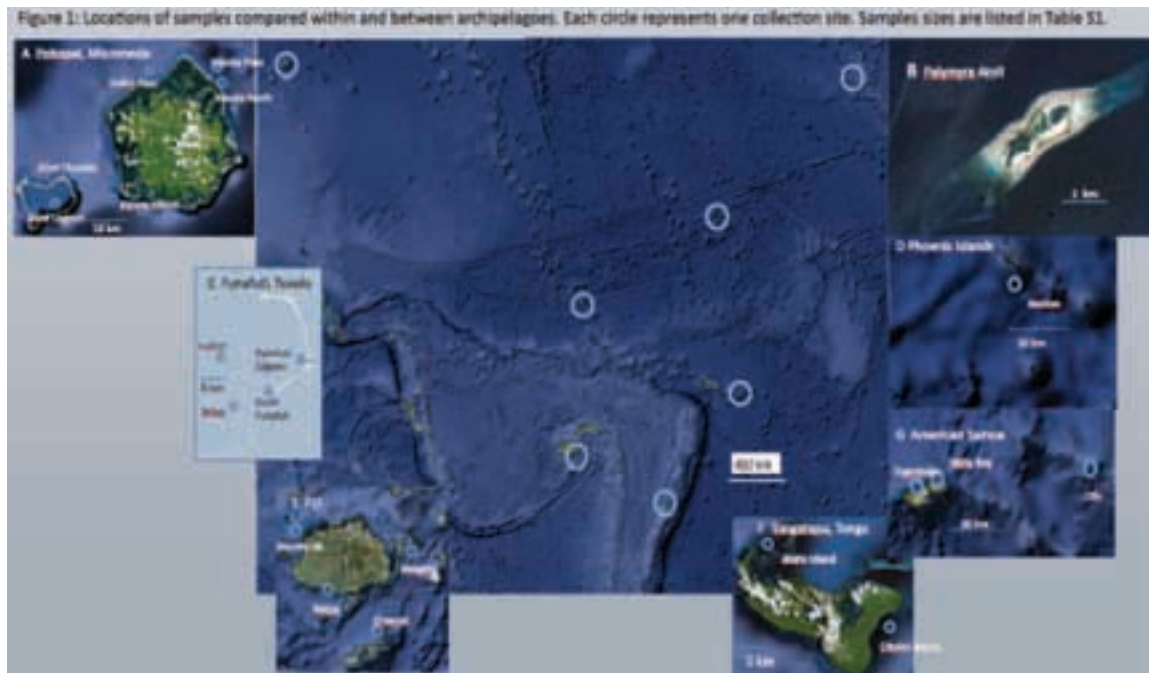
Hastings and Botsford (2006) laid out conditions under which separate protected areas together would form a network that sustained populations. Two protected areas that are each unsustainable singly are jointly sustainable when $(q_{12} * q_{21}) > |q_{11} * q_{22}|$ where q_{ij} is the movement of individuals from i to j during a generation (Hastings and Botsford 2006, eq. 5). Similar results were found for larger numbers of areas. These relationships show that spatial scale of dispersal plays a strong role in the ability of protected areas to jointly support threatened populations. One goal of research on population structure is to provide insight in the relative rates of dispersal (the q_{ij} 's) and local recruitment (the q_{ii} 's) in order to use this framework to make predictions about protected area design.

Reef building corals are architecture species that generate habitat for 1000s of other reef species. Despite the generally low productivity of local ocean water, corals and their photosynthetic symbionts help power one of the most productive ecosystems on Earth. Protecting coral populations is thus fundamental to the future of these productive ecosystems. Ayre and Hughes (Ayre & Hughes 2000) concluded coral populations on the Great Barrier Reef were essentially fully connected along the 2000 km length of the reef based on low genetic differentiation among populations. However, they also showed (Ayre & Hughes 2004) that populations of one coral, the table top coral *Acropora hyacinthus* on Lord Howe island, 700 km offshore of the GBR, had strong population differentiation. Palumbi *et al.* (see section 1 above) showed similarly high differentiation and inferred low dispersal across archipelagoes. Other studies have shown coral genetic differentiation, and inferred low dispersal, over spatial scales of 100s of km (Takabayashi *et al.* 2003; Vollmer & Palumbi 2007). Few studies have examined coral structure over short and large spatial scales at the same time (Baums *et al.* 2005; Baums *et al.* 2006) especially for free-spawning corals expected to have the highest dispersal. As a result, it remains unclear how local, regional and global population genetic structure differs for many reef building corals, especially in highly fragmented habitats such as the central

Pacific islands. It also remains unclear how to best design marine managed area networks to support coral populations.

Here we analyze the genetics of 1-6 local coral populations from each of seven different archipelagoes in the central Pacific in order to compare short scale dispersal patterns to the very low dispersal seen among these island groups. Our samples include populations 5 to 170 km apart within archipelagoes but also span a 6000 km and 30° latitudinal range (Figure 1, Table S1). We include samples from adjacent bays on small islands, and from among Pacific nations that control approximately 40% of the open ocean and reef area of the central Pacific. This geographic and political coverage allows the results to be compared to international efforts for effective coral protection and local marine managed area design.

We obtained DNA sequence data for four highly polymorphic loci (the mitochondrial control region, a nuclear intron and two nuclear exons, see Table S2) in the common tabletop coral, *Acropora hyacinthus* for 497 individual colonies from 20 populations (Figure 1, Table S1). Heterozygosity was high but variable among loci (range: 0.42-0.79).

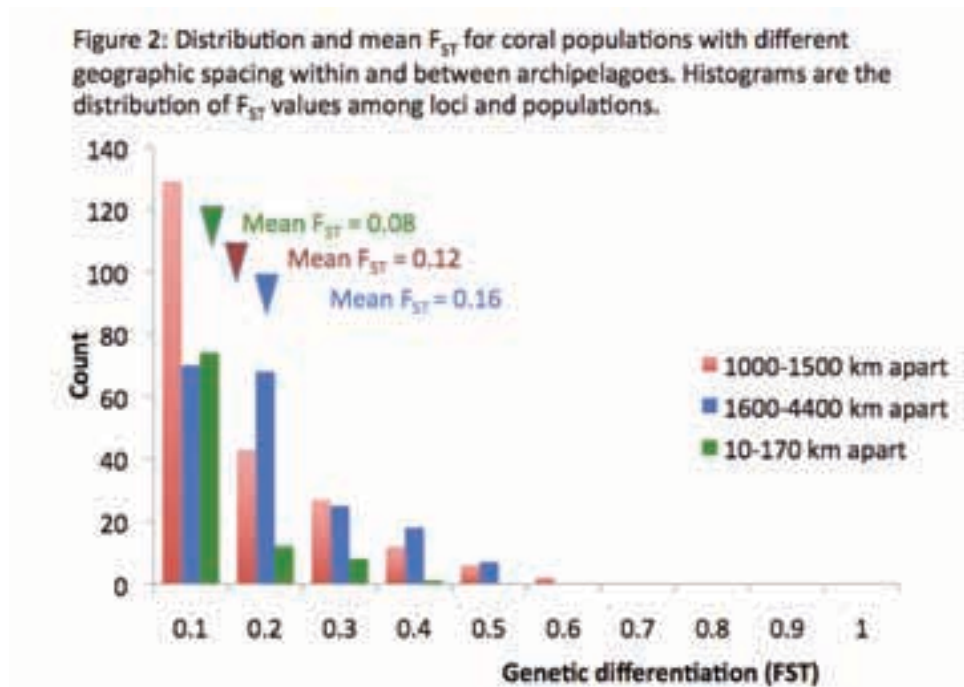


Patterns of genetic differentiation inferred from alleles among individuals at each locus showed that strong allele frequency differences were common. Genetic differentiation measured by F_{ST} was visible within all island groups (Table 1). Sixteen of 31 comparisons among population pairs within archipelagoes show genetic differentiation for at least one locus. F_{ST} within archipelagoes averages 0.08 for Control Region sequences, and ranges from 0.015 to 0.084 for the nuclear loci. Estimates of variation among populations within archipelagoes using Arlequin 3.0 were highly significant for three of four loci and ranged from 0.02 to 0.08. The populations compared have a mean

distance of 51 km (Table 1), and so these F_{ST} values represent high levels of local genetic differentiation for such closely spaced samples.

Some adjacent populations showed strong genetic distinctions. For example, populations at Manta Pass and Manta Reefs in Pohnpei, Micronesia were only 5 km apart, yet showed strong differentiation at two of four loci (Table 1). Such differences were not universal, however. Among the four populations sampled at Funafuti Atoll, one stood out as distinct (Fuafuti vs Funafuti Lagoon, Table 1) but the other comparisons (all within 20 km) were genetically similar. Other populations such as Dravuni in Fiji have low differentiation even from populations 100 km distant or more.

However, there were indications of increased genetic distance for population more distant than about 50 km. Average F_{ST} for populations closer than 50 km was lower (0.05) than for populations spaced 50 km apart or higher (0.07). Intra-archipelago population comparisons with significant F_{ST} had a higher average geographic distance (66 km) than did populations that were not significantly different (29 km). Traditional isolation by distance analyses show significant relationships of genetic distance to the log of geographic distance for three of four loci over scales of 1000 km or above (Figure S1). In addition, across all samples, intra-archipelago genetic differentiation was lower than for comparisons at greater spatial scales (Figure 2), indicating an overall increase in genetic differentiation with distance. Among different population pairs, there is a clear positive relationship between the geographic distance between populations and the fraction of comparisons across loci that are significantly different (Figure 3).



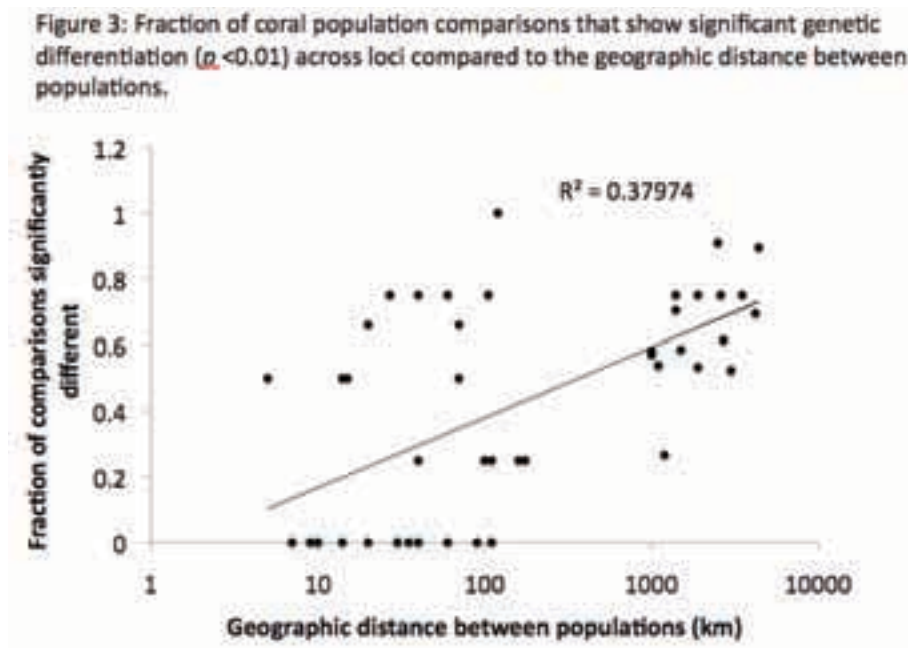
Patterns for each archipelago

Among six populations sampled for *A. hyacinthus* in Pohnpei, Micronesia (Figure 1A), one from Manta Pass stands out particularly as distinct from most others in the

archipelago. Populations from Ahnt Atoll, about 20 km distant from Pohnpei tend to be mildly distinct from the most distant, northeastern, Pohnpei populations but not the closer, southwestern Pohnpei populations.

In Tuvalu, all sampled populations were within 15 km of one another, situated on the ring of islands that forms the atoll of Funafuti (Figure 1C). Nevertheless, the populations of Fuafuti, on the western edge of the atoll and Funafuti Lagoon, on the eastern edge were significantly different at two of four loci (Table 1). Populations in South Funafuti, near one of the main channels into the lagoon, and Tefala to the west, are intermediate in gene frequencies.

In Fiji (Figure 1E), genetic differentiation is somewhat less, but is significant between the Mamanuca Islands (Bounty Island) on the west side of the largest island Viti Levu, Dravuni in the south, and Naigani-Makogai to the east. In Fiji, population differentiation was visible in populations 90 km apart and above. Populations closer than this (Naigani vs Makogai to the east, and Votua and Maui Bay on the south coast, both within 20-40 km) showed no population differentiation. This pattern is weakened by low sample sizes at Maui Bay where table top corals were very rare.



In Tonga, two locations on opposite sides of the main island of Tongatapu are significantly different from one another at three of four loci (Figure 1F). These populations are only 25 km distant and so the strength of genetic differentiation is much higher in Tongatapu than in Fiji. This implies very low genetic exchange among populations on this island.

In American Samoa, population differentiation is also high over small spatial scales. The population on Ofu Island was highly distinct from populations at Vatia Bay or Fagemalo Bay on the main island of Tutuila (Figure 1G). These two latter populations were also distinct, differing strongly at two of the four loci. Population differences were especially high for the mitochondrial Control Region, which showed levels of genetic differentiation (measured by F_{ST}) of about 0.20. We infer from these values that there is very low movement of coral larvae among islands of the American Samoa group or between bays on the island of Tutuila.

Patterns across archipelagoes

Coral populations on all seven central Pacific archipelagoes show high genetic differentiation from one another and very low dispersal (see section 1 above). Average F_{ST} among archipelagoes ranges from 0.02 to 0.15 across loci. Populations at the largest spatial scale, above 1500 km, show the largest genetic differentiation: F_{ST} averages 0.16 across pairwise population comparisons and loci (Figure 2). For pairs of locations separated by more than 1000 km, comparing all populations to one another at all loci shows that on average 50% of genetic tests are significantly different at the $p < 0.01$ level (Figure 3).

Implications for scales of coral dispersal

The trend for increased genetic distance at greater geographic distances is seen clearly at scales including 1000s of km (Figure S1), and implies that dispersal among archipelagoes is very limited. Other studies of coral population genetics have seen such differences over large scales (Ayre & Hughes 2000, 2004; Baums *et al.* 2005; Baums *et al.* 2006; Vollmer & Palumbi 2007). However, the structure we see in the central Pacific is stronger than that seen across locations in the Great Barrier Reef (Ayres and Hughes 2000) or among islands of the Caribbean (Galindo *et al.* 2006). It is possible that a combination of small adult population size on small atolls (compared to large islands or continental barrier reefs) combined with predominantly east-west currents (compared to the north-south orientation of our samples) increases genetic drift and decreases north-south dispersal.

By contrast, a relationship of genetic distance to geographic distance at scales less than 100 km is more difficult to discern (Figure 3). Partly this is due to the unpredictability of local coral differentiation. Many of the significant comparisons in our data set derive from a set of starkly divergent populations: Manta Pass in Pohnpei, Ofu Island in American Samoa, Fufuti in Funafuti and Oholei Beach in Tonga. These areas evidently represent highly closed coral populations with little demographic exchange with surrounding areas. That we found so many such populations, in nearly every archipelago, with our light sampling design suggests that such diverged populations are common.

The reason for this mosaic of genetic differentiation is not known. Differentiated populations may be in areas with high local larval retention and low dispersal due to ocean currents. High levels of local hybridization with conspecifics (Willis *et al.* 2006) may generate a local signature of genetic differentiation. Alternatively, episodic

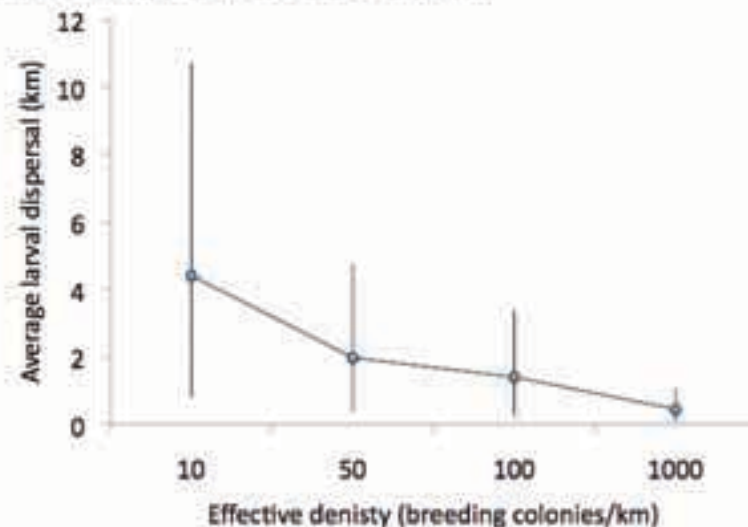
recruitment of large numbers of larvae may generate a spatial signature of genetic differentiation due to reproductive sweepstakes (Hedgecock 1994). None of these potential mechanisms has been well studied for local coral populations, and the mechanisms generating idiosyncratic local genetic structure remain unclear. Whether the less diverged populations are similarly closed, but show no genetic distinctions due to the vagaries of genetic drift (Waples 1998) or due to our small number of loci will require more intense study of local coral genetics.

Isolation by distance

Despite the variation in genetic differentiation over small scales, the chance of populations being genetically different is much higher above 50 km in geographic distance than below (39% vs 17%, Figure 3). F_{ST} values average 0.065 for populations 50 – 170 km distant within archipelagoes (Table 1), and slightly less (0.046) for populations spaced closer than 50 km. These genetic and geographic distances suggest limited dispersal potential.

Rousset (Rousset 1997) showed for a linear stepping stone population that the slope (m) of the build up of genetic distance ($F_{ST}/(1-F_{ST})$) over geographic distance (km) is related to average dispersal distance (d) by the relationship: $d = \sqrt{1/(4D_e m)}$ where D_e is the effective density of breeding adults per km of shoreline. Effective density, which is about equal to the number of breeding colonies per km, is not known for corals, but tends to be much less than ecological density (see discussion in Pinsky et al. submitted). If we assume the number of breeding colonies per km is between 10 and 1000, then we estimate average dispersal of free-spawning corals such as *A. hyacinthus* is between 1 and 10 km (Figure 4).

Figure 4: An estimate of coral larval dispersal rates within archipelagoes based on slopes of genetic isolation by distance curves. Points are dispersal distances calculated from the average genetic differentiation within archipelagoes. The error bars represent the range based on the maximum and minimum slopes observed. Dispersal estimates vary directly with effective density – and are shown for various effective estimates over three orders of magnitude.



Although this estimate has large uncertainty (see error bars in Figure 4), dispersal is probably on the low side of this range for highly distinctive populations such as the one at Manta Pass, Pohnpei. It may be on the high side of this range for populations that show little genetic divergence over 10s of km.

Other studies have shown dispersal distances consistent with these results. Sammarco (Sammarco & Andrews 1988; Sammarco & Andrews 1989) observed movement of coral larvae after a mass spawning event, and recorded settlement as a function of distance from Helix reef, the source. He found average movement of about 8 km in that instance. Ayre and Hughes (2000) suggested that on the order of 3-4 migrating coral larvae per generation move between local coral populations on the Great Barrier Reef. Our genetic data provide similar general inferences for populations above 50 km apart. Although this level of movement within archipelagoes may be high enough to suggest recolonization of reefs over millennial spans, it is probably low enough to slow down recovery over time spans of years or decades.

Implications for managed area design

From an ecological perspective, the samples we analyze here are drawn from a mosaic of coral populations with high, medium or low demographic connection to one another. The variety of these connection strengths has strong implications to the interaction among coral reef managed areas in the Pacific.

At large scales, our data suggest extremely low dispersal between archipelagoes. The large genetic divergences we found among corals from different island groups implies a very low level of demographic connection among them. Ayre and Hughes (2004) also inferred low dispersal rates for the isolated and genetically depauperate Lord Howe Island populations. Our data provide similar inferences for island populations that are not genetically depauperate, showing that the low connection among archipelagoes is likely to be a general feature of coral genetic structure.

In the framework of Hastings and Botsford's (2006) analysis of managed areas, our results imply that dispersal among archipelagoes is much lower than the rate of retention of larvae within archipelagoes, i.e. $q_{ij} \ll q_{ii}$. As a result, it is likely that $(q_{12} * q_{21}) < |q_{11} * q_{22}|$ for all pairs of populations, and the Hastings-Botsford criterion for network benefit will probably generally fail. This suggests that an unsustainable population in one archipelago will not be rescued by recruitment input from a distant archipelago. As a result, the network interaction of managed areas among these far flung archipelagoes will be minimal, and managed areas in one island nation will play little role in coral protection elsewhere. From a management standpoint, these results imply that conservation efforts within archipelagoes are critically important to sustain local coral populations.

Partially, this conclusion is based on the joint spatial scales of political boundaries, island distances and larval movement patterns. Unlike most ecologically important marine species, coral dispersal scales are smaller than scales of political boundaries in Pacific island nations, which stretch over 1000s km (Figure 1). As a result, conservation efforts

in distant archipelagoes will not add measurably to local success for corals. The same might not be true for other reef species such as reef fish.

Our results also shed light on the potential for marine managed area networks to sustain coral populations over short spatial scales. Recent models of managed area demography suggest that a managed area must be about twice as wide as average larval dispersal in order to capture enough local recruitment to be sustainable by itself (Botsford *et al.* 2001; Botsford *et al.* 2003). Alternatively, a managed area must receive substantial larval input from surrounding, non-protected zones. Coral dispersal of 1-10 km suggests a minimum size of managed areas on the order of 2 – 20 km. Few coral managed areas are this large, suggesting that few of them are protecting sustainable populations, or that they rely on input from elsewhere.

Alternatively, the success of managed areas for corals could derive from a network of managed areas that jointly provided one another enhanced populations of recruits (Hastings and Botsford 2006, Gaines *et al.* 2010). Because managed areas need to be within the average dispersal distance for this network effect to be strongly realized (Gaines *et al.* 2010), small coral managed areas must be spaced close together (<10 km) in order for them to form an effective network. Because the distance between islands within archipelagoes frequently exceeds these scales, such protected areas need to be included on all islands further apart than about 20 km. These considerations suggest two types of managed areas might be appropriate for corals. The first is a set of small coral gardens spaced closely along the reef. The second is a large continuous protected area.

It is possible that the genetic data we present provide an incomplete picture of coral dispersal. The average spatial scale of dispersal is clearly low, but whether average dispersal is typically 1 -10 km as suggested here depends on the effective density of colonies. Comparing the genetics of coral recruits and adults can help measure effective density (Pinsky *et al.* submitted). Other insight could come from comparison of coral populations over very small spatial scales of < 1km. In addition, the variable nature of coral genetic differentiation suggests that distance alone is not the only major determinant of larval dispersal. The wide occurrence of *A. hyacinthus* from Africa to Polynesia (Veron 1986) shows that long distance dispersal must occur. Conservative management might assume that coral dispersal is low but variable, and that reefs isolated by distance are most likely to be ecologically isolated as well.

Methods:

Four loci were amplified using PCR from coral genomic DNA. The mitochondrial control region, the PaxC intron and exons from two protein coding loci (Loc3684 and Loc5491) were amplified as described in section 1, and sequenced on an ABI 3100 sequencer. Diploid sequences were edited by hand to confirm heterozygous base calls and were analyzed with PHASE to determine the most likely haplotype content for each individual at each locus. Common alleles (occurring at least ten times in the data set) ranged from five in locus 5491 to 22 in the PaxC intron (Table 2). Haplotypes are defined by variation at 9 to 22 Single Nucleotide Polymorphisms (Table 2). Population structure

was tested with Arlequin 3.0 (Schneider *et al.* 2000) based on haplotype frequencies for each population and each locus. Geographic distance was calculated in Google Earth as the straight-line distance among populations. Correcting these distances by taking intervening island land masses into account did not affect the results.

Table 1: Genetic differentiation among populations within island groups. Values are F_{ST} 's based on haplotype distributions. Shaded cells represent significant values ($p < 0.01$). Analyses conducted with Arlequin 3.0 (Schneider et al. 2000).

	Intra-island pair			Fst			
			distance (km)	CR	PaxC	3684	5491
Am. Samoa	<i>Ofu</i>	<i>Vatia</i>	105	0.23	0.03	0.09	0.01
		<i>Fagemalo</i>	120	0.21	0.03	0.04	
	<i>Vatia</i>	<i>Fagemalo</i>	15	0.2	0		0.04
Fiji	<i>Bounty</i>	<i>Votua</i>	100	0.05	0.01	0.137	
		<i>Dravuni</i>	175	0.06	0.04	0.04	0.01
		<i>Naigani</i>	160	0.08	0.03	0.017	0
	<i>Dravuni</i>	<i>Votua</i>	90	0	0.006	0.03	
		<i>Naigani</i>	110	0.03	0.013	0.055	0.05
	<i>Votua</i>	<i>Naigani</i>	110	0.06	0.008	0.102	
Tuvalu	<i>Fuafuti</i>	<i>Funafuti</i>	14	0	0.06	0.127	0.02
		<i>S. Funafuti</i>	10	0.11	0	0	0.002
		<i>Tefala</i>	9	0	0	0	
	<i>Funafuti</i>	<i>S. Funafuti</i>	7	0.11	0.05	0.07	0
		<i>Tefala</i>	14	0	0.04	0.1	
	<i>S. Funafuti</i>	<i>Tefala</i>	7	0.03	0	0	
Tonga	<i>Atata</i>	<i>Oho</i>	27	0.32	0.07	0.09	0.001
Pohnpei	<i>Manta Pass</i>	<i>Manta Reef</i>	5	0.12	0.09	0.16	0
		<i>Palikir Pass</i>	20	0.04	0.16		
		<i>Kipara Isl</i>	40	0.22	0.14	0.25	
		<i>Ahnt Out</i>	60	0.23	0.19	0.27	
		<i>Ahnt Lagoon</i>	70	0.26	0.09		
	<i>Manta Reef</i>	<i>Palikir Pass</i>	20	0	0		
		<i>Kipara Isl</i>	40	0.02	0.005	0.05	
		<i>Ahnt Out</i>	60	0.08	0.004		
		<i>Ahnt Lagoon</i>	70	0.02	0	0.06	
	<i>Palikir Pass</i>	<i>Kipara Isl</i>	35	0.01	0.04		
		<i>Ahnt Out</i>	30	0.01	0.005		
<i>Ahnt Lagoon</i>		40	0.02	0			
<i>Kipara Isl</i>	<i>Ahnt Out</i>	10	0.02	0	0		
	<i>Ahnt Lagoon</i>	20	0.005	0.007			
	<i>Ahnt Out</i>	<i>Ahnt Lagoon</i>	7	0.004	0		

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Supplemental data:

Table S1: Sample sizes (number of alleles or haplotypes sequenced) and populations sampled for *A. hyacinthus*.

Population		Samples size		3684	5491
		CR	PaxC		
American Samoa					
	<i>Ofu</i>	60	79	68	104
	<i>Vatia Bay</i>	28	87	84	68
	<i>Fagemalo</i>	14	33		92
Fiji					
	<i>Bounty Isl.</i>	17	31	32	26
	<i>Dravuni</i>	37	73	69	20
	<i>Votua-Maui Bay</i>	27	34	27	42
	<i>Naigani-Makogai</i>	21	33	44	32
Tuvalu					
	<i>Fuafuti</i>	23	48	16	42
	<i>Funafuti Lagoon</i>	29	59	26	52
	<i>S. Funafuti</i>	29	46	46	28
	<i>Tefala</i>	7	22	22	
Tonga					
	<i>Atata Isl</i>	14	45	18	12
	<i>Oholei Beach</i>	6	42	36	10
Pohnpei					144
	<i>Manta Pass</i>	20	36	32	
	<i>Manta Reef</i>	27	40	50	
	<i>Kipara Isl</i>	65	124	200	
	<i>Palikir Pass</i>	9	18		
	<i>Ahnt Outside</i>	15	24	26	
	<i>Ahnt Lagoon</i>	24	33		
Phoenix		10	12	12	16
Palmyra		15	32	34	16

Total 497 951 842 688

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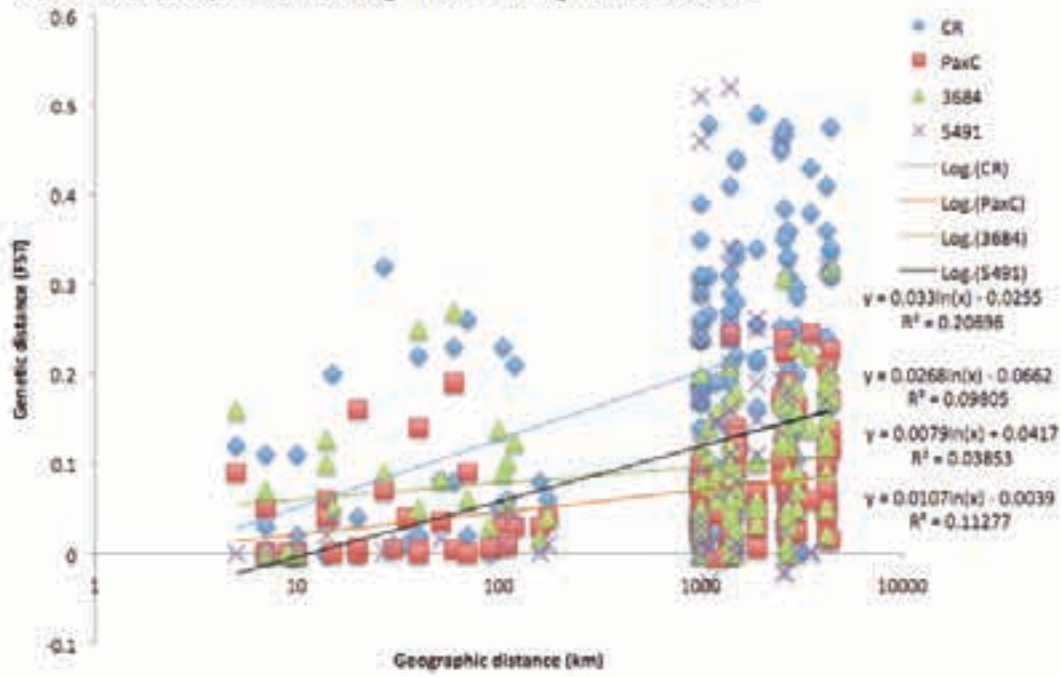
Table S2: Variability in the four loci sequenced.

	CR	PaxC	3684	5491
<i>bp sequenced</i>	417	247	289	348
<i># haplotypes</i>	17	22	10	5
<i># SNPs</i>	12	20	9	11

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Figure S1: Isolation by distance within and between archipelagoes. Each point is an F_{ST} value between populations. R-squared values represent correlation coefficients of genetic distance compared to log geographic distance. Correlations for all loci except 3684 are significant using Mantel tests.



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