Title: Strong genetic structure among coral populations within a conservation priority region, the Bird's Head Seascape (Papua and West Papua, Indonesia)

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Abstract: Marine Protected Areas (MPAs) are widely considered to be one of the best strategies available for protecting biodiversity and ecosystem processes in marine environments, particularly in developing, tropical nations. While data on connectivity and genetic structure of marine populations are critical to designing appropriately sized and spaced networks of MPAs, such data are rarely available. Here we present an assessment of genetic structure in reef-building corals from Papua and West Papua, Indonesia, among the most biologically diverse and least disturbed coral reef regions in the world, and the focus of the multi-institutional Bird's Head Seascape initiative to design and implement a functional network of MPAs. Microsatellite variation was assessed within and among populations of *Pocillopora damicornis* (Linnaeus, 1758) and *Seriatopora hystrix* (Dana 1846) (family: Pocilloporidae) from three regions, each currently under a different conservation regime: Teluk Cenderawasih, Raja Ampat, and southwest Papua. Analyses of molecular variance, assignment tests, and genetical bandwidth mapping revealed significant local-scale structure in both species, and a lack of regional filters to gene flow. Overall, *P. damicornis* populations were less structured (*F*ST = 0.139, p < 0.00001) than those of *S. hystrix* (*F*ST = 0.357, p < 0.00001). In order to maintain connectivity within and among regions, coral reef conservation on the local scale is needed. These data have been directly applied to the design of a MPA network in the Bird’s Head Seascape.
Introduction

Comprising only a small fraction of the surface of the Earth’s oceans, coral reefs are the world’s most biologically diverse marine ecosystems (Connell 1978, Reaka-Kudla 1997). Despite the ecological and economic importance of coral reefs, they are rapidly declining worldwide due to human influence (Hoegh-Guldberg et al. 2007). Within the past few decades, 19% of the world’s coral reefs have been destroyed and 15% are now at risk of imminent collapse in the next 10 to 20 years (Wilkinson 2008), with rates of decline that exceed those of tropical rain forests (Bruno and Selig 2007). Two thirds of the Caribbean and over 85% of Southeast Asian coral reefs are considered under threat (Burke et al. 2012)

Most troubling in these declines is the dramatic reduction in the abundance of reef-building corals (order: Scleractinia) threatening the very foundation of coral reef ecosystems. For example, the Coral Triangle (a region comprised of the Philippines, Malaysia, Indonesia, Papua New Guinea, the Solomon Islands, Brunei Darussalam, and Timor-Leste) has the highest proportion of ‘Vulnerable’ and ‘Near Threatened’ coral species based on IUCN Red List Criteria (Carpenter et al. 2008). Anthropogenic loss of corals and the degradation of coral reef environments are severely impacting the long term stability of coral communities (Adams and Ebersole 2010, Hughes et al. 2010) creating an urgent need for coral-focused conservation, especially within the Coral Triangle (Burke et al. 2012)
Marine protected areas (MPAs) are considered one of the best methods for protecting species diversity and ecosystem processes and functions. Despite their demonstrated effectiveness (Levitan and McGovern 2005), only 2% of the world’s coral reefs are within MPAs with adequate conditions for the conservation of biodiversity (Mora et al. 2006). Given that this amount is far less than the recommended 20-30% (Mora et al. 2006), the recent and projected growth of MPAs in the coming years increases the need for sound marine conservation science. While understanding connectivity has been identified as critical to developing long-term conservation strategies for marine ecosystems (Botsford et al. 2001, Cowen et al. 2006, Crowder et al. 2000, Palumbi 2003), it remains among the most crucial gaps in scientific knowledge necessary for marine conservation (Sale et al. 2005). In addition, genetic diversity has rarely been incorporated in international biodiversity conservation policy (Laikre 2010).

Coral reefs in the provinces of Papua and West Papua, Indonesia, (Figure 1) collectively referred to as the ‘Bird’s Head Seascape’ (BHS), are among the most diverse and pristine in the world (Allen 2008) and rank as the Indonesian government's number one priority region for marine biodiversity conservation development (Huffard et al. 2012a). This region is also the focus of the multi-institutional Bird’s Head Seascape initiative, comprised of NGOs and universities working with local governments to design and implement an ecosystem-based management plan that has as its centerpiece a network of MPAs that span the entire Bird’s Head Seascape (Mangubhai et al. 2012). Therefore, understanding patterns of genetic connectivity among populations of coral reef animals within this region has been an ongoing research priority for the past seven years. Results from genetic studies, including this one, have been fed directly into MPA network
planning and design in the Bird’s Head Seascape even before many of these studies were formally published (Huffard et al. 2012b).

Here we present fine scale spatial genetic patterns in *Pocillopora damicornis* (Linnaeus, 1758) and *Seriatopora hystrix* (Dana 1846), two scleractinian coral species that represent opposite ends of the genetic connectivity spectrum. We use analytical methods specifically designed for low and uneven sample sizes (necessary for investigators focusing on rare and threatened species) to test for limits to connectivity among the coral reefs of the Bird’s Head Seascape, a region designated a top conservation priority within the Coral Triangle, and to test the hypothesis that populations of *P. damicornis* will be more open with lower levels of genetic structure, while *S. hystrix* will exhibit higher genetic structure, resulting from more limited dispersal (Starger et al. 2010). We also hypothesize that these populations have undergone recent declines given the threatened nature of many Indonesian coral reefs. Our results improve our understanding of genetic structure of coral populations in remote and understudied areas while providing useful data for managers currently developing conservation strategies for the globally significant Bird’s Head Seascape.

Recent reports from Australia, Kenya and the Eastern Pacific have revealed previously unknown genetic diversity within *P. damicornis* and *S. hystrix* and some have suggested that this genetic variation may represent cryptic species (e.g. Souter 2010, Pinzón and LaJeunesse 2011, Schmidt-Roach et al. 2012, Pinzón et al. 2013). Despite these findings, most of the evidence for cryptic coral species presented in these publications is derived a limited number of molecular loci and no quantitative morphology resulting in poorly supported phylogenetic reconstructions and no clear
delimitations of cryptic species. In addition, studies rarely incorporate known sister taxa in a phylogenetic context except for Souter (2010), who tested East African *P. damicornis* against congers from Hawai’i and the Tropical Eastern Pacific, and Bongaerts et al. (2010), whose analysis of *S. hystrix* and *S. caliendrum* recovered *S. hystrix* as a monophyletic clade with marginal evidence of reproductive isolation among depth-distributed types. Furthermore, some of these recent methods, such as the use of symbiosis ecology to delineate coral species (Pinzón and LaJeunesse 2011), are already being invalidated (Cunning et al. 2013). Clearly not enough data currently exist to reject the null hypothesis that the original species designations are still valid and that our population genetic study and others (e.g. Ayre and Hughes 2004, Starger et al. 2010, Combosch and Vollmer 2011, Nir et al. 2011, Paz-Garcia et al. 2012) also remain valid.

**Methods**

**Species identification and site selection**

Coral samples were identified in the field using the species identification criteria and key of Veron (2000). Samples included in the present study (Table 1) were collected from three remote and relatively undisturbed regions within the Bird’s Head Seascape that are currently under different conservation management plans and that also represents distinct ‘coral ecoregions’ based on coral species composition (Veron et al. 2009): Raja Ampat, Teluk Cenderawasih, and Southwestern Papua (Figure 1). The coral reefs of Raja Ampat lay off the western most tip of the island of New Guinea and are at the center of the Bird’s Head Seascape. Human threats are minimal but increasing, and include destructive and unsustainable fishing (Varkeya et al. 2010).

There are currently 12 actively managed MPAs in the BHS ranging in size from 5000 to 1,453,500 ha and covering a total area of 3,594,702 ha (see Figure 1 and Table 2 in Mangubhai et al. 2012). A network of seven marine protected areas was first designated in Raja Ampat in May, 2007 and expanded in 2009 to cover a total of 1,125,940 ha, approximately 50% of Raja Ampat’s shallow reef areas, with MPAs ranging in size from 53,100 ha to 343,200 ha and the spacing between MPAs ranging from 20-100 km (Mangubhai et al. 2012). To the east of Raja Ampat is Teluk Cenderawasih, wherein lies the Taman Nasional Teluk Cenderawasih (TNTC, or Cenderawasih Bay National Park), an MPA covering 1,453,500 ha and approximately 30% of the reefs of Teluk Cenderawasih (Figure 1). To the Southwest, the Kaimana MPA covers all of Kaimana’s jurisdictional waters (597,747 ha) (Mangubhai et al. 2012).

Located along the New Guinea Coastal Current that flows westward toward Raja Ampat (Morey et al. 1999, Nof 1995), Teluk Cenderawasih may serve as a larval source for Raja Ampat. Alternatively, connectivity may be restricted due to the relatively sheltered nature of the bay, (DeBoer et al. 2008, Crandall et al. 2008, Wallace et al. 2011, Allen and Erdman 2012) limiting water and larval movement to outside populations. Although the reefs of Lemon, Adoki and Owi islands are technically not in Teluk Cenderawasih, they do lie within the ‘Cenderawasih Bay’ coral ecoregion (Veron et al. 2009) and are therefore pooled with reefs within the bay for our analysis. On the southern coast of the Bird’s Head Seascape lie Fakfak and Kaimana. Recent surveys in this region by Conservation International revealed a diverse and highly endemic fauna
(Allen 2008), and both the local and national governments are now committed to developing new MPAs in the region to protect this diversity (Huffard et al. 2012b).

Genetic analysis

A subset of previously published allele frequency data from Starger et al. (2010) was used to test new hypotheses for the Bird’s Head Seascape using new analytical methods. Briefly, Starger et al. (2010) analyzed specimens from across Indonesia, including the Bird’s Head Seascape, as possible source populations for the recovery of coral genetic diversity in the Sunda Strait following the 1883 eruption of the volcano Krakatau. For the present study, we used truncated allele frequency data files from Starger et al. (2010) to focus only on the populations of the Bird’s Head Seascape to address entirely different research questions. We subsequently employed new analysis methods to estimate connectivity and genetic diversity of these populations to inform an ongoing conservation initiative in the region that aims to promote a network of marine protected areas based on scientific data.

In order to test the hypothesis that significant genetic variation exists among sample locations, data from the Bird’s Head Seascape (Table 1) were analyzed for each species with AMOVA (Excoffier et al. 1992) as implemented in Arlequin 3.5.1.2 (Excoffier and Lischer 2010) assuming no regional genetic structure among sample locations. Hierarchical AMOVA was then performed to test the significance of the three coral ecoregions (Veron et al 2009): Raja Ampat, Teluk Cenderawasih, and Southwestern Papua. The significance of this structure was tested with 20,000 random permutations using both the infinite alleles model (IAM, represented by \( F \))
statistics, (Weir and Cockerham 1984)) and the distance-based, stepwise mutation model of microsatellite evolution (SMM, represented by R statistics, (Slatkin 1995)). Only those populations with ten or greater unique genotypes were considered in AMOVA calculations.

To examine genetic structure without a priori assumptions of population membership, we employed spatial and non-spatial Bayesian assignment methods implemented in BAPS 5.3 (Corander et al. 2008, Corander and Marttinen 2006) as described by Starger et al. (2010). Genetic structure and admixture were also assessed using the individual-based assignment test implemented in the program Structure 2.2.2 (Hubisz et al. 2009, Falush et al. 2003, Pritchard et al. 2000) using the admixture model with no prior information on population origin. All individuals were considered in this analysis. The assignment method was performed using 300,000 iterations, the first 100,000 of which were discarded as burn-in. K values from 2 to 15 were tested. The Delta K method of Evanno et al. (2005) was implemented to determine the most likely K value.

In order to assess population decline in these coral species, a critical component of conservation planning, we tested for recent population bottlenecks using a method developed by Garza and Williamson (2001). This approach calculates M, the ratio of the total number of alleles to the range in allele sizes, and is a good estimate of recent population decline that is commonly used to inform conservation decision making.

Finally, in order to identify putative barriers to dispersal, we applied a 'genetical bandwidth mapping' approach, which is based on 'wombling' (Womble 1951) and implemented in the
program GenbMap (Cercueil et al. 2007). Genetical bandwidth mapping identifies spatial
discontinuities in allele frequencies that may represent barriers to dispersal. Unlike model-based
approaches, genetical bandwidth mapping is nonparametric and does not assume a particular
measure of genetic distance. This method is particularly relevant to studies where fine scale
structure is stronger than regional structure, which can occur in low dispersal species, and for
studies with low and irregular sample sizes (Cercueil et al. 2007) which is appropriate in this
case. GenbMap was run with a resolution of 300 x 300 pixels, 200 iterations, and p=0.05. Since
GPS coordinates were only taken at each locality, each individual coral's GPS coordinates were
randomly perturbed by 10 m following the example of Cercueil et al. (2007). Statistical
significance of the resulting 'genetical regions' was tested using AMOVA.

Results

Allelic variation in microsatellites

For *P. damicornis*, 169 individuals (Table 1) were genotyped and analyzed at nine microsatellite
loci. The number of alleles per locus ranged from seven at locus Pd3-005 to 20 at locus PV2
(mean: 11.67). Five multilocus genotypes were observed in more than one individual however
only two of these were observed in more than two individuals. In total, nine clonal individuals
were removed from the analysis. For *S. hystrix*, 191 individuals (Table 1) were genotyped and
analyzed at seven microsatellite loci. The number of alleles per locus ranged from three at locus
Sh3-003 to 19 at locus Sh2-006 (mean: 10.57). Six multilocus genotypes were observed in more
than one individual however only one of these was observed in more than two individuals. In
total, six clonal individuals were removed from the analysis. The unique number of genotypes (Ng) and M values for each study location are presented in Tables 2 and 3. Statistics on heterozygosity and Hardy-Weinberg equilibrium are available in Starger et al. (2010).

### Population genetic structure

AMOVA analysis with no *a priori* assumptions indicated strong structure in both species with \( F_{ST} = 0.139 \) (\( R_{ST} = 0.130 \)) for *P. damicornis* and \( F_{ST} = 0.357 \) (\( R_{ST} = 0.246 \)) for *S. hystrix* (\( p < 0.00001 \) for all values) with 16-17% and 30-37% respectively of the variation due to differences among localities (Tables 4 and 5). Results from the hierarchical AMOVA (Tables 4 and 5) indicate that genetic structure does not result from differentiation among the three biogeographic regions (Figure 1). In *P. damicornis* both the infinite alleles model and stepwise mutation model indicate that regional genetic breaks explain none of the observed genetic variation. Regional structure is weak but significant in *S. hystrix* when based on the infinite alleles model (\( F_{CT} = 0.068, p = 0.03 \)), explaining 6.84% of the variation, but not significant when based on the stepwise mutation model (\( R_{CT} = 0.043, p = 0.18 \)). Instead, variation among populations within regions explained the majority of variation in both species: 86.84% of the variation in *P. damicornis* with \( F_{ST} = 0.132 \) (\( p < 0.00001 \)) and 63.02% of the variation in *S. hystrix*, with \( F_{ST} = 0.370 \) (\( p < 0.00001 \)). Similar results were achieved using the SMM (Tables 4 and 5).

M values (Tables 2 and 3) are generally lower for *P. damicornis*. Results from the non-spatial assignments test implemented in BAPS identified five genetic clusters from 12 *P. damicornis* localities, two of which were excluded due to low sample size (Table 2, Figure 2), and ten
genetic clusters in 11 *S. hystrix* populations (Table 3, Figure 3). Clusters containing multiple populations were generally but not always comprised of geographically proximal localities. For example, *P. damicornis* Cluster 1 includes four sites in Raja Ampat, however Cluster 2 consists of sites from Raja Ampat and Teluk Cenderawasih, suggesting genetic connectivity between these ecoregions. For *S. hystrix*, Cluster 1 contained adjacent sites Kri Island and Alyui in Raja Ampat. Spatial clustering results were identical to the non-spatial clustering for both species, with the exception of *P. damicornis* in which Kri Island, was assigned to Cluster 1 in the spatial analysis and clustered alone in the non-spatial analysis (not shown). Furthermore, log(likelihood) was higher in the non-spatial analysis compared to the spatial analysis for *P. damicornis* (-3,701.47 versus 3,718.95) and *S. hystrix* (-2,892.18 versus 2,916.11), indicating close agreement between spatial and non-spatial methods. While AMOVA results based on BAPS partitions indicate significant variation among groups explaining 6% and 28% of the variation among regions of *P. damicornis* and *S. hystrix* respectively, the majority of the variation was still observed within localities (Tables 4 and 5).

When using the individual-based analysis implemented in Structure 2.2.2, the ‘correct’ number of clusters that fit our data was not clear. Delta K indicated K=2 as the most likely value for *P. damicornis* and K=12 for *S. hystrix*, but in both species likelihood increased asymptotically as K values increased towards and then beyond the number of sampled localities (not shown). Results for K=2 for each species indicate mixing of clusters between Raja Ampat and Teluk Cenderawasih, while Kaimana and Fakfak contained mostly one cluster (Figure 2). As a heuristic, we also present K=6 for *P. damicornis* and K=11 for *S. hystrix* as indicated by BAPS as the most likely number of clusters (Table 2, Figure 2). Results of these analyses show a strong
correspondence between cluster assignment and locality in *S. hystrix* (Figure 3), whereas results from *P. damicornis* show more mixing of clusters among localities (Figure 2). In both species, admixture is evident because localities nearly always contain a mixed composition of individuals from various genetic clusters.

Genetical bandwidth mapping identified genetic discontinuities which are common to both coral species, and which may correspond to barriers to larval dispersal that were not clearly detected by other analysis methods. At least six distinct 'genetical regions' were delineated for each species within the Bird’s Head Seascape (Figures 4 and 5). Most notable in the genetical bandwidth maps for both species is a putative dispersal barrier between eastern and western localities within and above Teluk Cenderawasih, and genetic breaks in concordance with the land barrier formed by the Bird’s Head peninsula. The isolation of Mayalibit and Jefman from the other sites in Raja Ampat is also evident in both species, as is a genetic break between Adoki and Ambai, north of Teluk Cenderawasih. AMOVA based on the 'genetical regions' structure was only significant for *S. hystrix* when based on the infinite alleles model (\(F_{CT} = 0.142, p=0.006\) and Table 2).

**Discussion**

Microsatellite analyses of two Indo-Pacific, reef-building corals, *P. damicornis* and *S. hystrix*, indicate significant levels of genetic differentiation among populations within the Bird’s Head Seascape of Papua and West Papua, Indonesia. A mixture of traditional AMOVA, assignment tests, and the genetical bandwidth mapping approach all indicate significant structure among
localities within West Papua, suggesting limits to connectivity among these coral populations. Sample sizes were not large enough for traditional estimates of gene flow ($Nm$) however, as predicted, genetic structure was higher in *S. hystrix* ($F_{ST} = 0.360, p < 0.001$) than in *P. damicornis* ($F_{ST} = 0.139, p < 0.001$) suggesting more limited dispersal in the former, a result consistent with previous comparative research from Eastern Australia (Ayre and Hughes 2000, 2004) and across all of Indonesia (Starger et al. 2010).

Strong, significant genetic structure indicates substantial limits to genetic and demographic connectivity (Hedgecock et al. 2007) among coral populations of West Papua. However, while the data clearly indicate structure across the Bird’s Head Seascape in both species, this structure is not clearly explained by geography or the delineated coral ecoregions of Veron et al. (2009). AMOVA and assignment tests could not differentiate among Teluk Cenderawasih, Raja Ampat, and Southwestern Papua, but instead revealed fine scale patterns of genetic structure within Teluk Cenderawasih and within Raja Ampat. AMOVA results indicate significant levels of variation among localities within these regions, explaining 15.99% of the overall variation for *P. damicornis* and 30.14% for *S. hystrix*, with almost all the remaining genetic variation contained within localities (Table 2). Similar results were obtained by the Bayesian assignment method implemented in Structure and in the population-based analysis implemented in BAPS.

This pattern of strong structure on the local scale with weak differences among geographic regions was confirmed by the new technique of genetical bandwidth mapping, a technique that is specifically designed for data sets where sample sizes are irregular and occasionally small. This is characteristic of coral populations in eastern Indonesia —the extreme biodiversity and patchy
composition of coral communities in this region (Veron et al 2009) makes obtaining large sample sizes of individual species difficult. Genetical bandwidth mapping identified putative barriers to dispersal within Raja Ampat and within Teluk Cenderawasih indicating that the results from AMOVA and assignment tests are not artifacts of sample sizes. Interestingly, genetical bandwidth mapping also identified mainland West Papua as a region of genetic discontinuity in both species, supporting the presence of a dispersal barrier common to a wide range of marine invertebrates in this part of the Bird’s Head Seascape (Barber et al. 2006, Barber et al. 2010, Crandall et al. 2008, DeBoer et al. 2008, Carpenter et al. 2011, Barber et al. 2011). These patterns are concordant between the two coral species based on visual inspection of the maps (Figures 3 and 4). Although sample sizes and fixation indices were within the ranges where genetical bandwidth mapping can accurately infer genetic breaks (Cercueil et al. 2007), additional research could result in more accurate estimates of coral connectivity in the region. For example, taking a community genomics approach aligned with quantitative morphological and reproductive studies and oceanographic modeling (Treml and Halpin 2012) would improve our ability to detect subtle genetic structure and the presence of cryptic lineages (Chen et al. 2007, Souter 2010, Bongaerts et al. 2010), ecophenotypes (Nir et al. 2011), and cryptic species (discussed below) in corals of the Bird’s Head Seascape.

_Differences between species_

Results also indicate a clear difference in levels of genetic structure between _P. damicornis_ and _S. hystrix_, the latter having higher genetic structure. Genetic clustering analyses in BAPS and Structure indicate that nearly every _S. hystrix_ locality formed its own unique cluster with
minimal evidence of admixture among localities. The only clear geographic association was seen in the clustering of Alyui with Kri Island, which cluster together in both BAPS and Structure. Otherwise, each *S. hystrix* locality is genetically distinct, possibly suggestive of the occurrence of multiple ecophenotypes (Nir et al. 2011). Given the geographic proximity of our study sites, and previous evidence suggesting the monophyly of *S. hystrix* relative to its easily identifiable sister species *S. caliendrum* (Bongaerts et al. 2010), we find it unlikely, though not impossible, that our genetic clusters represent reproductively isolated cryptic species. *P. damicornis* populations exhibited lower levels of genetic structure based on fixation indices, and fewer clusters were resolved by BAPS and Structure, suggesting that this species has lower genetic structure than *S. hystrix*. Cryptic species in *P. damicornis* might also exist, but we find this even less likely than in *S. hystrix* given *P. damicornis*’s reproductive plasticity and long larval duration.

Differences in observed genetic structure among these two corals may be explained by differences in their larval dispersal abilities. The majority of larvae of both species have been observed to settle within a few days of release (Isomura and Nishihira 2001). However, aquarium-based research on the larval biology of *P. damicornis* indicates the potential for long distance dispersal via a maximum larval duration of at least 103 days (Richmond 1987). It is not known whether *S. hystrix* similarly possesses this ability, but as more corals are studied in this way, maximum larval life spans are proving to be much higher than previously thought (Graham et al. 2010). The presence of zooxanthellae in *S. hystrix* larvae, coupled with evidence of diverse reproductive strategies such as polyp bail-out (Sammarco 1982) and rafting (Jokiel 1984) suggest that extended larval durations may be possible in this species as well. However, the observation of higher structure in *S. hystrix* in comparison to *P. damicornis* in this and other studies (Ayre
and Hughes 2000, 2004; Starger et al. 2010) suggests that actual larval dispersal may be lower in
*S. hystrix*.

While our results are generally consistent with previous results comparing genetic structure
between these two coral species, we observed higher magnitudes of genetic structure over a
smaller spatial scale in both species in the Bird’s Head Seascape in comparison to results from
the Great Barrier Reef. Van Oppen et al. (2008) observed a mean pairwise *F*<sub>ST</sub> of 0.20 among *S.
hystrix* populations on the Great Barrier Reef, which is considerably lower than our observed
mean pairwise *F*<sub>ST</sub> of 0.36 in West Papua, even though our spatial scale is much smaller.
Physical oceanography, regional variation in reproduction, and more heterogeneous
environmental conditions in the Bird’s Head Seascape may explain the observed differences in
genetic structure between the Great Barrier Reef and the Bird’s Head Seascape. Furthermore,
coral populations on the Great Barrier Reef are largely arranged in a linear pattern along
Australia’s northeastern coastline and are subjected to relatively predictable patterns of sea
surface circulation, dominated by the Eastern Australian Current that flows southeast along the
Great Barrier Reef. Surface patterns are much less well understood in the Bird’s Head Seascape,
where the coastline of West Papua is far more complex and currents less predictable than they
are on the northeastern coast of Australia. This complexity may result in localized sea surface
circulation eddies and seasonal or irregular reversals which increase mean drift time between
geographically proximate reefs. Oceanographic modeling has found patterns similar to the
conservation planning boundaries at both the ecoregional and the priority seascape scales (Treml
and Halpin 2012). An additional explanation that is not mutually exclusive is that there may be
variations in reproductive strategies between corals of the Great Barrier Reef and those of the
Bird’s Head Seascape. It is well established that *P. damicornis* can be either a brooder or spawner depending on location (Baird et al. 2009), and may undergo ‘reverse metamorphosis’ from polyp to planula when stressed (Richmond 1985). Similarly, *S. hystrix* can undergo polyp bailout when stressed (Sammarco 1982). It is therefore possible that regional differences in reproductive strategy between the Great Barrier Reef and the Bird’s Head Seascape are contributing to the observed genetic differences. *P. damicornis* has also been observed rafting on pumice, which could increase drift times under rare circumstances (Bryan et al. 2012). Coral reproduction studies here would serve to shed light on this question.

**On coral species**

Although the possibility exists that some of the genetic variation we observed represents cryptic lineages or species, presently we find limited evidence in the literature for the existence of cryptic coral species. Therefore, we cannot reject the original species descriptions at this time. However, we do not discount the possibility that cryptic species can and probably do exist in the Bird’s Head Seascape where several undescribed coral species have recently been discovered (Mangubhai et al. 2012). Likewise it is possible that reproductive barriers may exist among some of the individuals and populations in our dataset. If this were true, it could potentially invalidate some of the assumptions made in our genetic analysis methods which assume cohesion. Unchanged, however, would be (1) our conclusions that genetic subdivision is widespread and complex within these nominal coral species in the Bird’s Head Seascape, and (2) the knowledge that the Bird’s Head Seascape is home to a remarkable assemblage of endemic coral species (Veron et al. 2009) and genetic variants requiring immediate conservation action. Applying
genomic methods and quantitative morphological characters in a phylogenetic context, as well as conducting reproductive and ecological studies on coral species, would help characterize biodiversity in the Bird’s Head Seascape, advance our understanding of the evolutionary processes that generate and maintain this diversity, and further inform MPA design and management.

Population decline and coral reef conservation

The Bird’s Head Seascape is home to some of the most diverse, modern day coral reef ecosystems (Mangubhai et al. 2012). However, one of the disturbing results from this study is that these reefs may not have been immune to population declines. The mean M values, a genetic measure used to infer population declines, for P. damicornis and S. hystrix populations in West Papua (averaging 0.64 and 0.65 respectively) are strikingly similar to those of the Mediterranean Monk Seal (M = 0.64) and the Northern Elephant Seal (M = 0.66) (Garza and Williamson 2001), two highly endangered species that have suffered massive population declines. This result strongly suggests a similar, recent population decline in these two coral species. Increasing human pressures on coral reefs in the Bird’s Head Seascape, coupled with increasing sea surface temperatures and episodes of coral bleaching, are likely to exacerbate coral decline throughout the region unless strategic conservation action is taken. Marine conservation initiatives in coral reef regions are increasingly focused on designing and implementing effective networks of MPAs (Roberts 2005, Clifton 2009, Horigue et al. 2012, Mangubhai et al. 2012) with the optimal size and spacing of the individual MPAs within a network being a critical aspect of applied MPA research (Shanks 2003, Mills et al. 2010). While difficulties obtaining the large sample sizes
needed precluded the use of more quantitative estimates of connectivity, and the presence of cryptic species remains possible, our results unequivocally identify fine-scale genetic structure, which strongly suggests limited genetic connectivity among reef building corals within the Bird’s Head Seascape on small spatial scales. This is especially clear in the clustering of *S. hystrix* individuals by location and the genetical bandwidth maps of both species showing genetic discontinuities within Raja Ampat and within Teluk Cenderawasih. As genetic connectivity requires far fewer dispersing individuals than does demographic connectivity, the strong genetic differentiation in both of these coral species indicates demographic independence of these populations throughout the Bird’s Head Seascape (Hedgecock et al. 2007).

While methods exist to infer connectivity through genetic assignment tests (e.g. BayesAss+), robust results generally require larger sample sizes than were logistically and biologically possible in our study. While our results cannot provide strong inferences of connectivity, our analyses do show strong evidence for the absence of connectivity. As the number of samples and loci required to detect genetic structure is inversely proportional to the strength of population subdivision (Hillis et al. 1996), the observation of strong genetic structure, even with sample sizes between 10 and 20 individuals, demonstrates that populations of these coral species are strongly isolated across the Bird’s Head Seascape. As such, designating a small number of large, widely-spaced "anchor" MPAs in the hopes that they will serve as larval sources, seeding adjacent unprotected areas, would be an ineffective strategy to protect these coral populations. A more effective strategy to maintain biodiversity and connectivity in the Bird’s Head Seascape is one that is currently being implemented: a network of numerous, relatively closely-spaced MPAs over a broad geographic area. This strategy is designed to provide protection of local reefs as
well as support regional genetic connectivity across the entire Bird’s Head Seascape. In fact, the preliminary results of the present study were directly incorporated into the Bird’s Head Seascape MPA network design process, which included an objective to limit the spacing between MPAs to 25-100 km (Huffard et al. 2012b). The network of seven MPAs in the Raja Ampat region is a good example of this approach, with an average MPA size of 160,000 ha and spacing between nearest MPAs averaging less than 60 km. However, further research is advisable to determine whether the number and spacing of these reserves is sufficient, and how many coral reef taxa will benefit from this arrangement. Similarly, Teluk Cenderawasih would also benefit from a network of numerous closely spaced reserves. The Taman Nasional Teluk Cenderawasih covers a large area, nearly 1.5 million hectares, but only includes the western half of the bay. Due to the genetic differentiation of most local populations, it would be advisable to also designate additional MPAs in the eastern half of the bay and to the northeast of the bay, in the vicinity of Adoki and Owi, both to protect local diversity as well as facilitate regional connectivity. Fortunately, the Indonesian Ministry of Marine Affairs and Fisheries and the local Biak government recently gazetted the Padaido Islands Marine Tourism Park in this northeast quadrant of Cendrawasih Bay, and additional MPAs are now being considered.

Genetic diversity has been historically overlooked in international conservation policy implementation (Laikre 2010). This is also true at the subnational level, where genetic data are very rarely incorporated in conservation planning. However, ours is case where genetic data can and do directly inform conservation action. For example, in addition to arranging MPAs to maintain connectivity, we recommended that the Bird’s Head Seascape MPA network should also serve to protect representative populations from each genetically unique cluster, thereby
conserving the maximum degree of coral genetic diversity. Our data from *S. hystrix*, where all but two of the sample localities (Kri Island and Alyui) represent distinct genetic clusters, argued for the inclusion of each of these localities within MPAs to maintain this unique genetic diversity into the future. Now, 9 of the 13 localities sampled in this study are indeed included in MPAs within the BHS network (Mangubhai et al. 2012). In the case of *P. damicornis*, 3 sites (Mauwara, Lemon and Alyui) represent unique genetic clusters that should be prioritized for inclusion in MPAs; in this case, Mauwara is now included in the Kaimana MPA, Alyui is largely protected by a pearl-farming concession and is bordered by the 155,000 ha Kawe MPA, and Lemon is currently under consideration for inclusion as a new MPA. As coral reefs face the coming onslaught of increased coral bleaching (Oliver et al. 2009) and ocean acidification (Pandolfi et al. 2011), it is imperative to maximize protection of genetic diversity to preserve the ability of local populations to adapt to changing environmental conditions.

Funding limitations in combination with political and socioeconomic realities that motivate unsustainable natural resource use only increase the need for sound science on which to base conservation strategies. Genetic investigations like this provide a disproportionately large amount of data relative to time spent in the field, and the results can help fill some of the most critical scientific gaps in MPA planning (Sale et al. 2005). Although not all reefs can be assessed in a scientifically rigorous manner, insights into the patterns and processes of biological diversity can be used to design effective management schemes that can be put to use in an effective time frame. In our case, the means to apply genetic data to conservation action already exist in ongoing, multi-institutional partnerships in the Bird’s Head Seascape (Green and Mous 2004, Huffard et al. 2012b, Mangubhai et al. 2012). Examination of additional taxa in a similar fashion...
to those presented here (Carpenter et al. 2011, Barber et al. 2011), including economically important species, will provide a wide range of results that resource managers may utilize in refining the optimum MPA network for the Bird’s Head Seascape and should serve as an important example for ongoing efforts to design further MPA networks within the Coral Triangle and elsewhere.

Acknowledgments:

We thank the Indonesian Institute of Sciences (LIPI) and all national and local authorities for research permission in Indonesia (permit # 2712/SU/KS/2005) and permission to export coral tissues in compliance with CITES (permit # 07218/IV/SATS-LN/2006). Funding for coral collections was provided by a Pew Conservation Fellowship to M.V. Erdmann as well as grants to P.H. Barber from NSF (OCE-0349177) and Conservation International. Laboratory work was supported by R. DeSalle and G. Amato at the Sackler Institute for Comparative Genomics at the American Museum of Natural History and an NSF grant to A. C. Baker (OCE-0099301). C.J. Starger was also supported by an NSF-GK12 Teaching Fellowship through Columbia University’s Chemistry Department.

Literature Cited:


Table 1: Sampling locations in Papua and West Papua, Indonesia

<table>
<thead>
<tr>
<th>Region</th>
<th>Locality</th>
<th>Latitude</th>
<th>Longitude</th>
<th>P. damicornis</th>
<th>S. hystrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raja Ampat</td>
<td>Alyui Bay</td>
<td>0° 10.47 S</td>
<td>130° 14.85 E</td>
<td>20</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Mayalibit</td>
<td>0° 17.85 S</td>
<td>130° 48.49 E</td>
<td>9</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Kri Island</td>
<td>0° 33.38 S</td>
<td>130° 40.68 E</td>
<td>30</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Jefman</td>
<td>0° 55.64 S</td>
<td>131° 07.41 E</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Gam Passage</td>
<td>0° 25.88 S</td>
<td>130° 33.16 E</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Teluk Cenderwasih</td>
<td>Lemon</td>
<td>0° 53.41 S</td>
<td>134° 04.90 E</td>
<td>18</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Rumberpon</td>
<td>1° 44.23 S</td>
<td>134° 12.15 E</td>
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<td>19</td>
</tr>
<tr>
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<td>135° 59.68 E</td>
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<td>12</td>
</tr>
<tr>
<td></td>
<td>Serui</td>
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<td>136° 13.65 E</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Owi</td>
<td>1° 15.26 S</td>
<td>136° 10.99 E</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Ambai</td>
<td>1° 57.64 S</td>
<td>136° 19.23 E</td>
<td>15</td>
<td>22</td>
</tr>
<tr>
<td>Fakfak / Kaimana</td>
<td>Mommon</td>
<td>3° 56.38 S</td>
<td>132° 48.21 E</td>
<td>4</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Mauwara</td>
<td>3° 49.65 S</td>
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<tr>
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<td>Namatote</td>
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<td>133° 52.93 E</td>
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</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>169</td>
<td>191</td>
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Table 2: Population statistics for *Pocillopora damicornis*: Give are the number of samples (N), number of unique genotypes (Ng), $M$ value (M), its variance (M var), and BAPS cluster.

<table>
<thead>
<tr>
<th>Locality (region)</th>
<th>N</th>
<th>Ng</th>
<th>M</th>
<th>M var</th>
<th>Cluster</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alyui Bay (R4)</td>
<td>20</td>
<td>16</td>
<td>0.61</td>
<td>0.07</td>
<td>1</td>
</tr>
<tr>
<td>Mayalibit (R4)</td>
<td>9</td>
<td>9</td>
<td>0.63</td>
<td>0.07</td>
<td>2</td>
</tr>
<tr>
<td>Kri Island (R4)</td>
<td>30</td>
<td>30</td>
<td>0.61</td>
<td>0.06</td>
<td>2</td>
</tr>
<tr>
<td>Jefman (R4)</td>
<td>22</td>
<td>22</td>
<td>0.72</td>
<td>0.06</td>
<td>3</td>
</tr>
<tr>
<td>Lemon (TC)</td>
<td>18</td>
<td>18</td>
<td>0.64</td>
<td>0.08</td>
<td>4</td>
</tr>
<tr>
<td>Rumberpon (TC)</td>
<td>13</td>
<td>13</td>
<td>0.62</td>
<td>0.04</td>
<td>3</td>
</tr>
<tr>
<td>Adoki Village (TC)</td>
<td>10</td>
<td>7</td>
<td>0.61</td>
<td>0.07</td>
<td>2</td>
</tr>
<tr>
<td>Owi (TC)</td>
<td>9</td>
<td>9</td>
<td>0.67</td>
<td>0.08</td>
<td>3</td>
</tr>
<tr>
<td>Ambai (TC)</td>
<td>15</td>
<td>15</td>
<td>0.62</td>
<td>0.05</td>
<td>3</td>
</tr>
<tr>
<td>Mauwara (F/K)</td>
<td>23</td>
<td>21</td>
<td>0.59</td>
<td>0.05</td>
<td>5</td>
</tr>
</tbody>
</table>
**Table 3:** Population statistics for *Seriatopora hystrix*: Give are the number of samples (N), number of unique genotypes (Ng), $M$ value (M), its variance ($M$ var), and BAPS cluster.

<table>
<thead>
<tr>
<th>Locality (region)</th>
<th>N</th>
<th>Ng</th>
<th>M</th>
<th>M var</th>
<th>Cluster</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alyui Bay (R4)</td>
<td>19</td>
<td>17</td>
<td>0.61</td>
<td>0.06</td>
<td>1</td>
</tr>
<tr>
<td>Mayalibit (R4)</td>
<td>20</td>
<td>20</td>
<td>0.49</td>
<td>0.09</td>
<td>2</td>
</tr>
<tr>
<td>Kri (R4)</td>
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<td>9</td>
<td>0.62</td>
<td>0.03</td>
<td>1</td>
</tr>
<tr>
<td>Jefman (R4)</td>
<td>22</td>
<td>17</td>
<td>0.66</td>
<td>0.07</td>
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</tr>
<tr>
<td>Lemon (TC)</td>
<td>20</td>
<td>20</td>
<td>0.67</td>
<td>0.09</td>
<td>4</td>
</tr>
<tr>
<td>Rumberpon (TC)</td>
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<td>19</td>
<td>0.79</td>
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</tr>
<tr>
<td>Adoki Village (TC)</td>
<td>12</td>
<td>12</td>
<td>0.7</td>
<td>0.11</td>
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<tr>
<td>Owi (TC)</td>
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<td>9</td>
<td>0.79</td>
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</tr>
<tr>
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<td>22</td>
<td>22</td>
<td>0.72</td>
<td>0.08</td>
<td>8</td>
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<td>Mommon (F/K)</td>
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<td>18</td>
<td>0.7</td>
<td>0.1</td>
<td>9</td>
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<tr>
<td>Namatote (F/K)</td>
<td>21</td>
<td>21</td>
<td>0.81</td>
<td>0.08</td>
<td>10</td>
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Table 4: Results from AMOVA for *Pocillopora damicornis*. Four genetic structures are tested. “All samples” indicates that there was no hierarchical structure imposed. ‘3 regions’ tests the significance of a priori geographic structure among Teluk Cenderawasih, Raja Ampat, and Fakfak/Kaimana. Finally, the structures inferred by BAPS and Genetical Bandwidth Mapping (GBM) are tested. Estimators are calculated based on both the infinite alleles model (*F* statistics) and stepwise mutation model (*R* statistics) of microsatellite evolution. Negative values are presented, but are effectively equal to zero.

<table>
<thead>
<tr>
<th></th>
<th>F statistic</th>
<th>p</th>
<th>% var</th>
<th>R statistic</th>
<th>p</th>
<th>% var</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>All samples</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among localities</td>
<td><em>F</em>&lt;sub&gt;ST&lt;/sub&gt;</td>
<td>0.139</td>
<td>&lt;0.00001</td>
<td><em>R</em>&lt;sub&gt;ST&lt;/sub&gt;</td>
<td>0.130</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>Within localities</td>
<td></td>
<td>86.060</td>
<td></td>
<td></td>
<td>87.000</td>
<td></td>
</tr>
<tr>
<td><strong>3 regions</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among groups</td>
<td><em>F</em>&lt;sub&gt;CT&lt;/sub&gt;</td>
<td>-0.028</td>
<td>0.874</td>
<td><em>R</em>&lt;sub&gt;CT&lt;/sub&gt;</td>
<td>0.017</td>
<td>0.382</td>
</tr>
<tr>
<td>Among localities within regions</td>
<td><em>F</em>&lt;sub&gt;SC&lt;/sub&gt;</td>
<td>0.156</td>
<td>&lt;0.00001</td>
<td><em>R</em>&lt;sub&gt;SC&lt;/sub&gt;</td>
<td>0.120</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>Within localities</td>
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<td>&lt;0.00001</td>
<td><em>R</em>&lt;sub&gt;ST&lt;/sub&gt;</td>
<td>0.135</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td><strong>Structure inferred by BAPS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among clusters</td>
<td><em>F</em>&lt;sub&gt;CT&lt;/sub&gt;</td>
<td>0.140</td>
<td>0.003</td>
<td><em>R</em>&lt;sub&gt;CT&lt;/sub&gt;</td>
<td>0.060</td>
<td>0.240</td>
</tr>
<tr>
<td>Among localities within clusters</td>
<td><em>F</em>&lt;sub&gt;SC&lt;/sub&gt;</td>
<td>0.030</td>
<td>0.007</td>
<td><em>R</em>&lt;sub&gt;SC&lt;/sub&gt;</td>
<td>0.079</td>
<td>0.013</td>
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<tr>
<td>Within localities</td>
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<td>&lt;0.00001</td>
<td><em>R</em>&lt;sub&gt;ST&lt;/sub&gt;</td>
<td>0.135</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td><strong>Structure inferred by GBM</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among clusters</td>
<td><em>F</em>&lt;sub&gt;CT&lt;/sub&gt;</td>
<td>-0.011</td>
<td>0.555</td>
<td><em>R</em>&lt;sub&gt;CT&lt;/sub&gt;</td>
<td>0.063</td>
<td>0.178</td>
</tr>
<tr>
<td>Among localities within clusters</td>
<td><em>F</em>&lt;sub&gt;SC&lt;/sub&gt;</td>
<td>0.148</td>
<td>&lt;0.00001</td>
<td><em>R</em>&lt;sub&gt;SC&lt;/sub&gt;</td>
<td>0.076</td>
<td>0.007</td>
</tr>
<tr>
<td>Within localities</td>
<td><em>F</em>&lt;sub&gt;ST&lt;/sub&gt;</td>
<td>0.139</td>
<td>&lt;0.00001</td>
<td><em>R</em>&lt;sub&gt;ST&lt;/sub&gt;</td>
<td>0.136</td>
<td>&lt;0.00001</td>
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</table>

Table 5: Results from AMOVA for *Seriatopora hystrix*. Four genetic structures are tested. “All samples” indicates that there was no hierarchical structure imposed. ‘3 regions’ tests the significance of a priori geographic structure among Teluk Cenderawasih, Raja Ampat, and Fakfak/Kaimana. Finally, the structures inferred by BAPS and Genetical Bandwidth Mapping (GBM) are tested. Estimators are calculated based on both the infinite alleles model ($F$ statistics) and stepwise mutation model ($R$ statistics) of microsatellite evolution. Negative values are presented, but are effectively equal to zero.

<table>
<thead>
<tr>
<th></th>
<th>F statistic</th>
<th>p</th>
<th>% var</th>
<th>R statistic</th>
<th>p</th>
<th>% var</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>All samples</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among localities</td>
<td>$F_{ST}$ 0.357</td>
<td>&lt;0.00001</td>
<td>35.710</td>
<td>$R_{ST}$ 0.246</td>
<td>&lt;0.00001</td>
<td>24.560</td>
</tr>
<tr>
<td>Within localities</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>3 regions</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among groups</td>
<td>$F_{CT}$ 0.068</td>
<td>0.034</td>
<td>6.840</td>
<td>$R_{CT}$ 0.043</td>
<td>0.177</td>
<td>4.290</td>
</tr>
<tr>
<td>Among localities within regions</td>
<td>$F_{SC}$ 0.324</td>
<td>&lt;0.00001</td>
<td>30.140</td>
<td>$R_{SC}$ 0.222</td>
<td>&lt;0.00001</td>
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<td>$F_{ST}$ 0.370</td>
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<td>$R_{ST}$ 0.255</td>
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<td>74.510</td>
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<tr>
<td><strong>Structure inferred by BAPS</strong></td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Among clusters</td>
<td>$F_{CT}$ 0.325</td>
<td>0.016</td>
<td>32.530</td>
<td>$R_{CT}$ 0.286</td>
<td>0.018</td>
<td>28.620</td>
</tr>
<tr>
<td>Among localities within clusters</td>
<td>$F_{SC}$ 0.050</td>
<td>0.088</td>
<td>3.400</td>
<td>$R_{SC}$ -0.054</td>
<td>0.919</td>
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</tr>
<tr>
<td>Within localities</td>
<td>$F_{ST}$ 0.359</td>
<td>&lt;0.00001</td>
<td>64.070</td>
<td>$R_{ST}$ 0.248</td>
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<td>75.220</td>
</tr>
<tr>
<td><strong>Structure inferred by GBM</strong></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Among clusters</td>
<td>$F_{CT}$ 0.142</td>
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<tr>
<td>Among localities within clusters</td>
<td>$F_{SC}$ 0.263</td>
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<tr>
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<td>&lt;0.00001</td>
<td>75.710</td>
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Figure 1: The Bird’s Head region of West Papua, Indonesia. Sampling localities are shown as white circles. The solid black line delineates the border of Teluk Cenderawasih National Park.
Figure 2: Results from Bayesian assignment methods implemented in Structure and BAPS for *Pocillopora damicornis*. X indicates exclusion from BAPS analysis due to Ng = 6 or less. K = 2 and K = 6 were used as heuristics as described in the text.
Figure 3: Results from Bayesian assignment methods implemented in Structure and BAPS for *Seriatopora hystrix*. K = 2 and K = 11 were used as heuristics as described in the text.
Figure 4: Genetical Bandwidth Map for *Pocillopora damicornis*. Green areas indicate regions of genetic homogeneity. White areas indicate putative barriers to larval dispersal and are highlighted with blue dashed lines. The solid black line indicates the borders of Taman Nasional Teluk Cenderawasih.
**Figure 5**: Genetical Bandwidth Map for *Seriatopora hystrix*. Green areas indicate regions of genetic homogeneity. White areas indicate putative barriers to larval dispersal and are highlighted with blue dashed lines. The solid black line indicates the borders of Taman Nasional Teluk Cenderawasih.