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

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Abstract. Marine Protected Areas (MPAs) are widely considered to be one of the best strategies available for protecting species diversity and ecosystem processes in marine environments. 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. This study examines genetic structure in reef-building corals from Papua and West Papua, Indonesia, one of the most biodiverse and least disturbed coral reef regions in the world. We focused on two common reef-building corals, *h* (Linnaeus 1758) and *o* (family: Pocilloporidae), from three regions under different management regimes: Teluk Cenderawasih, Raja Ampat, and southwest Papua. Analyses of molecular variance, assignment tests, and genetical bandwidth mapping based on microsatellite variation revealed significant genetic structure in both species, although there were no clear regional filters to gene flow among regions. Overall, *h* populations were less structured ($F_{ST} = 0.139$, $p < 0.00001$) than *o* ($F_{ST} = 0.357$, $p < 0.00001$). Despite occurring in one of the most pristine marine habitats in Indonesia, populations of both species showed evidence of recent declines. Furthermore, exclusion of individual populations from connectivity analyses resulted in marked increases in self-recruitment. Maintaining connectivity within and among regions of Eastern Indonesia will require coral conservation on the local scales and regional networks of MPAs.

Keywords. Coral Triangle, Marine Connectivity, Conservation, Papua, 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 anthropogenic stressors (Hoegh-Guldberg et al. 2007, Burke et al. 2012). On many reefs worldwide coral cover has declined by 50–80% over the last few decades (Gardner et al. 2003, Bruno & Selig 2007, De'ath et

al. 2012, Jackson et al. 2014). The loss of habitat-building reef corals compromises the very foundation of coral reef ecosystems (Adams and Ebersole 2010, Hughes et al. 2010), threatening marine biodiversity and the important economic goods and services that this diversity supports. In Southeast Asia, 95% of reefs are considered under threat and there is an urgent need for coral and coral reef-focused conservation (Burke et al. 2012).

Marine protected areas (MPAs) are considered one of the best methods for protecting spe-

cies diversity and ecosystem processes and functions (Levitan and McGovern 2005). As such, the Convention on Biodiversity (2006) set a goal that at least 10% of each of the world's marine and coastal ecoregions should be set aside as marine protected areas by 2020. Given that only ~3% of the world's marine ecosystems are currently within MPAs (Toropova et al. 2010, IUCN 2013¹), there should be significant growth in MPAs around the world, including coral reef ecosystems. Therefore, there is a pressing need for sound science to support marine conservation efforts. In particular, understanding connectivity, the exchange of dispersive larvae among populations that contributes to population demographics and gene flow, is critical to developing long-term conservation strategies for marine ecosystems (Crowder et al. 2000, Botsford et al. 2001, Palumbi 2003, Cowen et al. 2006). However, understanding patterns of connectivity remains among the most crucial gaps in scientific knowledge necessary for marine conservation (Sale et al. 2005).

The Coral Triangle (Veron et al. 2009), a region that includes Malaysia, the Philippines, Indonesia, Timor Leste, Papua New Guinea, and the Solomon Islands, is the most biologically diverse marine ecosystem in the world (Roberts 2002, Bellwood and Meyer 2009); it is also among the most threatened (Burke et al. 2012). Coral diversity peaks in the provinces of Papua and West Papua, Indonesia (Veron et al. 2009), a region collectively referred to as the 'Bird's Head Seascape'. A multi-institutional program that includes NGOs, universities, and local governments, the Bird's Head Seascape Initiative is working to confront the threats to marine habitats in this region by designing and implementing an ecosystem-based management plan, including an interconnected network of MPAs (Mangubhai et al. 2012). Therefore, understanding patterns of genetic connectivity among populations of corals and reef-associated species within this region has become a key research priority for conservation practitioners.

While the presence of genetic connectivity does not ensure demographic connectivity, restricted genetic connectivity is a clear sign that

demographic connectivity is extremely limited or absent (Hedgecock et al. 2007). As such, studies have used genetic connectivity to advance marine conservation goals from a variety of perspectives (e.g. Palumbi 2003, Laurie et al. 2004, Kool et al. 2011, Berger et al 2014, DeBoer et al. 2014, Serrano et al. 2014, Treml et al. 2015). In one particularly novel approach, Baums et al (2005) simulated how the loss of individual coral populations could impact regional patterns of genetic connectivity between Caribbean coral populations. This method is particularly useful in regions like West Papua, where rapid development requires informed decisions about which reefs should be prioritized for protection.

While phylogeography and genetic connectivity studies within the Coral Triangle have increased greatly in the past decade (see Carpenter et al. 2011 and Barber et al. 2011 for reviews), few of these studies focus on corals, highlighting a critical need for research on this foundational taxonomic group. Comparative population genetic studies on *h*

(Ayre and Hughes 2000, 2004) along the Great Barrier Reef suggest that these two species are on opposite sides of the genetic connectivity spectrum; typically *o* populations have higher levels of structure while *h* populations have minimal or no subdivision over spatial scales of 700–1200 km, although the latter can have substantial genetic structure on the periphery of its range (Ayre and Hughes 2004, Combsch and Vollmer 2011). Thus, these species provide an ideal range of dispersal ability for examining connectivity throughout the Bird's Head Seascape, the epicenter of coral diversity and the center of these corals' geographic ranges (Veron et al 2009).

In this study, we examine the genetic structure of *h* and *o*

to improve our understanding of connectivity of coral populations in the Bird's Head Seascape, and to help conservation practitioners develop effective management strategies for coral reefs in this region. Specifically, we test the hypothesis that populations of *h* are more open with lower levels of genetic structure,

¹ http://www.iucn.org/news_homepage/events/impac3/?13912/World-nearing-3-of-ocean-protection, last accessed 8/29/2015

while other populations are more structured, resulting from more limited dispersal. Further, because of significant loss of coral reef habitat in Indonesia (Burke et al. 2012), we examine diversity of microsatellite allele variation to test for declines in effective population size and examine how the loss of individual coral populations in the Bird's Head Seascape could impact connectivity across this region.

Methods

The Bird's Head Seascape is one of the most pristine marine ecosystems in Indonesia (McKenna et al. 2002, Burke et al. 2012), but threats to this ecosystem are increasing from a variety of sources (Varkeya et al. 2010). We focus on three regions – Teluk Cenderawasih, Raja Ampat and Southwestern Papua (Table 1, Fig. 1) – that represent distinct 'coral ecoregions' (Veron et al. 2009) with relatively limited connectivity among them (Trembl et al. 2015). Located on the northwestern shores of the island of New Guinea (Fig. 1), Teluk Cenderawasih could serve as important larval sources for Raja Ampat due to the New Guinea

Coastal Current (Nof 1995, Morey et al. 1999). However, Trembl et al. (2015) suggests that physical oceanography restricts connectivity between Teluk Cenderawasih and Raja Ampat, a prediction supported by genetic isolation (Crandall et al. 2008, DeBoer et al. 2008, Nuryanto and Kochzius 2009, DeBoer et al. 2014, Jackson et al. 2014) and range restricted endemics (Wallace et al. 2011, Allen and Erdman 2012) within the bay. Although technically outside Teluk Cenderawasih, Lemon, Adoki and Owi islands lie within the 'Cenderawasih Bay' coral ecoregion (Veron et al. 2009) and cluster with Teluk Cenderawasih in the analyses of Trembl et al. (2015). Similarly, models by Trembl et al. (2015) indicate that Southwestern Papua, represented by the populations Fakfak and Kaimana, is also relatively isolated.

The 12 actively managed MPAs in the Bird's Head Seascape range in size from 5000 to 1,453,500 ha, covering a total area of 3,594,702 ha (see Mangubhai et al. 2012). Approximately 50% of Raja Ampat's reefs are included in a network of seven marine protected areas ranging in size from 34,000 ha to 343,200 ha and separated by 20–100 km (Varkeya et al. 2010). A single MPA

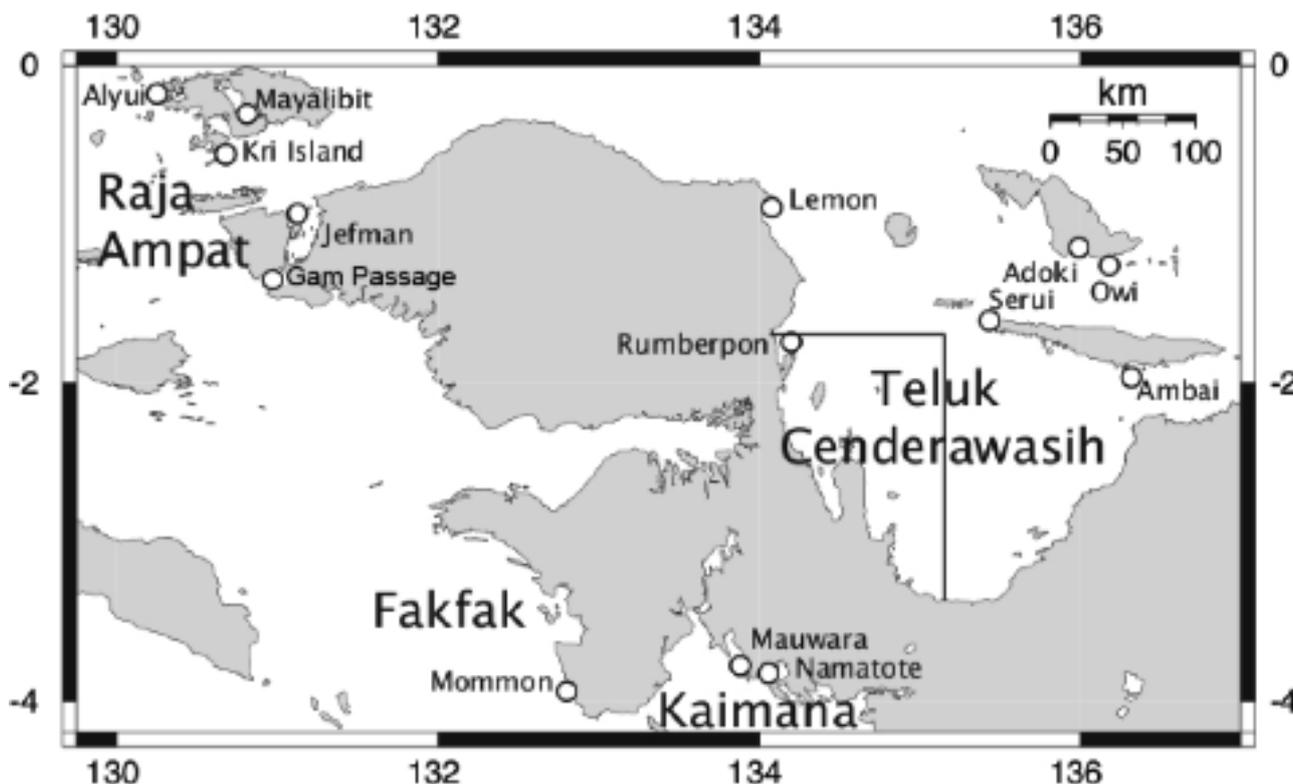


Figure 1. The Bird's Head region of West Papua, Indonesia. Sampling localities are shown as white circles. The solid black line delineates the border of Teluk Cenderawasih National Park.

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

Region	Locality	Latitude	Longitude	Number of samples	
				<i>P. damicornis</i>	<i>S. hystrix</i>
Raja Ampat	Alyui Bay	0° 10.47 S	130° 14.85 E	20	19
	Mayalibit	0° 17.85 S	130° 48.49 E	9	20
	Kri Island	0° 33.38 S	130° 40.68 E	30	9
	Jefman	0° 55.64 S	131° 07.41 E	22	22
	Gam Passage	0° 25.88 S	130° 33.16 E	4	0
Teluk Cenderwasih	Lemon	0° 53.41 S	134° 04.90 E	18	20
	Rumberpon	1° 44.23 S	134° 12.15 E	13	19
	Adoki Village	1° 08.53 S	135° 59.68 E	10	12
	Serui	1° 54.32 S	136° 13.65 E	6	0
	Owi	1° 15.26 S	136° 10.99 E	9	9
	Ambai	1° 57.64 S	136° 19.23 E	15	22
Fakfak / Kaimana	Mommon	3° 56.38 S	132° 48.21 E	4	18
	Mauwara	3° 49.65 S	134° 03.51 E	23	0
	Namatote	3° 46.73 S	133° 52.93 E	0	21
Total				169	191

of 1,453,500 ha covers 30% of Teluk Cenderawasih (The Taman Nasional Teluk Cenderawasih, or Cenderawasih Bay National Park, Fig. 1), and the Kaimana MPA covers all of Kaimana's jurisdictional waters (597,747 ha) (Mangubhai et al. 2012).

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Field collection and microsatellite analysis of 14 h and o populations in the Bird's Head Seascape (Table 1) followed Starger et al. (2008). Hardy-Weinberg equilibrium and allelic diversity measures for these populations are available in Starger et al. (2010).

To test for genetic structure among sample locations, we analyzed data from each species with AMOVA (Excoffier et al. 1992) as implemented in Arlequin 3.5.1.2 (Excoffier and Lischer 2010). We first assumed no regional genetic structure among sample locations, then performed hierarchical AMOVA partitioning populations into Raja Ampat, Teluk Cenderawasih, and Southwestern Papua coral ecoregions (Veron et al. 2009). Signifi-

cance was tested with 20,000 random permutations using the infinite alleles model (IAM, represented by γ statistics; Weir and Cockerham 1984) and the distance-based, stepwise mutation model of microsatellite evolution (SMM, represented by k statistics; Slatkin 1995). To prevent artifacts due to clonal reproduction, only unique genets (samples with non-identical genotypes) were included in the analyses.

To examine genetic structure without assumptions, we employed spatial and non-spatial Bayesian assignment methods implemented in BAPS 5.3 (Corander and Marttinen 2006, Corander et al. 2008) as described by Starger et al. (2010). We also employed individual-based assignment tests implemented in Structure 2.2.2 (Pritchard et al. 2000, Falush et al. 2003, Hubisz et al. 2009) using the admixture model with no prior information on population origin. We performed 300,000 iterations, discarding the first 100,000 as burn-in. We tested K values from 2 to 15 and used the Delta K method (Evanno et al. 2005) to determine the most likely K value.

To further explore dispersal barriers, we

used 'genetical bandwidth mapping' as implemented in the GenbMap (Cercueil et al. 2007). This method identifies spatial discontinuities in allele frequencies that may represent barriers to dispersal, but unlike model-based approaches, this nonparametric method does not assume a particular measure of genetic distance. Genetical bandwidth mapping 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) as is common with corals in the hyper-diverse Coral Triangle. GenbMap was run with a resolution of 300 x 300 pixels (1 pixel = 2.1km), 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.

To test for population declines in coral populations in this region, we calculated the statistic "M" following Garza and Williamson (2001). Briefly, M is the ratio of the number of alleles to range in allele size. Ratios of 0.8 and above are common for stable populations, but populations that have experienced reductions in effective population size have values below 0.70. As h and o are hermaphroditic (Veron 1986) and effective population size cannot be skewed by unequal sex ratio, fluctuations in effective population can only be driven by changes in actual population size.

Finally, we examined the functional loss of individual coral populations on regional connectivity by employing the jackknifing procedure of Baums et al (2005). Briefly, we estimated pairwise immigration rates between populations with $n \geq 9$ using a Bayesian assignment method implemented in the program BayesAss+ 1.3 (Wilson and Rannala 2003) which estimates migration among all populations simultaneously. The first 999,999 iterations of the MCMC were discarded as burn-in. The chain was then run for an additional 2 million iterations with a sampling frequency of 2,000, allowing convergence of likelihood scores (data not

shown). Finally, we generated additional migration matrices for each species, but with a single locality removed, and then calculated the mean effect of removal of each locality on mean self-recruitment of the remaining sites by subtracting self-recruitment rates of the truncated matrices from the complete genetic connectivity matrix and averaging across localities.

Results

We genotyped 169 individual *h*

(Table 1) at nine microsatellite loci. Number of alleles per locus ranged from seven (Pd3-005) to 20 (PV2) with a mean of 11.67 (Table 2). Five multilocus genotypes were observed in more than one individual, suggesting the possibility of clonality, and two of these were observed in more than two individuals. In total, nine clonal individuals were removed from the analysis. Similarly, we genotyped 191 individual *o* x (Table 1) at seven microsatellite loci. The number of alleles per locus ranged from three (Sh3-003) to 19 (Sh2-006) with a mean of 10.57 (Table 3). Six multilocus genotypes were observed in more than one individual, suggesting clonality, and one of these was observed in more than two individuals. These six potentially clonal individuals were removed from subsequent analyses. Details of Hardy-Weinberg equilibrium (HWE), linkage disequi-

Table 2. Population statistics for *h* : Given are the number of samples (N), number of unique genotypes (Ng), M value (M), its variance (M var), and BAPS cluster.

Locality (region)	N	Ng	M	M var	Cluster
Alyui Bay (R4)	20	16	0.61	0.07	1
Mayalibit (R4)	9	9	0.63	0.07	2
Kri Island (R4)	30	30	0.61	0.06	2
Jefman (R4)	22	22	0.72	0.06	3
Lemon (TC)	18	18	0.64	0.08	4
Rumberpon (TC)	13	13	0.62	0.04	3
Adoki Village (TC)	10	7	0.61	0.07	2
Owi (TC)	9	9	0.67	0.08	3
Ambai (TC)	15	15	0.62	0.05	3
Mauwara (F/K)	23	21	0.59	0.05	5

Table 3. Population statistics for *O. nuxi*: Given are the number of samples (N), number of unique genotypes (Ng), *U* value (M), its variance (M var), and BAPS cluster.

Locality (region)	N	Ng	M	M var	Cluster
Alyui Bay (R4)	19	17	0.61	0.06	1
Mayalibit (R4)	20	20	0.49	0.09	2
Kri (R4)	9	9	0.62	0.03	1
Jefman (R4)	22	17	0.66	0.07	3
Lemon (TC)	20	20	0.67	0.09	4
Rumberpon (TC)	19	19	0.79	0.09	5
Adoki Village (TC)	12	12	0.7	0.11	6
Owi (TC)	9	9	0.79	0.09	7
Ambai (TC)	22	22	0.72	0.08	8
Mommon (F/K)	18	18	0.7	0.1	9
Namatote (F/K)	21	21	0.81	0.08	10

librium and tests for null alleles are reported in Starger et al 2010 and Supplemental Table 1. Briefly, no locus was consistently out of HWE in all localities, and patterns suggest genetic subdivision at the local scale, combined with admixture of populations (Underwood et al. 2007).

AMOVA analysis with no assumptions indicated strong structure in both species with $F_{ST} = 0.139$ ($k_{ST} = 0.130$) for *h* and $F_{ST} = 0.357$ ($k_{ST} = 0.246$) for *o* ($p < 0.00001$ 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), however, did not support differentiation among the three biogeographic regions (Fig. 1). This hypothesis explained 0% of the genetic variation in *h* and only 6.84% of the variation in *o* using the infinite alleles model ($F_{CT} = 0.068$, $p = 0.03$); results of the stepwise mutation model were not significant ($k_{CT} = 0.043$, $p = 0.18$). Instead, variation among populations within regions explained 86.84% of the variation in *h* with $F_{ST} = 0.132$ ($p < 0.00001$) and 63.02% of the variation in *o*, with $F_{ST} = 0.370$ ($p < 0.00001$). Similar results were achieved using the stepwise mutation model (Tables 4 and 5).

Table 4. Results from AMOVA for *h*. 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 (k statistics) of microsatellite evolution. Negative values are presented, but are effectively equal to zero.

	F stat	st c	p	% var	R stat	st c	p	% var
All samples								
Among localities	F_{ST}	0.139	<0.00001	13.940	k_{ST}	0.130	<0.00001	13.000
Within localities				86.060				87.000
3 regions								
Among groups	F_{CT}	-0.028	0.874	-2.830	k_{CT}	0.017	0.382	1.660
Among localities within regions	F_{SC}	0.156	<0.00001	15.990	k_{SC}	0.120	<0.00001	11.810
Within localities	F_{ST}	0.132	<0.00001	86.840	k_{ST}	0.135	<0.00001	86.540
Structure inferred by BAPS								
Among clusters	F_{CT}	0.140	0.003	14.000	k_{CT}	0.060	0.240	6.020
Among localities within clusters	F_{SC}	0.030	0.007	2.610	k_{SC}	0.079	0.013	7.460
Within localities	F_{ST}	0.166	<0.00001	83.400	k_{ST}	0.135	<0.00001	86.520
Structure inferred by GBM								
Among clusters	F_{CT}	-0.011	0.555	-1.070	k_{CT}	0.063	0.178	5.930
Among localities within clusters	F_{SC}	0.148	<0.00001	14.940	k_{SC}	0.076	0.007	7.160
Within localities	F_{ST}	0.139	<0.00001	86.130	k_{ST}	0.136	<0.00001	86.530

Table 5. Results from AMOVA for *O. hirtella* and *O. nuxi*. 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 (k statistics) of microsatellite evolution. Negative values are presented, but are effectively equal to zero.

	F statistics			R statistics		
	F_{ST}	p	% var	k_{ST}	p	% var
All samples						
Among localities	0.357	<0.00001	35.710	0.246	<0.00001	24.560
Within localities			64.290			75.440
3 regions						
Among groups	0.068	0.034	6.840	0.043	0.177	4.290
Among localities within regions	0.324	<0.00001	30.140	0.222	<0.00001	21.210
Within localities	0.370	<0.00001	63.020	0.255	<0.00001	74.510
Structure inferred by BAPS						
Among clusters	0.325	0.016	32.530	0.286	0.018	28.620
Among localities within clusters	0.050	0.088	3.400	-0.054	0.919	-3.830
Within localities	0.359	<0.00001	64.070	0.248	<0.00001	75.220
Structure inferred by GBM						
Among clusters	0.142	0.006	14.170	-0.031	0.566	-3.080
Among localities within clusters	0.263	<0.00001	22.610	0.270	<0.00001	27.370
Within localities	0.368	<0.00001	63.220	0.243	<0.00001	75.710

Results from BAPS identified five genetic clusters from 12 *h. nuxi* localities, two of which were excluded due to low sample size (Table 2, Fig. 2), and ten genetic clusters in 11 *O. hirtella* populations (Table 3, Fig. 3). Clusters containing multiple populations were generally, but not always, composed of geographically proximal localities. For example, *h. nuxi* Cluster 1 includes four sites in Raja Ampat; however Cluster 2 consists of sites from Raja Ampat and Teluk Cenderawasih. For *O. hirtella*, 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 *h. nuxi* in which Kri Island was assigned to Cluster 1 in the spatial analysis and clustered alone in the non-spatial analysis (not shown). The log(likelihood) values in the non-spatial analysis and spatial analysis for *h. nuxi* (-3,701.47 versus -3,718.95) and *O. hirtella* (-2,892.18 versus -2,916.11) were extremely similar, indicating close

agreement between the two methods, although the non-spatial analysis was still the best model. While AMOVA results based on BAPS partitions indicate significant variation among groups explaining 6% and 28% of the variation among regions of *h. nuxi* and *O. hirtella* respectively, the majority of the variation was still observed within localities (Tables 4 and 5).

The 'correct' number of clusters recovered in Structure 2.2.2 was unclear. Delta K indicated $K = 2$ as the most likely value for *h. nuxi* and $K = 12$ for *O. hirtella*, 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 multiple clusters in both Raja Ampat and Teluk Cenderawasih, while Kaimana and Fakfak were contained mostly in one cluster (Figs 2 and 3). As a heuristic, we also present $K = 6$ for *h. nuxi* and $K = 11$ for *O. hirtella* the most likely number of clusters indicated by BAPS (Table

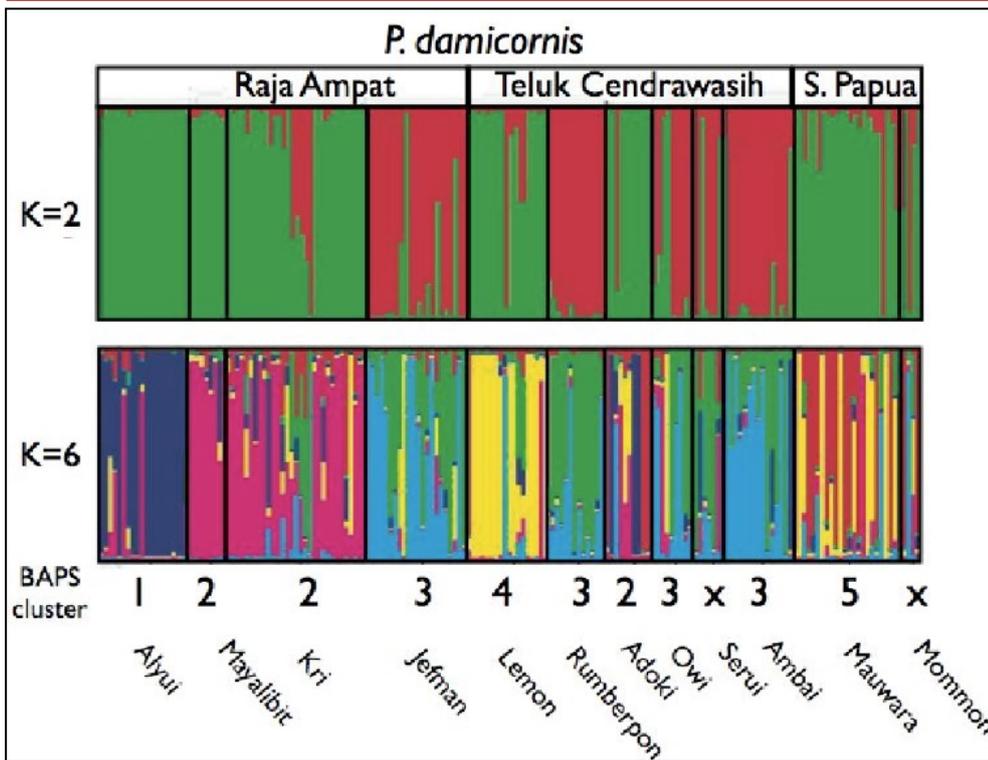


Figure 2. Results from Bayesian assignment methods implemented in Structure and BAPS for h . X indicates populations excluded from BAPS analysis due to $N \leq 6$. Numbers of population clusters $K = 2$ and $K = 6$ were used to explore a range of cluster numbers as described in the text.

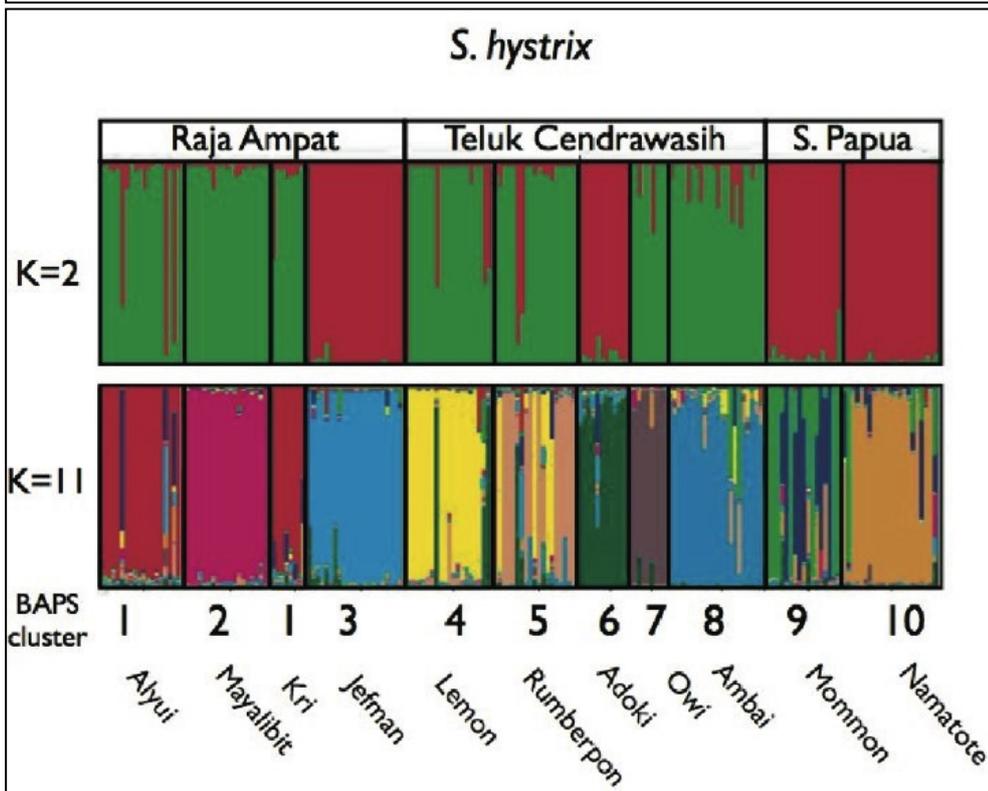


Figure 3. Results from Bayesian assignment methods implemented in Structure and BAPS for o . $K = 2$ and $K = 11$ were used to explore a range of cluster numbers as described in the text.

2, Fig. 2). Results show a strong correspondence between cluster assignment and locality in o (Fig. 3), whereas results from h show less concordance between clusters and location (Fig. 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. At least six distinct 'genetical regions' were delineated for each species within the Bird's Head Seascape (Figs 4 and 5). Most notable are both a putative dispersal barrier between eastern and western localities within and above Teluk Cendrawasih, and genetic breaks in concordance with the land barrier

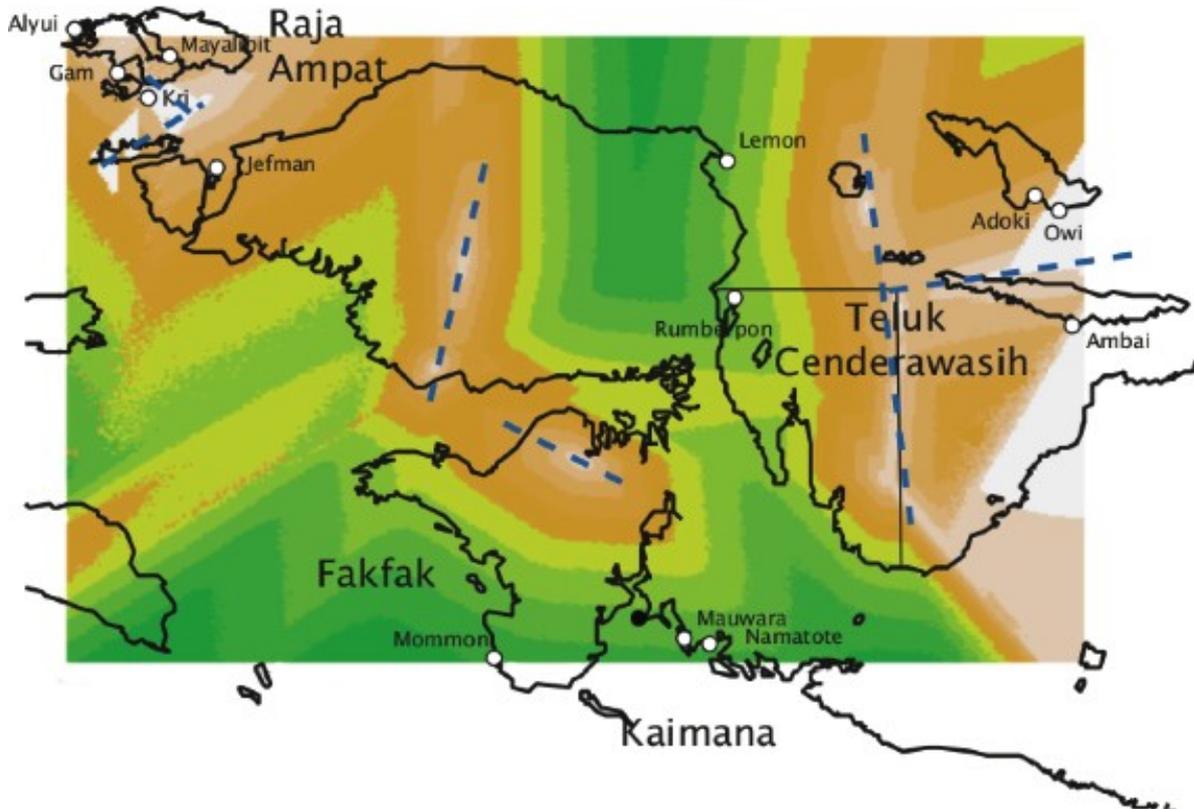


Figure 4. Genetical bandwidth map for h . Green areas indicate regions of genetic homogeneity. White areas indicate putative barriers to larval dispersal and are highlighted with blue dashed lines. The solid black line indicates the borders of Taman Nasional Teluk Cenderawasih.

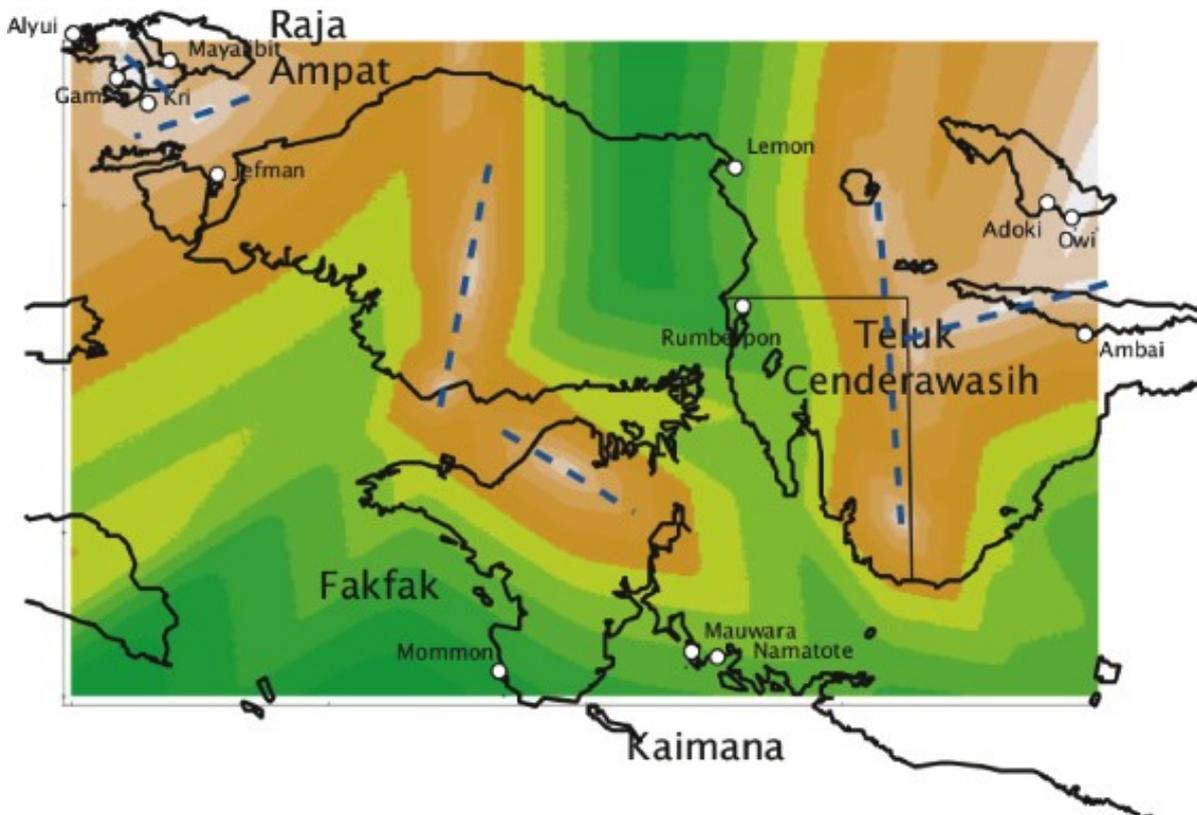


Figure 5. Genetical Bandwidth Map for o . Green areas indicate regions of genetic homogeneity. White areas indicate putative barriers to larval dispersal and are highlighted with blue dashed lines. The solid black line indicates the borders of Taman Nasional Teluk Cenderawasih.

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 o when based on the infinite alleles model ($\chi^2_{CT} = 0.142$, $p = 0.006$ and Table 2).

Results from BayesAss+ showed high levels of self-recruitment. Results from BayesAss+ revealed an average self-recruitment rate of 76% (SD = 1%) for h and 93% (SD = 1%) for o . The removal of individual localities increased self-recruitment an average of 1.8% in the remaining localities for h and an average of 2.6% in the remaining localities for o (Fig. 6). The exclusion of o in Rumberpon and h in Adoki were the only instances in which self-recruitment decreased in the remaining localities.

Discussion

Microsatellite analyses using AMOVA, assignment tests, and genetical bandwidth mapping indicate significant genetic differentiation among h and o populations within the Bird's Head Seascape, Eastern Indonesia. Genetic structure was much stronger in o than in h , consistent with previous comparative studies from Eastern Australia (Ayre and Hughes 2000, 2004) and Indonesia (Starger et al. 2010). Levels of divergence in both species were substantially higher than observed over similar geographic ranges in the Great Barrier Reef (Ayre and Hughes 2000, 2004) and Western Australia (Underwood et al. 2007), and were much more similar to values seen in the extreme of these species' ranges (Ayre and Hughes 2004, Combsch and Vollmer 2011).

Strong, significant genetic structure in coral populations of West Papua indicates substantial limits to genetic and demographic connectivity (Hedgecock et al. 2007), yet there was no clear regional pattern to this structure. Although biophysical models predict limited connectivity among Teluk Cenderawasih, Raja Ampat, and Southwestern Papua (Trembl et al. 2015), AMOVA

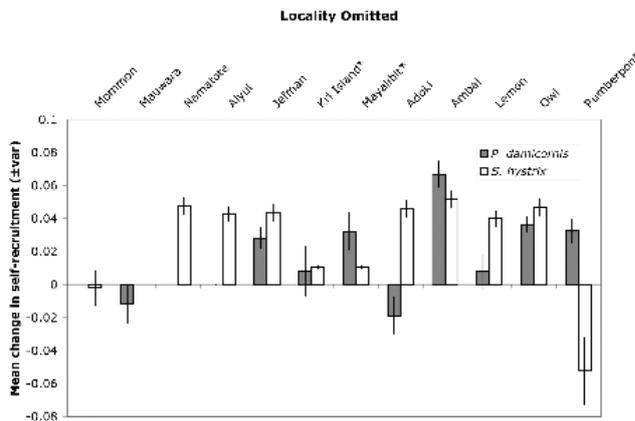


Figure 6. Jackknife analysis of self-recruitment rates depicting mean percent change in self-recruitment rates (\pm variance) among localities when one locality (labeled on the x-axis) is omitted. A negative value indicates a mean decrease in self-recruitment into the remaining localities when one locality is omitted. h was not sampled in Mommon or Namatote. o was not sampled in Mauwara. *indicates sites that lie within protected areas.

and assignment tests could not differentiate these three regions. The lack of clear regional genetic structure contrasts with results from a variety of other reef-dwelling invertebrate species that show pronounced genetic differentiation between Teluk Cenderawasih and other parts of the Bird's Head Seascape (Barber et al. 2006, Crandall et al. 2008, Barber et al. 2011, DeBoer et al. 2014).

Instead of regional structure, analyses revealed fine scale patterns of genetic structure within Teluk Cenderawasih and Raja Ampat. Lack of strong regional differentiation with pronounced genetic structure on the local scale was confirmed by genetical bandwidth mapping. This technique identified putative dispersal barriers within Raja Ampat and Teluk Cenderawasih, confirming that results from AMOVA and assignment tests are not artifacts of sample size. Mainland West Papua was also identified as a region of genetic discontinuity in both species (Figures 3 and 4), supporting the divergence of Teluk Cenderawasih and Raja Ampat as seen in a wide range of marine invertebrates in this part of the Bird's Head Seascape (Barber et al. 2011, Carpenter et al. 2011).

While both species exhibited significant genetic

structure across the Bird's Head Seascape, genetic structure was highest in *O. aspera*. With the exception of Alyui with Kri Island, all other *O. aspera* localities were genetically distinct. In contrast, *h. aspera* populations exhibited much lower levels of genetic structure based on fixation indices, and clustering analyses, suggesting that this species has very different patterns of connectivity across the Bird's Head Seascape.

These differences in genetic structure may result from larval dispersal abilities. While the majority of larvae of both species have been observed to settle within a few days of release (Isomura and Nishihira 2001), maximum larval life spans may be higher than previously thought (Graham et al. 2010). In particular, *h. aspera* larvae have survived 103 days in aquaria, indicating the potential for long distance dispersal (Richmond 1987). The presence of zooxanthellae in *O. aspera* larvae coupled with evidence of diverse reproductive strategies such as polyp bailout (Sammarco 1982) and rafting (Jokiel 1984) suggests that extended larval durations may be possible in this species as well. However, the observation of higher structure in *O. aspera* in comparison to *h. aspera* in this and other studies (Ayre and Hughes 2000, 2004, Starger et al. 2010) suggests that *O. aspera* must have lower larval dispersal abilities.

While our results are generally consistent with previous studies that compare 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. Van Oppen et al. (2008) observed a mean pairwise F_{ST} of 0.20 among *O. aspera* populations on the Great Barrier Reef, compared to $F_{ST} = 0.36$ across the Bird's Head Seascape, even though the spatial scale is considerably smaller. Physical oceanography, regional variation in reproduction, and more heterogeneous environmental conditions may explain the observed differences in connectivity among populations in these two coral reef ecosystems. For example, coral populations on the Great Barrier Reef are largely arranged in a linear pattern and are subjected to relatively predictable sea surface cir-

ulation patterns dominated by the Eastern Australian Current. Ocean circulation is much less well understood in the Bird's Head Seascape where coastlines are far more complex. This complexity may result in localized sea surface circulation eddies and seasonal or irregular reversals that could increase mean drift time between geographically proximate reefs.

An additional, non-mutually exclusive explanation 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 *h. aspera* 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). In contrast, *O. aspera* is not known to spawn, but 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 differences in observed genetic patterns. Similarly, *h. aspera* has been observed rafting on pumice (Bryan et al. 2012), which could also facilitate higher dispersal and lower genetic structure in this species.

An increasing number of studies indicate the presence of cryptic species in corals (e.g. Chen et al. 2007, Bongaerts et al. 2010, Souter 2010, Pinzon and LaJeunesse 2011). In particular, recent work by Pinzón et al. (2013) and Schmidt-Roach et al. (2013) indicate that *h. aspera* is a species complex. Schmidt-Roach et al. (2013) identifies at least 5 cryptic lineages in the Western Pacific based on DNA sequences from the control region, internal transcribed spacer 2 (ITS2), and heat shock protein 70 and Combosch and Vollmer (2013) successfully differentiate ITS types 1, 3 and 5 based on based on 6,769 Single Nucleotide Polymorphisms (SNPs) obtained from RAD-Seq data.

While the above suggests that cryptic diversity within our samples likely impacts our results, particularly given that BAPS recovers 5 clusters, there are several reasons to believe that our re-

sults cannot simply be dismissed as the result of cryptic species diversity. First, Genetical Bandwidth Mapping recovers nearly identical patterns for both h' and o' . The most parsimonious explanation for this result is that the two species are being structured by similar physical processes (Avice 2000) rather than arising from concordant non-random distributions of cryptic lineages. In fact, while Bongaerts et al. (2010) suggest that there could be divergence among deep and shallow o' , their results suggest there is no cryptic divergence among shallow-water o' populations, such as those sampled in our study. Secondly, results show that populations generally fall into clusters based on geographic proximity. Given that many of the cryptic lineages can be distributed and genetically homogeneous over 1000s of km (Pinzón et al. 2013), it seems unlikely that multiple cryptic species in the Bird's Head Seascape would each dominate specific geographic regions. Lastly, results from Torda et al. (2013) on h' along the Great Barrier Reef are similar to previous research (e.g. Ayre and Hughes 2000, 2004) and show that the major genetic patterns are observed whether or not samples are segregated by cryptic lineage. As such, while cryptic lineages likely introduce noise into the h' results it is unlikely that patterns of genetic structure are simply an artifact of taxonomic uncertainty.

h'

While the Bird's Head Seascape is relatively pristine (Mangubhai et al. 2012), our results suggest that corals may have suffered population declines in this region. M values averaged 0.64 for h' and 0.65 for o' with the majority of values falling below 0.70. These values are strikingly similar to those of the highly endangered Mediterranean Monk Seal ($M = 0.64$) and the Northern Elephant Seal ($M = 0.66$), two marine species that have suffered massive population declines (Garza and Williamson 2001), suggesting similar declines may have occurred 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 declines throughout the region unless 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 results indicate connectivity was largely limited among coral populations within the Bird's Head Seascape, results also indicated that MPA networks in this region could be impacted by the loss of individual populations. The jackknifing procedure of Baums et al (2005) showed that loss of individual populations raised mean self-recruitment rates in both species; in only 2 cases for each species did loss of a populations not impact self-recruitment.

Substantial increases in self-recruitment were seen in both species with the removal of Jefman, Ambai, and Owi, indicating that these locations are especially important for facilitating connectivity among populations in the Bird's Head Seascape. While it might be tempting to conclude that these populations are the most important to prioritize for conservation, designating a limited number of populations as strategically placed MPAs in hopes that they will seed adjacent unprotected areas would be an ineffective strategy to protect these coral populations. Likely, a more effective strategy would be a network that includes numerous, relatively closely spaced MPAs over a broad geographic area to provide protection of local reefs as well as support regional genetic connectivity. The network of seven MPAs in Raja Ampat is a good example of this approach, with an average MPA size of 160,000 ha and spacing averaging less than 60 km. However, further research is required to determine whether the number and spacing of these reserves is sufficient, and how many coral reef taxa will benefit from this arrangement. In contrast, the Taman Nasional Teluk Cenderawasih covers a large area, over 1 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 designate additional MPAs in the eastern north-east portions of the bay in the vicinity of Adoki and Owi to facilitate regional connectivity throughout Teluk Cenderawasih, as well as preserve the maximum amount of genetic diversity, protecting adaptive potential of these populations in the face of growing threats like climate change (Oliver et al. 2009) and ocean acidification (Pandolfi et al. 2011).

Increasing global and local threats to coral reefs is increasing the need for science to support conservation planning. Genetic investigations 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 understanding connectivity among MPAs (Sale et al. 2005). Although not all reefs can be assessed in this manner, insights into the patterns and processes of biological diversity can be used to design or refine management plans. In our case, the means to apply genetic data to conservation action already exists in the ongoing, multi-institutional partnerships of the Bird's Head Seascape Initiative (Green and Mous 2004). Examination of additional taxa in a similar fashion to that presented here (Barber et al. 2011, Carpenter et al. 2011) will provide a wide range of results that resource managers may take into account when designing an optimum MPA network for the Bird's Head Seascape and elsewhere.

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