

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

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4 **Authors:** Craig John Starger^{1,2,3,4}; Paul Henry Barber⁴; Mark van Nydeck Erdmann⁵; Abdul
5 Hamid A. Toha⁶; Andrew Charles Baker^{7,8}

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7 **Authors' addresses:**

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9 1. Science & Technology Policy Fellowships, Center of Science, Policy & Society
10 Programs, American Association for the Advancement of Science, 1200 New York
11 Avenue NW, Washington DC, 22205 USA.
- 12 2. Department of Ecology, Evolution and Environmental Biology, Columbia University,
13 New York, NY, USA
- 14 3. Sackler Institute for Comparative Genomics, American Museum of Natural History, New
15 York, NY, USA.
- 16 4. Department of Ecology and Evolutionary Biology, University of California Los Angeles,
17 Los Angeles, California, USA.
- 18 5. Conservation International, Indonesia Marine Program, Renon, Bali, Indonesia.
- 19 6. Faculty of Animal Sciences, Fisheries and Marine Science, State University of Papua,
20 Manokwari, West Papua, Indonesia.
- 21 7. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami,
22 Florida, USA
- 23 8. Marine Conservation Program, Wildlife Conservation Society, Bronx, New York, USA

24 **Abstract:** Marine Protected Areas (MPAs) are widely considered to be one of the best strategies
25 available for protecting biodiversity and ecosystem processes in marine environments,
26 particularly in developing, tropical nations. While data on connectivity and genetic structure of
27 marine populations are critical to designing appropriately sized and spaced networks of MPAs,
28 such data are rarely available. Here we present an assessment of genetic structure in reef-
29 building corals from Papua and West Papua, Indonesia, among the most biologically diverse and
30 least disturbed coral reef regions in the world, and the focus of the multi-institutional Bird's Head
31 Seascape initiative to design and implement a functional network of MPAs. Microsatellite
32 variation was assessed within and among populations of *Pocillopora damicornis* (Linnaeus,
33 1758) and *Seriatopora hystrix* (Dana 1846) (family: Pocilloporidae) from three regions, each
34 currently under a different conservation regime: Teluk Cenderawasih, Raja Ampat, and
35 southwest Papua. Analyses of molecular variance, assignment tests, and genetical bandwidth
36 mapping revealed significant local-scale structure in both species, and a lack of regional filters to
37 gene flow. Overall, *P. damicornis* populations were less structured ($F_{ST} = 0.139$, $p < 0.00001$)
38 than those of *S. hystrix* ($F_{ST} = 0.357$, $p < 0.00001$). In order to maintain connectivity within and
39 among regions, coral reef conservation on the local scale is needed. These data have been
40 directly applied to the design of a MPA network in the Bird's Head Seascape.

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47 **Introduction**

48

49 Comprising only a small fraction of the surface of the Earth's oceans, coral reefs are the world's
50 most biologically diverse marine ecosystems (Connell 1978, Reaka-Kudla 1997). Despite the
51 ecological and economic importance of coral reefs, they are rapidly declining worldwide due to
52 human influence (Hoegh-Guldberg et al. 2007). Within the past few decades, 19% of the world's
53 coral reefs have been destroyed and 15% are now at risk of imminent collapse in the next 10 to
54 20 years (Wilkinson 2008), with rates of decline that exceed those of tropical rain forests (Bruno
55 and Selig 2007). Two thirds of the Caribbean and over 85% of Southeast Asian coral reefs are
56 considered under threat (Burke et al. 2012)

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58

59 Most troubling in these declines is the dramatic reduction in the abundance of reef-building
60 corals (order: Scleractinia) threatening the very foundation of coral reef ecosystems. For
61 example, the Coral Triangle (a region comprised of the Philippines, Malaysia, Indonesia, Papua
62 New Guinea, the Solomon Islands, Brunei Darussalam, and Timor-Leste) has the highest
63 proportion of 'Vulnerable' and 'Near Threatened' coral species based on IUCN Red List Criteria
64 (Carpenter et al. 2008). Anthropogenic loss of corals and the degradation of coral reef
65 environments are severely impacting the long term stability of coral communities (Adams and
66 Ebersole 2010, Hughes et al. 2010) creating an urgent need for coral-focused conservation,
67 especially within the Coral Triangle (Burke et al. 2012)

68

69 Marine protected areas (MPAs) are considered one of the best methods for protecting species
70 diversity and ecosystem processes and functions. Despite their demonstrated effectiveness
71 (Levitan and McGovern 2005), only 2% of the world's coral reefs are within MPAs with
72 adequate conditions for the conservation of biodiversity (Mora et al. 2006). Given that this
73 amount is far less than the recommended 20-30% (Mora et al. 2006), the recent and projected
74 growth of MPAs in the coming years increases the need for sound marine conservation science.
75 While understanding connectivity has been identified as critical to developing long-term
76 conservation strategies for marine ecosystems (Botsford et al. 2001, Cowen et al. 2006, Crowder
77 et al. 2000, Palumbi 2003), it remains among the most crucial gaps in scientific knowledge
78 necessary for marine conservation (Sale et al. 2005). In addition, genetic diversity has rarely
79 been incorporated in international biodiversity conservation policy (Laikre 2010).

80
81 Coral reefs in the provinces of Papua and West Papua, Indonesia, (Figure 1) collectively referred
82 to as the 'Bird's Head Seascape' (BHS), are among the most diverse and pristine in the world
83 (Allen 2008) and rank as the Indonesian government's number one priority region for marine
84 biodiversity conservation development (Huffard et al. 2012a). This region is also the focus of the
85 multi-institutional Bird's Head Seascape initiative, comprised of NGOs and universities working
86 with local governments to design and implement an ecosystem-based management plan that has
87 as its centerpiece a network of MPAs that span the entire Bird's Head Seascape (Mangubhai et
88 al. 2012). Therefore, understanding patterns of genetic connectivity among populations of coral
89 reef animals within this region has been an ongoing research priority for the past seven years.
90 Results from genetic studies, including this one, have been fed directly into MPA network

91 planning and design in the Bird's Head Seascape even before many of these studies were
92 formally published (Huffard et al. 2012b).

93

94 Here we present fine scale spatial genetic patterns in *Pocillopora damicornis* (Linnaeus, 1758)
95 and *Seriatopora hystrix* (Dana 1846), two scleractinian coral species that represent opposite ends
96 of the genetic connectivity spectrum. We use analytical methods specifically designed for low
97 and uneven sample sizes (necessary for investigators focusing on rare and threatened species) to
98 test for limits to connectivity among the coral reefs of the Bird's Head Seascape, a region
99 designated a top conservation priority within the Coral Triangle, and to test the hypothesis that
100 populations of *P. damicornis* will be more open with lower levels of genetic structure, while *S.*
101 *hystrix* will exhibit higher genetic structure, resulting from more limited dispersal (Starger et al.
102 2010). We also hypothesize that these populations have undergone recent declines given the
103 threatened nature of many Indonesian coral reefs. Our results improve our understanding of
104 genetic structure of coral populations in remote and understudied areas while providing useful
105 data for managers currently developing conservation strategies for the globally significant Bird's
106 Head Seascape.

107

108 Recent reports from Australia, Kenya and the Eastern Pacific have revealed previously unknown
109 genetic diversity within *P. damicornis* and *S. hystrix* and some have suggested that this genetic
110 variation may represent cryptic species (e.g. Souter 2010, Pinzón and LaJeunesse 2011, Schmidt-
111 Roach et al. 2012, Pinzón et al. 2013). Despite these findings, most of the evidence for cryptic
112 coral species presented in these publications is derived a limited number of molecular loci and no
113 quantitative morphology resulting in poorly supported phylogenetic reconstructions and no clear

114 delimitations of cryptic species. In addition, studies rarely incorporate known sister taxa in a
115 phylogenetic context except for Souter (2010), who tested East African *P. damicornis* against
116 congeners from Hawai'i and the Tropical Eastern Pacific, and Bongaerts et al. (2010), whose
117 analysis of *S. hystrix* and *S. caliendrum* recovered *S. hystrix* as a monophyletic clade with
118 marginal evidence of reproductive isolation among depth-distributed types. Furthermore, some
119 of these recent methods, such as the use of symbiosis ecology to delineate coral species (Pinzón
120 and LaJeunesse 2011), are already being invalidated (Cunning et al. 2013). Clearly not enough
121 data currently exist to reject the null hypothesis that the original species designations are still
122 valid and that our population genetic study and others (e.g. Ayre and Hughes 2004, Starger et al.
123 2010, Combosch and Vollmer 2011, Nir et al. 2011, Paz-Garcia et al. 2012) also remain valid.

125 **Methods**

127 *Species identification and site selection*

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

137 and terrigenous pollution from logging and coastal development (McKenna et al 2002, Burke et
138 al. 2012, Mangubhai et al. 2012).

139

140 There are currently 12 actively managed MPAs in the BHS ranging in size from 5000 to
141 1,453,500 ha and covering a total area of 3,594,702 ha (see Figure 1 and Table 2 in Mangubhai
142 et al. 2012). A network of seven marine protected areas was first designated in Raja Ampat in
143 May, 2007 and expanded in 2009 to cover a total of 1,125,940 ha, approximately 50% of Raja
144 Ampat's shallow reef areas, with MPAs ranging in size from 53,100 ha to 343,200 ha and the
145 spacing between MPAs ranging from 20-100 km (Mangubhai et al. 2012). To the east of Raja
146 Ampat is Teluk Cenderawasih, wherein lies the Taman Nasional Teluk Cenderawasih (TNTC, or
147 Cenderawasih Bay National Park), an MPA covering 1,453,500 ha and approximately 30% of
148 the reefs of Teluk Cenderawasih (Figure 1). To the Southwest, the Kaimana MPA covers all of
149 Kaimana's jurisdictional waters (597,747 ha) (Mangubhai et al. 2012).

150

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

160 (Allen 2008), and both the local and national governments are now committed to developing new
161 MPAs in the region to protect this diversity (Huffard et al. 2012b).

162

163 *Genetic analysis*

164

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

175

176 In order to test the hypothesis that significant genetic variation exists among sample locations,
177 data from the Bird's Head Seascape (Table 1) were analyzed for each species with AMOVA
178 (Excoffier et al. 1992) as implemented in Arlequin 3.5.1.2 (Excoffier and Lischer 2010)
179 assuming no regional genetic structure among sample locations. Hierarchical AMOVA was then
180 performed to test the significance of the three coral ecoregions (Veron et al 2009): Raja Ampat,
181 Teluk Cenderawasih, and Southwestern Papua. The significance of this structure was tested with
182 20,000 random permutations using both the infinite alleles model (IAM, represented by F

183 statistics, (Weir and Cockerham 1984)) and the distance-based, stepwise mutation model of
184 microsatellite evolution (SMM, represented by *R* statistics, (Slatkin 1995)). Only those
185 populations with ten or greater unique genotypes were considered in AMOVA calculations.

186

187 To examine genetic structure without *a priori* assumptions of population membership, we
188 employed spatial and non-spatial Bayesian assignment methods implemented in BAPS 5.3
189 (Corander et al. 2008, Corander and Marttinen 2006) as described by Starger et al. (2010).

190 Genetic structure and admixture were also assessed using the individual-based assignment test
191 implemented in the program Structure 2.2.2 (Hubisz et al. 2009, Falush et al. 2003, Pritchard et
192 al. 2000) using the admixture model with no prior information on population origin. All
193 individuals were considered in this analysis. The assignment method was performed using
194 300,000 iterations, the first 100,000 of which were discarded as burn-in. *K* values from 2 to 15
195 were tested. The Delta *K* method of Evanno et al. (2005) was implemented to determine the most
196 likely *K* value.

197

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

203

204 Finally, in order to identify putative barriers to dispersal, we applied a 'genetical bandwidth
205 mapping' approach, which is based on 'wombling' (Womble 1951) and implemented in the

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

217 **Results**

219 *Allelic variation in microsatellites*

220
221 For *P. damicornis*, 169 individuals (Table 1) were genotyped and analyzed at nine microsatellite
222 loci. The number of alleles per locus ranged from seven at locus Pd3-005 to 20 at locus PV2
223 (mean: 11.67). Five multilocus genotypes were observed in more than one individual however
224 only two of these were observed in more than two individuals. In total, nine clonal individuals
225 were removed from the analysis. For *S. hystrix*, 191 individuals (Table 1) were genotyped and
226 analyzed at seven microsatellite loci. The number of alleles per locus ranged from three at locus
227 Sh3-003 to 19 at locus Sh2-006 (mean: 10.57). Six multilocus genotypes were observed in more
228 than one individual however only one of these was observed in more than two individuals. In

229 total, six clonal individuals were removed from the analysis. The unique number of genotypes
230 (Ng) and M values for each study location are presented in Tables 2 and 3. Statistics on
231 heterozygosity and Hardy-Weinberg equilibrium are available in Starger et al. (2010).

232

233 *Population genetic structure*

234

235 AMOVA analysis with no *a priori* assumptions indicated strong structure in both species with
236 $F_{ST} = 0.139$ ($R_{ST} = 0.130$) for *P. damicornis* and $F_{ST} = 0.357$ ($R_{ST} = 0.246$) for *S. hystrix* ($p <$
237 0.00001 for all values) with 16-17% and 30-37% respectively of the variation due to differences
238 among localities (Tables 4 and 5). Results from the hierarchical AMOVA (Tables 4 and 5)
239 indicate that genetic structure does not result from differentiation among the three biogeographic
240 regions (Figure 1). In *P. damicornis* both the infinite alleles model and stepwise mutation model
241 indicate that regional genetic breaks explain none of the observed genetic variation. Regional
242 structure is weak but significant in *S. hystrix* when based on the infinite alleles model ($F_{CT} =$
243 0.068 , $p=0.03$), explaining 6.84% of the variation, but not significant when based on the stepwise
244 mutation model ($R_{CT} = 0.043$, $p = 0.18$). Instead, variation among populations within regions
245 explained the majority of variation in both species: 86.84% of the variation in *P. damicornis* with
246 $F_{ST} = 0.132$ ($p < 0.00001$) and 63.02% of the variation in *S. hystrix*, with $F_{ST} = 0.370$ ($p <$
247 0.00001). Similar results were achieved using the SMM (Tables 4 and 5).

248

249 M values (Tables 2 and 3) are generally lower for *P. damicornis*. Results from the non-spatial
250 assignments test implemented in BAPS identified five genetic clusters from 12 *P. damicornis*
251 localities, two of which were excluded due to low sample size (Table 2, Figure 2), and ten

252 genetic clusters in 11 *S. hystrix* populations (Table 3, Figure 3). Clusters containing multiple
253 populations were generally but not always comprised of geographically proximal localities. For
254 example, *P. damicornis* Cluster 1 includes four sites in Raja Ampat, however Cluster 2 consists
255 of sites from Raja Ampat and Teluk Cenderawasih, suggesting genetic connectivity between
256 these ecoregions. For *S. hystrix*, Cluster 1 contained adjacent sites Kri Island and Alyui in Raja
257 Ampat. Spatial clustering results were identical to the non-spatial clustering for both species,
258 with the exception of *P. damicornis* in which Kri Island, was assigned to Cluster 1 in the spatial
259 analysis and clustered alone in the non-spatial analysis (not shown). Furthermore, log(likelihood)
260 was higher in the non-spatial analysis compared to the spatial analysis for *P. damicornis* (-
261 3,701.47 versus 3,718.95) and *S. hystrix* (-2,892.18 versus 2,916.11), indicating close agreement
262 between spatial and non-spatial methods. While AMOVA results based on BAPS partitions
263 indicate significant variation among groups explaining 6% and 28% of the variation among
264 regions of *P. damicornis* and *S. hystrix* respectively, the majority of the variation was still
265 observed within localities (Tables 4 and 5).

266
267 When using the individual-based analysis implemented in Structure 2.2.2, the ‘correct’ number
268 of clusters that fit our data was not clear. Delta K indicated K=2 as the most likely value for *P.*
269 *damicornis* and K=12 for *S. hystrix*, but in both species likelihood increased asymptotically as K
270 values increased towards and then beyond the number of sampled localities (not shown). Results
271 for K=2 for each species indicate mixing of clusters between Raja Ampat and Teluk
272 Cenderawasih, while Kaimana and Fakfak contained mostly one cluster (Figure 2). As a
273 heuristic, we also present K=6 for *P. damicornis* and K=11 for *S. hystrix* as indicated by BAPS
274 as the most likely number of clusters (Table 2, Figure 2). Results of these analyses show a strong

275 correspondence between cluster assignment and locality in *S. hystrix* (Figure 3), whereas results
276 from *P. damicornis* show more mixing of clusters among localities (Figure 2). In both species,
277 admixture is evident because localities nearly always contain a mixed composition of individuals
278 from various genetic clusters.

279

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

291

292 **Discussion**

293

294 Microsatellite analyses of two Indo-Pacific, reef-building corals, *P. damicornis* and *S. hystrix*,
295 indicate significant levels of genetic differentiation among populations within the Bird's Head
296 Seascape of Papua and West Papua, Indonesia. A mixture of traditional AMOVA, assignment
297 tests, and the genetical bandwidth mapping approach all indicate significant structure among

298 localities within West Papua, suggesting limits to connectivity among these coral populations.
299 Sample sizes were not large enough for traditional estimates of gene flow (Nm) however, as
300 predicted, genetic structure was higher in *S. hystrix* ($F_{ST} = 0.360$, $p < 0.001$) than in *P.*
301 *damicornis* ($F_{ST} = 0.139$, $p < 0.001$) suggesting more limited dispersal in the former, a result
302 consistent with previous comparative research from Eastern Australia (Ayre and Hughes 2000,
303 2004) and across all of Indonesia (Starger et al. 2010).

304
305 Strong, significant genetic structure indicates substantial limits to genetic and demographic
306 connectivity (Hedgecock et al. 2007) among coral populations of West Papua. However, while
307 the data clearly indicate structure across the Bird's Head Seascape in both species, this structure
308 is not clearly explained by geography or the delineated coral ecoregions of Veron et al. (2009).
309 AMOVA and assignment tests could not differentiate among Teluk Cenderawasih, Raja Ampat,
310 and Southwestern Papua, but instead revealed fine scale patterns of genetic structure within
311 Teluk Cenderawasih and within Raja Ampat. AMOVA results indicate significant levels of
312 variation among localities within these regions, explaining 15.99% of the overall variation for *P.*
313 *damicornis* and 30.14% for *S. hystrix*, with almost all the remaining genetic variation contained
314 within localities (Table 2). Similar results were obtained by the Bayesian assignment method
315 implemented in Structure and in the population-based analysis implemented in BAPS.

316
317 This pattern of strong structure on the local scale with weak differences among geographic
318 regions was confirmed by the new technique of genetical bandwidth mapping, a technique that is
319 specifically designed for data sets where sample sizes are irregular and occasionally small. This
320 is characteristic of coral populations in eastern Indonesia —the extreme biodiversity and patchy

321 composition of coral communities in this region (Veron et al 2009) makes obtaining large sample
322 sizes of individual species difficult. Genetical bandwidth mapping identified putative barriers to
323 dispersal within Raja Ampat and within Teluk Cenderawasih indicating that the results from
324 AMOVA and assignment tests are not artifacts of sample sizes. Interestingly, genetical
325 bandwidth mapping also identified mainland West Papua as a region of genetic discontinuity in
326 both species, supporting the presence of a dispersal barrier common to a wide range of marine
327 invertebrates in this part of the Bird's Head Seascape (Barber et al. 2006, Barber et al. 2010,
328 Crandall et al. 2008, DeBoer et al. 2008, Carpenter et al. 2011, Barber et al. 2011). These
329 patterns are concordant between the two coral species based on visual inspection of the maps
330 (Figures 3 and 4). Although sample sizes and fixation indices were within the ranges where
331 genetical bandwidth mapping can accurately infer genetic breaks (Cercueil et al. 2007),
332 additional research could result in more accurate estimates of coral connectivity in the region.
333 For example, taking a community genomics approach aligned with quantitative morphological
334 and reproductive studies and oceanographic modeling (Treml and Halpin 2012) would improve
335 our ability to detect subtle genetic structure and the presence of cryptic lineages (Chen et al.
336 2007, Souter 2010, Bongaerts et al. 2010), ecophenotypes (Nir et al. 2011), and cryptic species
337 (discussed below) in corals of the Bird's Head Seascape.

338

339 *Differences between species*

340

341 Results also indicate a clear difference in levels of genetic structure between *P. damicornis* and
342 *S. hystrix*, the latter having higher genetic structure. Genetic clustering analyses in BAPS and
343 Structure indicate that nearly every *S. hystrix* locality formed its own unique cluster with

344 minimal evidence of admixture among localities. The only clear geographic association was seen
345 in the clustering of Alyui with Kri Island, which cluster together in both BAPS and Structure.
346 Otherwise, each *S. hystrix* locality is genetically distinct, possibly suggestive of the occurrence of
347 multiple ecophenotypes (Nir et al. 2011). Given the geographic proximity of our study sites, and
348 previous evidence suggesting the monophyly of *S. hystrix* relative to its easily identifiable sister
349 species *S. caliendrum* (Bongaerts et al. 2010), we find it unlikely, though not impossible, that our
350 genetic clusters represent reproductively isolated cryptic species. *P. damicornis* populations
351 exhibited lower levels of genetic structure based on fixation indices, and fewer clusters were
352 resolved by BAPS and Structure, suggesting that this species has lower genetic structure than *S.*
353 *hystrix*. Cryptic species in *P. damicornis* might also exist, but we find this even less likely than in
354 *S. hystrix* given *P. damicornis*'s reproductive plasticity and long larval duration.

355
356 Differences in observed genetic structure among these two corals may be explained by
357 differences in their larval dispersal abilities. The majority of larvae of both species have been
358 observed to settle within a few days of release (Isomura and Nishihira 2001). However,
359 aquarium-based research on the larval biology of *P. damicornis* indicates the potential for long
360 distance dispersal via a maximum larval duration of at least 103 days (Richmond 1987). It is not
361 known whether *S. hystrix* similarly possesses this ability, but as more corals are studied in this
362 way, maximum larval life spans are proving to be much higher than previously thought (Graham
363 et al. 2010). The presence of zooxanthellae in *S. hystrix* larvae, coupled with evidence of diverse
364 reproductive strategies such as polyp bail-out (Sammarco 1982) and rafting (Jokiel 1984) suggest
365 that extended larval durations may be possible in this species as well. However, the observation
366 of higher structure in *S. hystrix* in comparison to *P. damicornis* in this and other studies (Ayre

367 and Hughes 2000, 2004; Starger et al. 2010) suggests that actual larval dispersal may be lower in
368 *S. hystrix*.

369

370 While our results are generally consistent with previous results comparing genetic structure
371 between these two coral species, we observed higher magnitudes of genetic structure over a
372 smaller spatial scale in both species in the Bird's Head Seascape in comparison to results from
373 the Great Barrier Reef. Van Oppen et al. (2008) observed a mean pairwise F_{ST} of 0.20 among *S.*
374 *hystrix* populations on the Great Barrier Reef, which is considerably lower than our observed
375 mean pairwise F_{ST} of 0.36 in West Papua, even though our spatial scale is much smaller.
376 Physical oceanography, regional variation in reproduction, and more heterogeneous
377 environmental conditions in the Bird's Head Seascape may explain the observed differences in
378 genetic structure between the Great Barrier Reef and the Bird's Head Seascape. Furthermore,
379 coral populations on the Great Barrier Reef are largely arranged in a linear pattern along
380 Australia's northeastern coastline and are subjected to relatively predictable patterns of sea
381 surface circulation, dominated by the Eastern Australian Current that flows southeast along the
382 Great Barrier Reef. Surface patterns are much less well understood in the Bird's Head Seascape,
383 where the coastline of West Papua is far more complex and currents less predictable than they
384 are on the northeastern coast of Australia. This complexity may result in localized sea surface
385 circulation eddies and seasonal or irregular reversals which increase mean drift time between
386 geographically proximate reefs. Oceanographic modeling has found patterns similar to the
387 conservation planning boundaries at both the ecoregional and the priority seascape scales (Trembl
388 and Halpin 2012). An additional explanation that is not mutually exclusive is that there may be
389 variations in reproductive strategies between corals of the Great Barrier Reef and those of the

390 Bird's Head Seascape. It is well established that *P. damicornis* can be either a brooder or
391 spawner depending on location (Baird et al. 2009), and may undergo 'reverse metamorphosis'
392 from polyp to planula when stressed (Richmond 1985). Similarly, *S. hystrix* can undergo polyp
393 bailout when stressed (Sammarco 1982). It is therefore possible that regional differences in
394 reproductive strategy between the Great Barrier Reef and the Bird's Head Seascape are
395 contributing to the observed genetic differences. *P. damicornis* has also been observed rafting on
396 pumice, which could increase drift times under rare circumstances (Bryan et al. 2012). Coral
397 reproduction studies here would serve to shed light on this question.

398

399 *On coral species*

400

401 Although the possibility exists that some of the genetic variation we observed represents cryptic
402 lineages or species, presently we find limited evidence in the literature for the existence of
403 cryptic coral species. Therefore, we cannot reject the original species descriptions at this time.
404 However, we do not discount the possibility that cryptic species can and probably do exist in the
405 Bird's Head Seascape where several undescribed coral species have recently been discovered
406 (Mangubhai et al. 2012). Likewise it is possible that reproductive barriers may exist among some
407 of the individuals and populations in our dataset. If this were true, it could potentially invalidate
408 some of the assumptions made in our genetic analysis methods which assume cohesion.
409 Unchanged, however, would be (1) our conclusions that genetic subdivision is widespread and
410 complex within these nominal coral species in the Bird's Head Seascape, and (2) the knowledge
411 that the Bird's Head Seascape is home to a remarkable assemblage of endemic coral species
412 (Veron et al. 2009) and genetic variants requiring immediate conservation action. Applying

413 genomic methods and quantitative morphological characters in a phylogenetic context, as well as
414 conducting reproductive and ecological studies on coral species, would help characterize
415 biodiversity in the Bird's Head Seascape, advance our understanding of the evolutionary
416 processes that generate and maintain this diversity, and further inform MPA design and
417 management.

418

419 *Population decline and coral reef conservation*

420

421 The Bird's Head Seascape is home to some of the most diverse, modern day coral reef
422 ecosystems (Mangubhai et al. 2012). However, one of the disturbing results from this study is
423 that these reefs may not have been immune to population declines. The mean M values, a genetic
424 measure used to infer population declines, for *P. damicornis* and *S. hystrix* populations in West
425 Papua (averaging 0.64 and 0.65 respectively) are strikingly similar to those of the Mediterranean
426 Monk Seal (M =0.64) and the Northern Elephant Seal (M = 0.66) (Garza and Williamson 2001),
427 two highly endangered species that have suffered massive population declines. This result
428 strongly suggests a similar, recent population decline in these two coral species. Increasing
429 human pressures on coral reefs in the Bird's Head Seascape, coupled with increasing sea surface
430 temperatures and episodes of coral bleaching, are likely to exacerbate coral decline throughout
431 the region unless strategic conservation action is taken. Marine conservation initiatives in coral
432 reef regions are increasingly focused on designing and implementing effective networks of
433 MPAs (Roberts 2005, Clifton 2009, Horigue et al. 2012, Mangubhai et al. 2012) with the optimal
434 size and spacing of the individual MPAs within a network being a critical aspect of applied MPA
435 research (Shanks 2003, Mills et al. 2010). While difficulties obtaining the large sample sizes

436 needed precluded the use of more quantitative estimates of connectivity, and the presence of
437 cryptic species remains possible, our results unequivocally identify fine-scale genetic structure,
438 which strongly suggests limited genetic connectivity among reef building corals within the
439 Bird's Head Seascape on small spatial scales. This is especially clear in the clustering of *S.*
440 *hystrix* individuals by location and the genetical bandwidth maps of both species showing
441 genetic discontinuities within Raja Ampat and within Teluk Cenderawasih. As genetic
442 connectivity requires far fewer dispersing individuals than does demographic connectivity, the
443 strong genetic differentiation in both of these coral species indicates demographic independence
444 of these populations throughout the Bird's Head Seascape (Hedgecock et al. 2007).

445
446 While methods exist to infer connectivity through genetic assignment tests (e.g. BayesAss+),
447 robust results generally require larger sample sizes than were logistically and biologically
448 possible in our study. While our results cannot provide strong inferences of connectivity, our
449 analyses do show strong evidence for the absence of connectivity. As the number of samples and
450 loci required to detect genetic structure is inversely proportional to the strength of population
451 subdivision (Hillis et al. 1996), the observation of strong genetic structure, even with sample
452 sizes between 10 and 20 individuals, demonstrates that populations of these coral species are
453 strongly isolated across the Bird's Head Seascape. As such, designating a small number of large,
454 widely-spaced "anchor" MPAs in the hopes that they will serve as larval sources, seeding
455 adjacent unprotected areas, would be an ineffective strategy to protect these coral populations. A
456 more effective strategy to maintain biodiversity and connectivity in the Bird's Head Seascape is
457 one that is currently being implemented: a network of numerous, relatively closely-spaced MPAs
458 over a broad geographic area. This strategy is designed to provide protection of local reefs as

459 well as support regional genetic connectivity across the entire Bird's Head Seascape. In fact, the
460 preliminary results of the present study were directly incorporated into the Bird's Head Seascape
461 MPA network design process, which included an objective to limit the spacing between MPAs to
462 25-100 km (Huffard et al. 2012b). The network of seven MPAs in the Raja Ampat region is a
463 good example of this approach, with an average MPA size of 160,000 ha and spacing between
464 nearest MPAs averaging less than 60 km. However, further research is advisable to determine
465 whether the number and spacing of these reserves is sufficient, and how many coral reef taxa
466 will benefit from this arrangement. Similarly, Teluk Cenderawasih would also benefit from a
467 network of numerous closely spaced reserves. The Taman Nasional Teluk Cenderawasih covers
468 a large area, nearly 1.5 million hectares, but only includes the western half of the bay. Due to the
469 genetic differentiation of most local populations, it would be advisable to also designate
470 additional MPAs in the eastern half of the bay and to the northeast of the bay, in the vicinity of
471 Adoki and Owi, both to protect local diversity as well as facilitate regional connectivity.
472 Fortunately, the Indonesian Ministry of Marine Affairs and Fisheries and the local Biak
473 government recently gazetted the Padaido Islands Marine Tourism Park in this northeast
474 quadrant of Cendrawasih Bay, and additional MPAs are now being considered.

475
476 Genetic diversity has been historically overlooked in international conservation policy
477 implementation (Laikre 2010). This is also true at the subnational level, where genetic data are
478 very rarely incorporated in conservation planning. However, ours is case where genetic data can
479 and do directly inform conservation action. For example, in addition to arranging MPAs to
480 maintain connectivity, we recommended that the Bird's Head Seascape MPA network should
481 also serve to protect representative populations from each genetically unique cluster, thereby

482 conserving the maximum degree of coral genetic diversity. Our data from *S. hystrix*, where all
483 but two of the sample localities (Kri Island and Alyui) represent distinct genetic clusters, argued
484 for the inclusion of each of these localities within MPAs to maintain this unique genetic diversity
485 into the future. Now, 9 of the 13 localities sampled in this study are indeed included in MPAs
486 within the BHS network (Mangubhai et al. 2012). In the case of *P. damicornis*, 3 sites
487 (Mauwara, Lemon and Alyui) represent unique genetic clusters that should be prioritized for
488 inclusion in MPAs; in this case, Mauwara is now included in the Kaimana MPA, Alyui is largely
489 protected by a pearl-farming concession and is bordered by the 155,000 ha Kawe MPA, and
490 Lemon is currently under consideration for inclusion as a new MPA. As coral reefs face the
491 coming onslaught of increased coral bleaching (Oliver et al. 2009) and ocean acidification
492 (Pandolfi et al. 2011), it is imperative to maximize protection of genetic diversity to preserve the
493 ability of local populations to adapt to changing environmental conditions.

494
495 Funding limitations in combination with political and socioeconomic realities that motivate
496 unsustainable natural resource use only increase the need for sound science on which to base
497 conservation strategies. Genetic investigations like this provide a disproportionately large
498 amount of data relative to time spent in the field, and the results can help fill some of the most
499 critical scientific gaps in MPA planning (Sale et al. 2005). Although not all reefs can be assessed
500 in a scientifically rigorous manner, insights into the patterns and processes of biological diversity
501 can be used to design effective management schemes that can be put to use in an effective time
502 frame. In our case, the means to apply genetic data to conservation action already exist in
503 ongoing, multi-institutional partnerships in the Bird's Head Seascape (Green and Mous 2004,
504 Huffard et al. 2012b, Mangubhai et al. 2012). Examination of additional taxa in a similar fashion

505 to those presented here (Carpenter et al. 2011, Barber et al. 2011), including economically
506 important species, will provide a wide range of results that resource managers may utilize in
507 refining the optimum MPA network for the Bird's Head Seascape and should serve as an
508 important example for ongoing efforts to design further MPA networks within the Coral Triangle
509 and elsewhere.

510

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512

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522

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852

853 **Table 1:** Sampling locations in Papua and West Papua, Indonesia
 854

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

855

856 **Table 2:** Population statistics for *Pocillopora damicornis*: Give are the number of samples (N),
857 number of unique genotypes (Ng), *M* value (M), its variance (M var), and BAPS cluster.
858

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

859

860 **Table 3:** Population statistics for *Seriatopora hystrix*: Give are the number of samples (N),
861 number of unique genotypes (Ng), *M* value (M), its variance (M var), and BAPS cluster.
862

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

863

864 **Table 4:** Results from AMOVA for *Pocillopora damicornis*. Four genetic structures are tested.
 865 “All samples” indicates that there was no hierarchical structure imposed. '3 regions' tests the
 866 significance of a priori geographic structure among Teluk Cenderawasih, Raja Ampat, and
 867 Fakfak/Kaimana. Finally, the structures inferred by BAPS and Genetical Bandwidth Mapping
 868 (GBM) are tested. Estimators are calculated based on both the infinite alleles model (*F* statistics)
 869 and stepwise mutation model (*R* statistics) of microsatellite evolution. Negative values are
 870 presented, but are effectively equal to zero.
 871

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

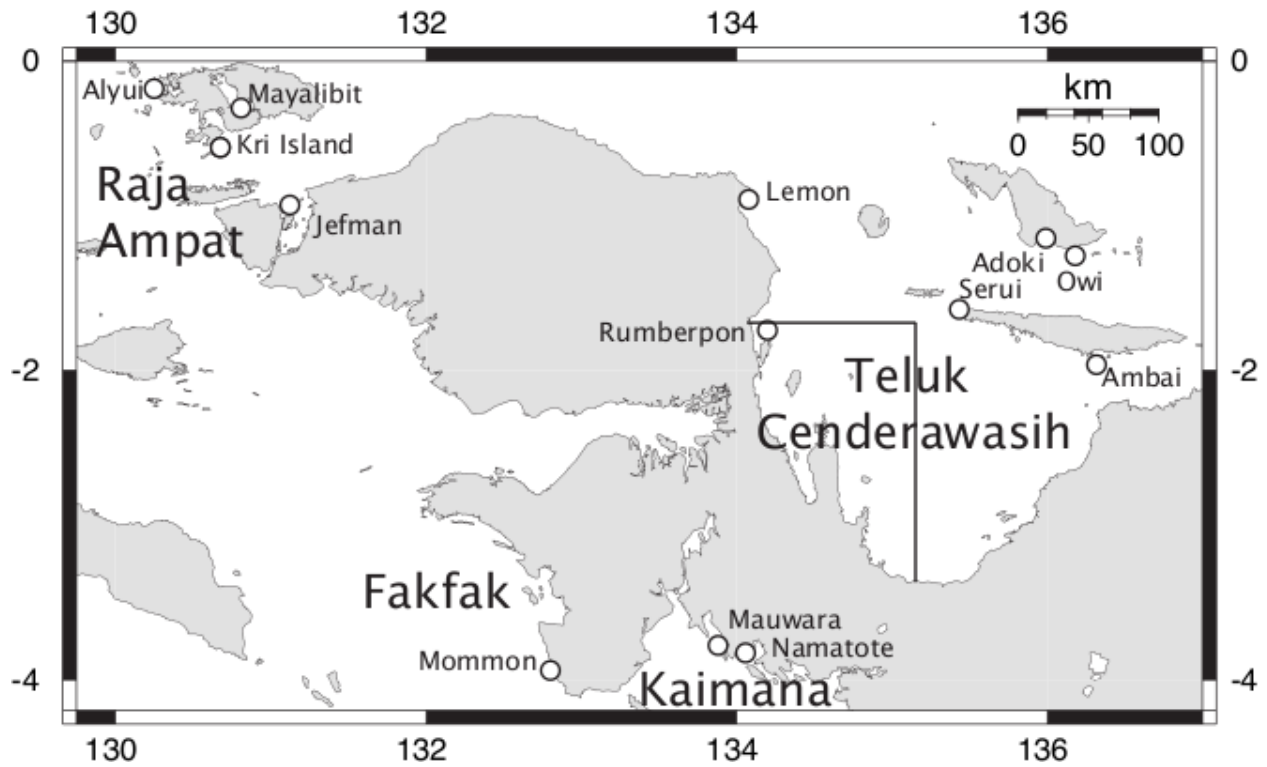
872

873 **Table 5:** Results from AMOVA for *Seriatopora hystrix*. Four genetic structures are tested. “All
 874 samples” indicates that there was no hierarchical structure imposed. '3 regions' tests the
 875 significance of a priori geographic structure among Teluk Cenderawasih, Raja Ampat, and
 876 Fakfak/Kaimana. Finally, the structures inferred by BAPS and Genetical Bandwidth Mapping
 877 (GBM) are tested. Estimators are calculated based on both the infinite alleles model (*F* statistics)
 878 and stepwise mutation model (*R* statistics) of microsatellite evolution. Negative values are
 879 presented, but are effectively equal to zero.
 880

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

881

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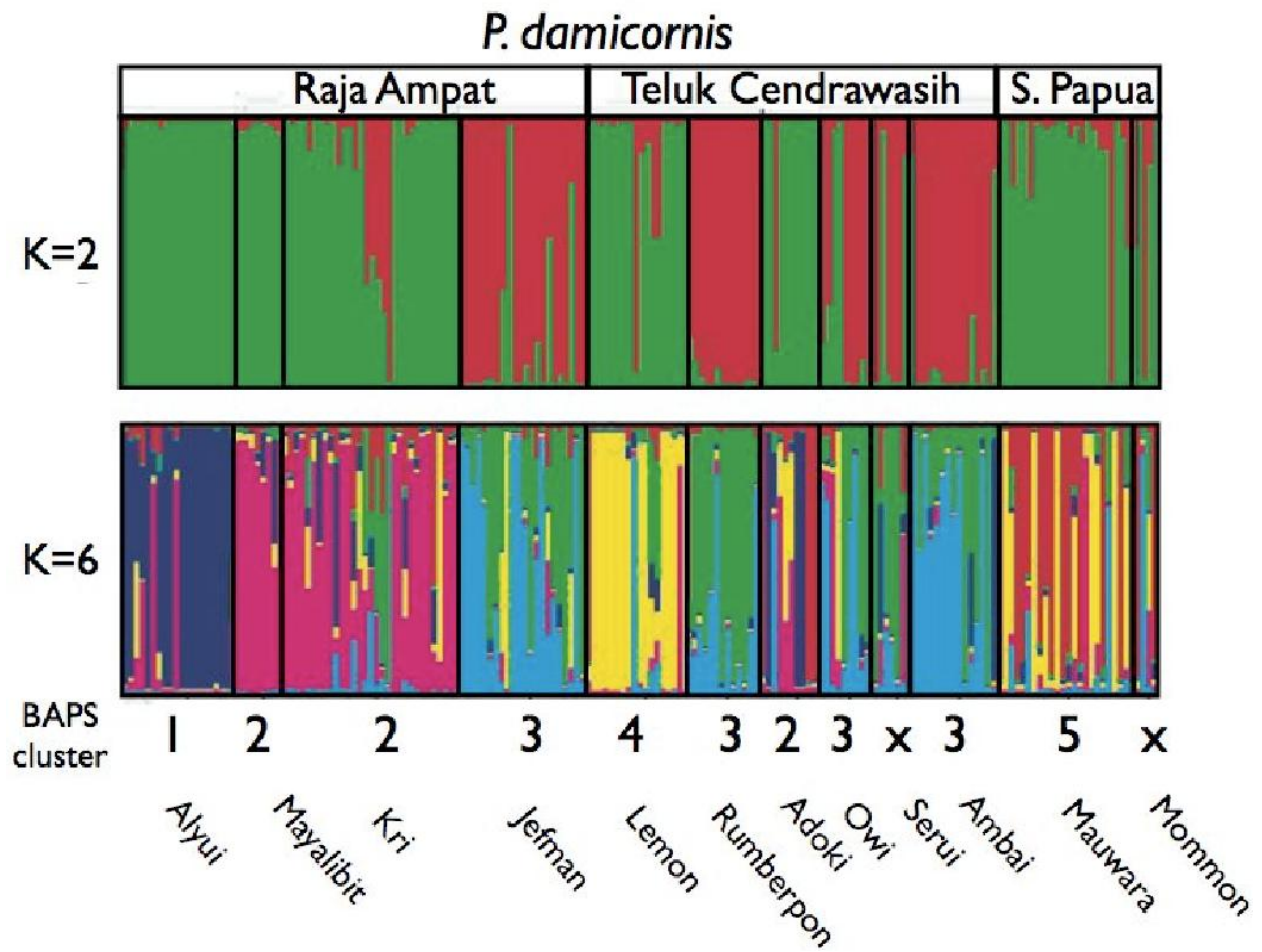


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887 **Figure 2:** Results from Bayesian assignment methods implemented in Structure and BAPS for
 888 *Pocillopora damicornis*. X indicates exclusion from BAPS analysis due to $N_g = 6$ or less. $K = 2$
 889 and $K = 6$ were used as heuristics as described in the text.

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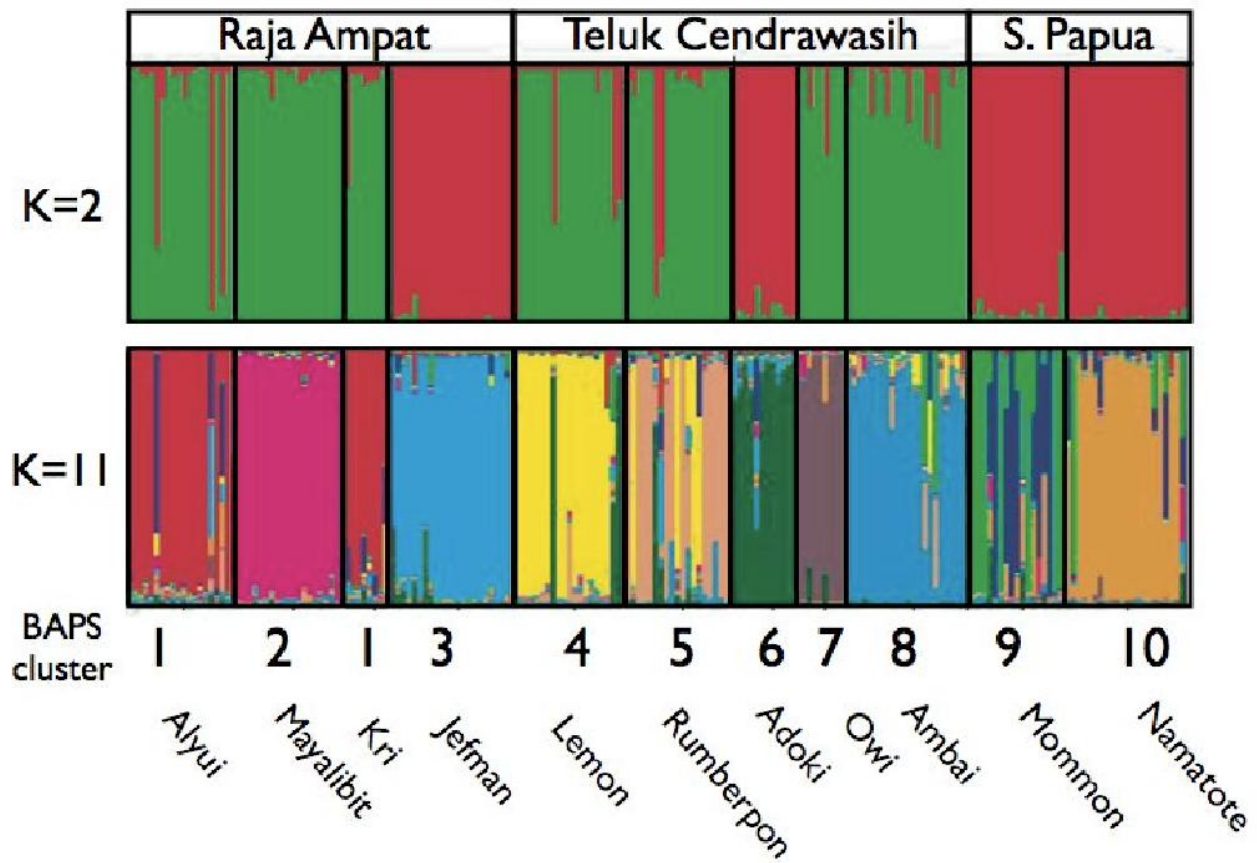
891

892 **Figure 3:** Results from Bayesian assignment methods implemented in Structure and BAPS for
893 *Seriatopora hystrix*. K = 2 and K = 11 were used as heuristics as described in the text.

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S. hystrix

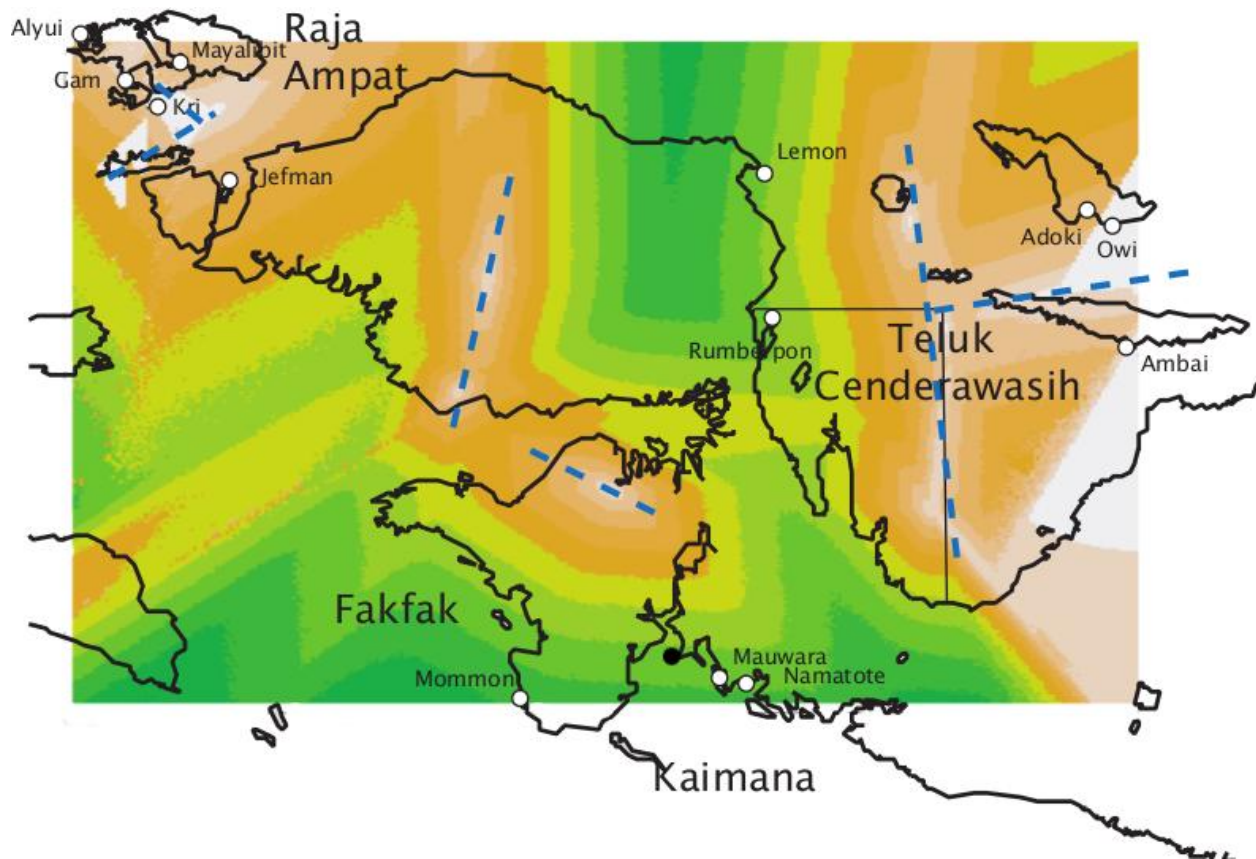


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898 **Figure 4:** Genetical Bandwidth Map for *Pocillopora damicornis*. Green areas indicate regions of
899 genetic homogeneity. White areas indicate putative barriers to larval dispersal and are
900 highlighted with blue dashed lines. The solid black line indicates the borders of Taman Nasional
901 Teluk Cenderawasih.

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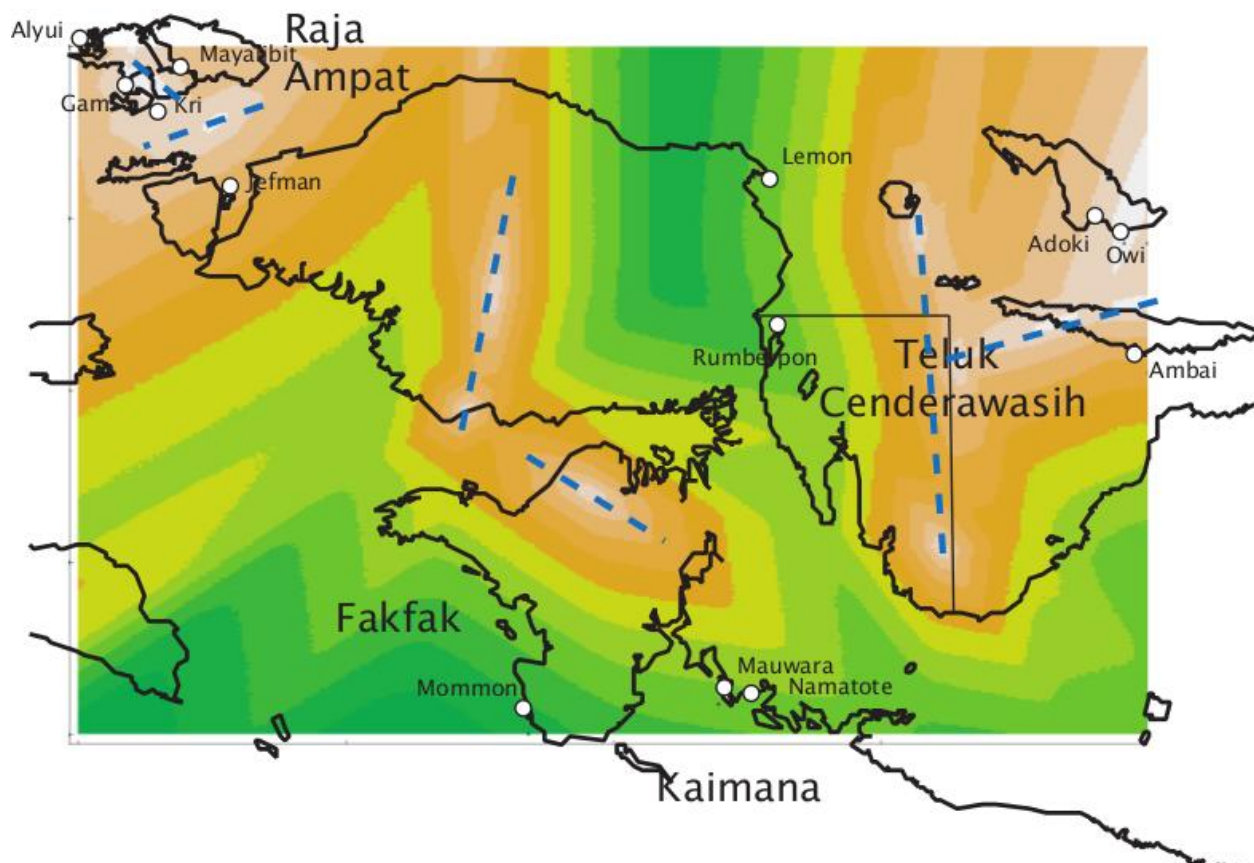


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905

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

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