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1   BIOLOGICAL SCIENCES: Ecology

2   **A connectivity portfolio effect stabilizes marine reserve performance**

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16

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19

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21   GPJ designed the field studies and collected samples; HBH, MB and MLB assembled and

22   analyzed the data; HBH wrote the original draft and all authors contributed to reviewing and

23   editing.

24

25   **This PDF file includes**

26   Main Text
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30   **Abstract**

31   **Well-managed and enforced no-take marine reserves generate important larval subsidies**

32   **to neighboring habitats and thereby contribute to the long-term sustainability of fisheries.**

33   **However, larval dispersal patterns are variable, which leads to temporal fluctuations in**

34   **the contribution of a single reserve to the replenishment of local populations. Identifying**

35   **management strategies that mitigate the uncertainty in larval supply will help ensure the**

36   **stability of recruitment dynamics and minimize the volatility in fishery catches. Here, we**

37   **use genetic parentage analysis to show extreme variability in both the dispersal patterns**

38   **and recruitment contribution of four individual marine reserves across six discrete**

39   **recruitment cohorts for coral grouper (*Plectropomus maculatus*) on the Great Barrier Reef.**

40   **Together though, the asynchronous contributions from multiple reserves create temporal**

41   **stability in recruitment via a connectivity portfolio effect. This dampening effect reduces**

42   **the variability in larval supply from individual reserves by a factor of 1.8, which effectively**

43   **halves the uncertainty in the recruitment contribution of individual reserves. Thus, not**

44   **only does the network of four marine reserves generate valuable larval subsidies to**

45   **neighboring habitats, the aggregate effect of individual reserves mitigates temporal**

46   **fluctuations in dispersal patterns and the replenishment of local populations. Our results**

47   **indicate that small networks of marine reserves yield previously unrecognized stabilizing**

48   **benefits that ensure a consistent larval supply to replenish exploited fish stocks.**

49

50   **Significance Statement**

51   Networks of no-take marine reserves support local fisheries by ensuring a consistent supply

52   of juvenile fish. We measured larval dispersal patterns for a highly exploited coral grouper

53   and quantified temporal fluctuations in the recruitment contribution from a network of no-

54   take marine reserves on the Great Barrier Reef. Although recruitment contributions from

55   individual reserves are extremely variable, the reserve network generates a connectivity

56   portfolio effect that successfully dampens the volatility of larval supply to nearby coral

57   reefs. Our findings demonstrate that effective reserve networks can yield previously

58   unrecognized stabilizing benefits that ensure a consistent replenishment of exploited fish

59   stocks.

60

61   **Main Text**

62   **Introduction**

63   Marine reserves are a comprehensive tool to mitigate the over-exploitation of marine

64   resources and to enhance the recovery of marine ecosystems following disturbances (1-3).

65   They are being implemented globally to preserve biodiversity (4, 5), improve livelihoods in

66   coastal communities (6), and indirectly benefit local fisheries by protecting spawning stocks

67   and replenishing exploited populations beyond reserve boundaries (7). In principle, the

68   greater biomass of exploited species in reserves (8, 9), combined with greater per-capita

69   reproductive outputs (10, 11), generates positive ecological and socio-economic value to

70   fisheries by contributing to the replenishment of local populations and enhancing

71   population persistence via the supply of larval offspring (12-15). However, larval

72   contributions from individual reserves are likely to be highly variable (16, 17), both because

73   local population abundances vary and because complex oceanographic processes and larval

74   behaviors produce spatial and temporal variability in connectivity patterns (16-19). Such

75   volatility in larval supply can lead to temporal fluctuations in recruitment (20, 21) and

76   uncertainty concerning the value of marine reserves to either biodiversity conservation or

77   fisheries management (20, 22-24). Clearly, the long-term ecological and economic benefits

78   of no-take marine reserves depend on significant and consistent larval supply among

79   reserves, and from reserves to neighboring habitats (7, 22-24). This has yet to be

80   established.

81

82   Decades of ecological theory on risk-spreading in spatially structured populations shows

83   how variability in the contribution of separate sub-populations can deliver net benefits for

84   metapopulation growth and persistence (25-28). In general, more subpopulations and

85   greater population connectivity reduce the probability of local extinctions via a "rescue

86   effect", and dampen local fluctuations in population replenishment (29-32) and fishery

87   catches (33, 34). If correct, effective networks of no-take marine reserves could mitigate

88   against the volatility of larval supply provided the network can dampen the spatially and

89   temporally variable contributions of individual reserves (20, 21). In the context of optimal

90   reserve design, variability in the aggregate performance of a reserve network hinges on

91   covariation among its individual components (34, 35) so that overall stability in larval supply

92   can theoretically be achieved despite volatility in the performance of individual reserves.

93

94   Such variance dampening has more recently been referred to as a *portfolio effect,* and

95   negative spatial covariation in population sizes (a *subpopulation portfolio effect*) has been

96   observed in a diversity of biological systems, including the population dynamics of fishes

97   (36-38). Modern portfolio theory emerged from financial economics and is increasingly

98   applied in resource management settings to optimize the design of reserve networks and

99   mitigate against disturbance events (39-42). In marine ecology, individual populations can

100   be thought of as different financial stocks and their larval supply are the returns they

101 generate. Creating a marine reserve will reliably increase the abundance in a protected

102 population and generate larger larval supply (43), like purchasing more of a particular stock.

103 Just as a diverse portfolio of uncorrelated financial assets minimizes an investor's exposure

104 to stock market volatility (44), replication of reserves in an interconnected network could

105 mitigate against fluctuations in larval supply and minimize the risk of recruitment failure.

106 However, to date there has been no empirical estimation of the portfolio effect for any

107 existing network of reserves. This knowledge gap is significant given the large and rapidly

108 increasing global investment in interconnected networks of marine reserves, the success of

109 which hinges on the assumption that networks have emergent benefits that are greater

110 than the sum of the constituent reserves.

111

112 For any established marine reserve network, a portfolio effect for a protected species can

113 be measured by observing temporal fluctuations in the recruitment contribution of multiple

114 reserves, over multiple recruitment cohorts. Here we evaluate variability in the aggregate

115 performance of no-take marine reserves in the Great Barrier Reef Marine Park (GBRMP),

116 using a unique dataset of six discrete recruitment cohorts of juvenile coral grouper

117 (*Plectropomus maculatus*, Serranidae), spanning 6 years. We use genetic parentage analysis

118 on a sample of adult fish from four no-take marine reserves and juvenile fish that recruited

119 to nearby coral reefs to reveal temporal trends in larval connectivity patterns. These results

120 allow us to measure fluctuations in the performance of individual reserves, and reveal the

121 existence of a *connectivity portfolio effect*; a reduction in the volatility of larval recruitment

122 that results from asynchronous variation in larval connectivity patterns.

123

124   In the GBRMP, coral grouper (*Plectropomus* spp.) are highly targeted by commercial and

125   recreational fishers, and have responded positively to protection inside no-take marine

126   reserves (1). In the Keppel Islands, the biomass of coral grouper is 2-3 times higher on no-

127   take reserve reefs than on neighboring fished reefs (45), hence we expect their contribution

128   to local larval replenishment to be high relative to fished reefs (11). We collected tissue

129   samples of adult coral grouper from four reserves in the Keppel Islands (Fig. 1A) during the

130   peak reproductive season in the austral summers of 2007-08 and 2011-12 (*Methods*). Our

131   sample of 877 adults represents 19.2% $\pm$ 3.0% SE and 22.5% $\pm$ 4.7% SE of the reproductively

132   mature population of coral grouper in reserves during the sampling periods (*SI Appendix,*

133   Table S1). We also collected 981 juveniles from reserve and fished reefs throughout the

134   island group. Six discrete recruitment cohorts were identified based on interruptions

135   between periods of unimodal distributions of spawning times of juvenile fish (Fig. 1B, *SI*

136   *Appendix*), providing information on recruitment and dispersal patterns at an unusually high

137   temporal resolution.

138

139

140   **Results**

141   Based on the unique genetic profiles of adult and juvenile coral trout collected in the Keppel

142   Islands, we identified 125 juvenile fish as the progeny of adults sampled within the four

143   reserves (*Methods*). Assigned juvenile fish were distributed among six recruitment cohorts

144   that represent an exhaustive sample of all juvenile fish that settled in the island group (Fig.

145   1C, *SI Appendix,* Table S2). In each cohort we identified juvenile fish that dispersed from no-

146   take marine reserves to both fished areas (85 juveniles) and other reserves (40 juveniles).

147   However, dispersal patterns varied substantially among recruitment cohorts, showing no

148   consistent trend or single underlying structure among dispersal networks (Fig. 1D, average

149   Pearson correlation: 0.43 $\pm$ 0.03 SE). The distance, direction and strength of larval

150   connections from each of the four reserves (*SI Appendix,* Figs. S2-S3) were inconsistent

151   among successive cohorts, indicating highly variable connectivity patterns among reserve

152   reefs and neighboring reefs.

153

154   Adjusting for unsampled adults, we estimate the performance of each reserve as their

155   proportional contribution to the overall recruitment in the island group (*Methods*). The

156   results show that the aggregate network of four no-take marine reserves consistently

157   generates between 26% and 58% of all local recruitment for any given cohort (Fig. 2A). On

158   average, the aggregate performance of the reserve network, which represents only 14% of

159   coral reef habitat, is responsible for 41% $\pm$ 11% SD of all recruitment in the island group. Our

160   findings reinforce the importance of reserves as a source of juvenile fish for local population

161   replenishment. However, they also reveal substantial fluctuations and uncertainty in the

162   performance of individual reserves. The median contribution of a single reserve to local

163   recruitment varied between 5% and 15% with a coefficient of variation (CV) of 0.71 (Fig. 2B),

164   meaning that the degree of variation between reserves and between cohorts is extremely

165   high. Incidentally, the time series also reveals asynchronous fluctuations in the local

166   recruitment contribution of the four reserves across the six cohorts (synchrony index: 0.25,

167   where 0 is maximally asynchronous and 1 is maximally synchronous (46), Fig. 2A). So, while

168   the performance of a single reserve varies with each cohort, it varies independently of other

169   reserves in the network. This weak covariation in the performance of individual reserves

170   dampens the temporal variance in the recruitment contribution of the aggregate network of

171   marine reserves (CV = 0.26).

172

173   The high variance in the performance individual reserves and the negative covariance within

174   the aggregate network generates a substantial portfolio effect that reduces the overall

175   volatility in the larval contributions of the reserve network. If we measure the mean and

176   variance in the local recruitment contribution of reserves across all six cohorts, we see that

177   reserves with greater average contribution to local recruitment also have greater variance

178   among discrete cohorts (Fig. 3A, *Methods*). Such mean-variance scaling relationships are

179   common in ecological systems and typically follow a power-law with an exponent z lower

180   than 2. A portfolio effect indicates the temporal variance of the aggregate components is

181   less than predicted based on its average performance over time. Here, the observed

182   variance in the aggregate network of reserves in the Keppel Islands is 1.8 (95% CI 1.2 – 2.4)

183   times less than predicted based on the mean-variance relationship of individual reserves

184   (Fig. 3A). This indicates that the combined performance of the four reserves exhibits a

185   substantial portfolio effect to minimize volatility in the recruitment contribution of

186   individual reserves.

187

188   We can extend these findings by using the observed variation in the performance of marine

189   reserves in the Keppel Islands to estimate the shape and strength of the connectivity

190   portfolio effect with increasing number of marine reserves. From the recruitment

191   contribution of reserves in the Keppel Islands, we estimate that the volatility in the local

192   recruitment contribution of a single marine reserve would be on average 0.66 ± 0.16 SD

193   (Fig. 3B). This indicates that the supply of juvenile fish from a single reserve can fluctuate

194   widely between recruitment cohorts. By bootstrap resampling from the set of reserves, we

195   predict that volatility will fall rapidly with every additional reserve in the network (Fig. 3B),

196 so that it is halved with only four reserves (0.34 ± 0.08 SD). Therefore, by dampening the

197 volatility of their aggregate contribution to recruitment, networks of marine reserves

198 increase temporal stability in the replenishment of local populations.

199

200 **Discussion**

201 Consistent with previous findings (12, 13), our results reveal no-take marine reserves

202 generate considerable larval subsidies to neighboring habitats and are responsible for

203 generating a disproportionally large proportion of local recruitment. However, our unique

204 temporal dataset also reveals high spatial and temporal variability in connectivity patterns

205 with extreme fluctuations in the recruitment contribution of individual reserves through

206 time. Furthermore, scale dependency in the performance of marine reserves indicates that

207 large mean contributions to local recruitment are also associated with larger fluctuations in

208 their performance. While individual no-take marine reserves clearly enhance long-term

209 recruitment in the island group, the benefits of a single reserve are spatially and temporally

210 unpredictable.

211

212 Despite the volatility in larval dispersal patterns, asynchrony in the larval supply from

213 reserves promotes the temporal stability of local recruitment patterns in the Keppel Islands.

214 The presence of a portfolio effect from the aggregate performance of the network of

215 reserves effectively dampens temporal fluctuations in larval supply to yield previously

216 unrecognized stabilizing benefits that ensure a consistent source of local recruitment. In

217 doing so, networks of no-take marine reserves minimize the risk of recruitment failure to

218 local fisheries and promote positive ecological and socio-economic values beyond the

219 simple increase in fish biomass and larval subsidies (6, 7, 22-24).

220

221 Portfolio effects are common to a variety of ecological systems where demographic and

222 environmental processes fluctuate asynchronously or are negatively correlated over time

223 (34). The connectivity portfolio effect is analogous to other ecological portfolio effects in

224 that it is driven by a highly stochastic process: larval dispersal. The successful dispersal and

225 recruitment of marine larvae depend on both behavioral and physical processes (16, 17, 20,

226 21), which creates uncertainty in connectivity patterns between coral reef habitats. We

227 therefore expect to see evidence of the connectivity portfolio effect in all marine

228 populations regulated by larval exchange.

229

230 Our results are based on one of the most intensive and extensive genetic parentage

231 assignment datasets available (47), but positive parentage assignments still only represent a

232 subsample of the recruitment occurring at each location. Although our sampling of juvenile

233 fish was well-distributed among reefs, the presence of uncorrelated sampling noise would

234 augment the strength of the connectivity portfolio effect however, it does not create it. We

235 would strongly expect connectivity patterns to contain the negatively correlated structure

236 that drives portfolio effects. Physical drivers of oceanographic flows contain large stochastic

237 components (16-19), and advective current structures will naturally create negative

238 connectivity correlations in a reef matrix.

239

240 Since the supply of larval offspring is linked to the size and structure of populations (10, 11),

241 we also anticipate the connectivity portfolio effect works in conjunction with subpopulation

242 portfolio effects previously described in marine fishes (34). When fluctuations in population

243 size lead to fluctuations in larval supply, these are likely to accentuate the spatial and

244 temporal variance of recruitment patterns. Networks of no-take marine reserves, which

245 accumulate larger biomass of exploited species (8, 9) and generate substantial larval

246 subsidies, may therefore effectively mitigate local fluctuations in spawning stock biomass,

247 larval supply and rates of population replenishment.

248

249 Our findings demonstrate that effective reserve networks take advantage of a connectivity

250 portfolio effect that mitigates temporal volatility in larval supply to ensure the stability of

251 recruitment dynamics, with potential long-term sustainability benefits for exploited fish

252 stocks. Replication of no-take marine reserves within networks provides an essential hedge

253 against uncertainty in the dynamic processes that sustain fisheries stocks (48, 49) and may

254 moderate the effects of large-scale climatic disturbances (1-3) that are projected to escalate

255 as global warming progresses (39, 40, 42).

256

257

258 **Methods**

259 ***Sample collections and cohort identification.*** This study focuses on the bar-cheek coral

260 grouper (*Plectropomus maculatus,* Serranidae). Like most species of groupers, it is heavily

261 targeted by commercial, recreational, and subsistence fishers throughout the Indo-Pacific

262 region (50). We sampled adult and juvenile coral grouper from fringing coral reefs in the

263 Keppel Islands between September 2007 to April 2013. We sampled adult fish intensively

264 from reefs in four focal no-take marine reserves, and juvenile fish on all protected and

265 fished reefs in the island group, with effort distributed proportionally to the area of each

266 reef (Fig. 1A). We measured the size of each fish and aged juvenile fish from sagittal otolith

267 to determine the age-length relationship for juvenile *P. maculatus* in the Keppel Islands (*Age*

268 = *Total Length* x 1.159 – 4.283, R^2 = 0.81) and estimate the date-of-spawn (*SI Appendix*, Fig.

269 S1). We defined six discrete recruitment cohorts in the data, which we believe correspond

270 to six different adult spawning events (*SI Appendix*, Table S2). A spawning event was defined

271 as a unimodal pulse of reproduction which resulted in the observed dispersal and

272 recruitment patterns.

273 ***UVC surveys and population size estimates.*** We conducted underwater visual census (UVC)

274 of *P. maculatus* populations to quantify their density, biomass and length-frequency

275 distributions on all focal reserve and fished reefs. These UVC surveys were part of a broader

276 long-term reef biodiversity monitoring program that was initiated in the Keppel Island group

277 in 2002 (*see* (45) for a detailed methodology). For the present study, we conducted

278 standard UVC surveys along 50 m by 6 m belt transects on reef slope, crest and flat habitat-

279 strata for nine monitoring sites on focal reserve reefs (Middle island, Clam Bay, Halfway

280 island and Egg Rock) prior to each round of sample collection. To quantify reef habitat areas,

281 we used a combination of high-resolution satellite imagery and stratified habitat surveys

282 (reef slope, crest, flat) to map reef habitats areas within each focal reserve. All spatial

283 analyses were conducted using ArcGIS (ESRI, Redlands, CA). We estimated total population

284 size for each focal reserve, and the proportion of adults sampled, by scaling up length-

285 specific *P. maculatus* density estimates to the total area within each reef habitat strata (*SI*

286 *Appendix,* Table S1) (12, 51).

287 ***Parentage analysis.*** We first extracted genomic DNA from ~2 mm^2 of fin or muscle tissue

288 and screened each individual at 23 microsatellite loci (52)**.** We identified parent-offspring

289 pairs in two periods, with each period composed of three successive cohorts. Period 1

290 included all sampled juvenile fish that recruited to reefs in the Keppel Islands between

291 September 2007 and March 2009 (n = 686) and all sampled adult fish that were mature

292 during the same period (n = 559), including large adults (> 500 mm) captured between

293 September 2011 and April 2013. Period 2 included juveniles that recruited between

294 September 2011 and April 2013 (n = 891) and adults that were mature during that period (n

295 = 454), including individuals captured between September 2007 and March 2009. For each

296 period, we used a maximum likelihood approach implemented in the software program

297 FAMOZ (53, 54) to reveal parent-offspring relationships in our samples.

298 **_Reserve performance._** In the context of this study, the performance of a single no-take

299 marine reserve is measured by its relative contribution to local recruitment across all

300 sampled reefs in the island group in each cohort. Since we sampled only a fraction of all

301 reproductively mature adults in each reserve (_SI Appendix_, Table S2), the observed number

302 of assigned juveniles (Fig. 1D) represents only a fraction of a reserve's contribution to local

303 recruitment. In order to compare the performance of each reserves across different cohort,

304 we estimated the number of juveniles we would have assigned to each reserve had all

305 adults been sampled in the populations. Since we can assign parentage to fathers, mothers

306 or both, the relationship between the number assignments and the proportion of parents

307 sampled is non-linear (12). The expected recruitment contribution (_R_) accounts for the

308 number of assigned juveniles given the proportion of adults sampled from reserve _i_ so that:

309
$$R(i) = n \times \frac{1}{1 - (1 - P)^2}$$

310 where _n_ represents the number of assigned juveniles and _P_ is the proportion of sampled

311 adults in the focal reef or reefs. We assume that all adult _P. maculatus_ within each reserve

312 boundary have an equal probability of contributing to local recruitment and that our sample

313 of juveniles represents a random sample of recruitment in the study area for each cohort. We

314   then estimate the percent contribution to local recruitment contribution of reserves by

315   standardising for the number juveniles sampled in each cohort.

316   ***Measuring the mean-variance corrected portfolio effect.*** We correct our estimates of the

317   portfolio effect by accounting for the natural scale-dependence of population processes. In

318   financial systems, the variance in returns scales linearly with the mean return (since every

319   stock yields the same dividend). In ecological systems by contrast, larger populations exhibit

320   lower variability than we would expect from proportional scaling. Such mean-variance scaling

321   is common across ecological systems and predicts that the temporal variance of individual

322   components (σ^2) increases with the mean value (μ) according to a power-law relationship

323   with exponent $z < 2$ (38, 55). Using the mean-variance exponent fit to the sampled reserves

324   ($z = 1.87$), we predict the average recruitment contribution and variance of a single reserve

325   with a mean output equal to the sum of the mean outputs of the four individual reserves. We

326   compare the predicted coefficient of variation of this hypothetical single reserve $CV_{Total} =$

327   0.459 to the observed coefficient of variation of the contributions made by the portfolio of

328   four reserves $CV_{Portfolio} = 0.256$, to calculate the strength of the connectivity portfolio

329   effect. We analysed the sensitivity of our results to the definition of cohorts, and found that

330   the results were almost identical.

331   A bootstrap resampling protocol estimates the volatility in the recruitment contribution of an

332   arbitrary number of reserves. First, we create a set of n reserves by randomly resampling

333   (with replacement) from the observed recruitment contribution timeseries of the reserves in

334   the Keppel Islands ($1 \leq n \leq 20$). We repeat this procedure 100 times for each value of n to

335   estimate the mean and standard deviation of the CV. This method assumes that recruitment

336 timeseries from additional reserves would have similar correlation structure to those

337 observed in the Keppel Islands.

338 **Data and code availability.** All R scripts for the calculation of the CPE as well as the data

339 presented in this manuscript are available in the online supplementary information.

340

341 **Acknowledgments**

351

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478   **Figure legends**

479

480   **Figure 1. Realized larval dispersal patterns of coral grouper from a network of no-take**

481   **marine reserves.** (**A**) The Keppel Islands in the southern Great Barrier Reef, where adult

482   coral grouper (*Plectropomus maculatus*) were sampled in four no-take marine reserves

483   (Middle Island, Halfway Island, Clam Bay and Egg Rock). Juveniles were sampled from all

484   known suitable coral reef habitat throughout the island group. Focal reefs are highlighted by

485   colored dots, consistent across panels. (**B**) We used daily otolith increments and length-age

486   relationships (*SI Appendix*, Fig. S1) to identify six distinct spawning periods and settlement

487   cohorts (C1 – C6) between September 2007 and April 2013 among the 981 sampled juvenile

488   fish. (**C**) Parentage analysis identified 125 parent-offspring pairs spanning all six cohorts. (**D**)

489   All assignments were to parents sampled from four no-take marine reserves. For each

490   dispersal network, colored circles (network nodes) represent reserves and grey circles

491   correspond to other reefs in the Keppel Islands. Lines (network edges) represent juvenile

492 fish that successfully dispersed from reserves to neighboring reefs, where line thickness

493 indicates the number assigned juveniles and line color indicates their origin.

494

495 **Figure 2. Variable and asynchronous performance of no-take marine reserves.** (**A**) Our

496 time series of larval dispersal patterns indicate temporal fluctuations in the contribution of

497 no-take marine reserves to local recruitment in the Keppel Islands (colored lines). However,

498 when combined (grey bars) the four reserves generate between 26% and 58% of all local

499 recruitment for any given cohort (C1-C6). (**B**)**.** Boxplots of the relative performance of each

500 reserve indicate they contribute unevenly to local recruitment. The median contribution of

501 individual reserves ranges from 5% to 15% and reveals an extremely high degree of variance

502 in their performance through time. Collectively, the median contribution of the aggregate

503 reserve network is higher and less variable.

504

505 **Figure 3. The connectivity portfolio effect (CPE) reduces volatility in reserve performance.**

506 (**A**) We calculate the CPE from the temporal mean (μ) and variance (σ^2) of each reserve's

507 contribution to local recruitment of coral grouper on log-log axes and extrapolate the mean-

508 variance relationships (z) to the aggregate mean contribution of the reserve network across

509 the six discrete cohorts in the Keppel Islands. The difference between the predicted (circle)

510 and observed variability (diamond) represents the strength of the connectivity portfolio

511 effect. (**B**) Based on the measured performance of reserves in the Keppel Islands for each

512 cohort (Fig. 2B), we estimate the coefficient of variation (CV) in the aggregate recruitment

513 contribution of reserves in a network. We use a bootstrap resampling procedure to estimate

514 the mean and standard deviation of CV, which reflects the volatility in reserve performance

515 (*Methods*).

516