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Supplementary Information for

A connectivity portfolio effect stabilizes marine reserve performance

Hugo B. Harrison, Michael Bode, David H. Williamson,
Michael L. Berumen, Geoffrey P. Jones.

Correspondence to: hugo.harrison@jcu.edu.au

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Materials and Methods

Study species. This study focuses on the bar-cheek coral grouper (*Plectropomus maculatus*, Serranidae). *Plectropomus maculatus* are protogynous hermaphrodites (change sex from female to male) with females reaching maturity at approximately 30 cm total length (TL) and 2 – 3 years of age (1, 2). The mean size and age of sex change is 35 – 40 cm TL and 4 years, but is highly variable and may be influenced by multiple factors including population density, size structure and fishing intensity (1). *Plectropomus maculatus* can live for at least 16 years, reach 125 cm in length and exceed 20 kg in weight (3). Like many other grouper species, *P. maculatus* can form large spawning aggregations at predictable locations and times, while small group spawning has also been documented (4). No known spawning aggregation sites are present in the Keppel Islands although courtship and small group spawning has been observed.

Coral groupers are prized table fish, targeted by commercial, recreational, and subsistence fishers throughout the Indo-Pacific region. As a consequence, they have been depleted through overfishing throughout much of their ranges (5). *Plectropomus maculatus* are abundant on inshore coral reefs of the Great Barrier Reef Marine Park (GBRMP) and are targeted by both commercial and recreational fisheries. The fishery catch of coral grouper in the GBRMP is managed with a range of controls including a minimum legal-size limit of 38 cm TL, limited-entry licensing, a total allowable commercial catch with individual transferable quotas, and possession limits for recreational fishers (6). Since 2013-14, the total annual harvest of all coral grouper in Queensland waters has averaged 983 metric tons, of which 82% is commercial harvest and 18% is recreational (6). The vast majority of the Queensland catch is sourced from coral reefs within the GBRMP, and most commercially harvested coral grouper are exported live to Asian markets (6).

Sample collections. We sampled adult and juvenile coral grouper from fringing coral reefs in the Keppel Islands between September 2007 to April 2013. Adult fish were intensively sampled from reefs in four focal no-take marine reserves, and juvenile fish were sampled on all NTMR and fished reefs in the island group, with effort distributed proportionally to the area of each reef. Adult fish were sampled using either hook-and-line or modified tissue

biopsy probes (PneuDart, USA). Fish captured using hook-and-line were visually identified, measured for total length, externally tagged with a single T-bar anchor tag (Hallprint, Australia), fin-clipped for a tissue (DNA) sample, and then returned to the water. Biopsy probes were mounted on spear guns and divers using SCUBA or snorkel undertook sampling. All fish sampled with biopsy probes were identified to species and their total length estimated to the nearest 5 cm category. At the time of collection, adults ranged from 290 mm to 780 mm (mean: 495 mm \pm 104 mm standard deviation). Juvenile fish were collected by divers using low-caliber spear guns, hand spears, clove oil and small fence nets. Sampling effort was distributed equally amongst reefs and continued until a point where we could no longer find juvenile fish on the reef. All collected juveniles were measured for total length and their sagittal otoliths removed for age determination. At the time of collection, juveniles ranged from 22 mm to 329 mm in total length (mean: 145 mm \pm 65 mm standard deviation). All tissue samples were preserved in 95% ethanol. Collections were undertaken under Marine Parks Permit numbers G06/17981.1 and G11/33554.2, Queensland General Fisheries Permit numbers 87381 and 148534 and James Cook University animal ethics permits A1001 and A1625.

Table S1. Estimated population size, and sample size, of adult *Plectropomus maculatus* in four reserves in the Keppel islands (population size / sample size).

Period	Clam Bay	Egg Rock	Halfway Is	Middle Is
2007-09	1262 / 200	599 / 165	1027 / 154	748 / 132
2011-12	2127 / 257	599 / 185	1201 / 208	539 / 163
Reef area (ha)	48.2	4.1	11.2	36.4

Length-age relationship. Sagittal otoliths were removed from a sub-sample of 312 juvenile *P. maculatus* (length range 23 – 246 mm TL) collected from Keppel Islands reefs between April 2008 and June 2012. One of each pair of otoliths was sectioned and mounted onto glass slides; daily growth rings were counted to determine the age-length relationship for juvenile *P. maculatus* in the Keppel Islands ($Age = Total\ Length \times 1.159 - 4.283$, $R^2 = 0.81$) (Fig. S1). The spawn date of each sampled individual was thereby back-calculated from their

total length and the date of collection. The estimated ages of sampled juveniles ranged from 16 days to 314 days. All cohorts were defined by the distribution of back-calculated spawning dates of juvenile fish caught in the Keppel Islands (Table S2). While the cohorts differ in their durations, each reflects a single prior spawning event and are separated by periods of no spawning. C4 and C5 could possibly overlap, but also have clear modes, and are separated by a period of low spawning. Inconsistencies in the size (i.e., numbers of recruits) and timing of cohorts are expected and point to the variability in dispersal and recruitment patterns discussed here. All cohorts were sampled within each period and irrespective of their size or their timespan they represent a clearly defined population process. C6 followed a major flooding event from the Fitzroy River in January 2013. The freshwater plume impacted on shallow water coral reef habitats in the Keppel Islands, an important recruitment habitat for coral trout. It was clear during the sampling of C6 that recruitment had been poor. We analysed the sensitivity of our results to the definition of cohorts, and found that the results were almost identical.

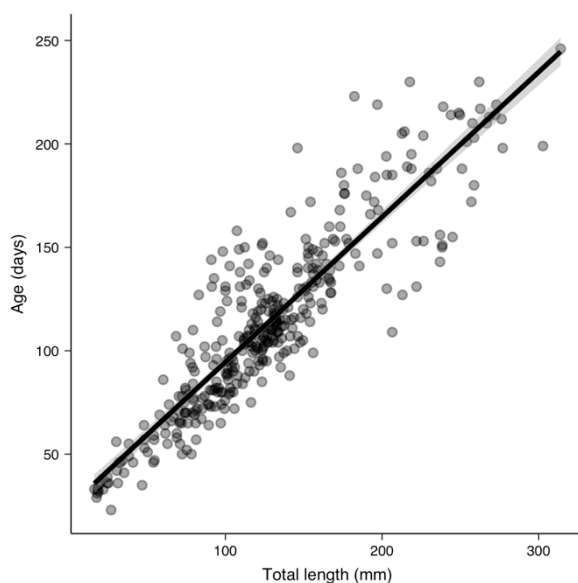


Fig. S1. Age-Length relationship of 312 juvenile *Plectropomus maculatus* sampled from reefs in the Keppel Islands between April 2008 and June 2012. Daily growth rings were examined to determine the age (in days) of juvenile fish from the date of hatch. Individual ages are plotted against the total length of each fish; shading indicates overlapping points. (*Estimated age = Total Length* \times 1.159 – 4.283, $R^2 = 0.81$)

Table S2. Juvenile *Plectropomus maculatus* assigned to parents sampled in four reserves in the Keppel Islands. Juvenile fish were allocated to 6 distinct cohorts based on the estimated date on which they were spawned, subsequently juveniles were assigned to parent fish using parentage analysis. A total of 125 parent-offspring pairs were identified.

Settlement reef	Juvenile cohorts					
	C1	C2	C3	C4	C5	C6
Clam Bay (MPZ)	2	8	5	4	3	1
Corroboree Is	-	-	1	-	1	-
Halfway Is.	5	4	6	11	6	5
Halfway Is (MPZ)	-	-	1	-	-	-
Humpy Is.	6	2	-	-	1	-
Long Beach	-	-	-	1	1	-
Middle Is.	2	2	2	3	3	1
Monkey Bay	-	-	-	-	1	-
North Keppel (MPZ)	12	5	4	1	4	2
North Keppel West	-	-	-	-	1	1
Pumpkin Is.	-	-	-	-	4	-
Wreck Bay	-	-	-	-	-	1
Wyndham Cove	1	-	-	-	1	-
Total assignments	28	21	19	20	26	11
Total sampled	46/153	67/105	30/102	32/80	112/159	25/65

Parentage analysis. Genomic DNA was extracted from ~2 mm² of fin or muscle tissue and screened at 25 microsatellite loci for *P. maculatus* following a previously described protocol (7). Two loci (*Pma112*, *Pma036*) were excluded from the data for parentage analysis due to significant departure from Hardy-Weinberg expectations and the presence of a large number of rare alleles that may have skewed the parentage analyses. Parent-offspring pairs were identified in two periods, with each period composed of three successive cohorts. Period 1 included all sampled juvenile fish that recruited to reefs in the Keppel Islands between September 2007 and March 2009 (n = 686), and all sampled adult fish that were reproductively mature (>300 mm) during the same period (n = 559), including large adults (> 500 mm) captured between September 2011 and April 2013. Period 2 included juveniles that recruited between September 2011 and April 2013 (n = 891), and adults that were

reproductively mature (>300 mm) during that period (n = 454), including individuals captured between September 2007 and March 2009.

For each period, juveniles were screened against the pool of adults to reveal parent-offspring relationships using a maximum likelihood approach implemented in the software program FAMOZ (8, 9). The program computes log of the odds ratio (LOD) scores for assigning individuals to candidate parents based on the observed allelic frequencies at each locus. Minimum LOD score thresholds for accepting assignments to single parents and parent pairs were determined from the distribution of simulated LOD scores from 50,000 known parent-offspring pairs and 50,000 unrelated pairs as well as custom simulations to measure the accuracy of assignments (10, 11). All putative parent-offspring pairs with LOD scores above 2.0 were retained. Parentage test simulations estimated the probability of falsely accepting (false positive – type I error) or excluding (false negative – type II error) parent-offspring pairs associated with these parameters (10, 11). The resulting probability of assigning a juvenile to a parent that was not its true parent, knowing that the true parent was not sampled, was 2% (false positive – type I error) in *P. maculatus*. Conversely, the probability of a true parent-offspring pair not being identified knowing that the true parent was sampled was less than 0.01% (false negative – type II error). Any parent-offspring pairs that also presented over four confirmed mismatches between parent and offspring genotypes were excluded from the final list of assigned pairs. Additional simulations demonstrated that the panels of microsatellite markers provided robust assignment of parent-offspring pairs in the Keppel islands.

Dispersal networks. We represented the observed dispersal patterns between source reserves and destination reefs as a directed network in the R package ‘*igraph*’ (12) with reefs as *nodes* and the observed dispersal events as *edges*. In the case of dispersal networks of *P. maculatus* in the Keppel Islands, each connection is based on empirical observations of dispersal between reefs and connection weights are measured as the number of juveniles that dispersed from each reserve.

We measured the correlation of edge weights between dispersal networks corresponding to each of the six cohorts (C1-C6) to assess the consistency of dispersal patterns in the Keppel islands. Pearson correlations between matrices ranged from 0.28 to 0.66 and averaged 0.43 ± 0.03 SE.

The distance between all reefs in the Keppel Islands was measured to determine the distribution of all possible dispersal distances (Fig. S2A). The distance of dispersal events was measured as the Euclidian (straight-line) distance between source and destination reefs in the R package ‘*geosphere*’ (13) and plotted in ‘*ggplot2*’ (14) for all assigned juveniles (Fig. S2-b) and for each individuals cohort (Fig. S2C). The mean observed dispersal distance among reefs was $9.2 \text{ km} \pm 0.64 \text{ SE}$ (Fig. S2B) and although we observed variation among settlement cohorts (Fig. S2C), it did not vary substantially from the mean. However, the distribution of dispersal distances was statistically independent of the distance between reserves and available settlement habitat ($\chi^2 = 122.65$, d.f. = 64, $P < 0.001$).

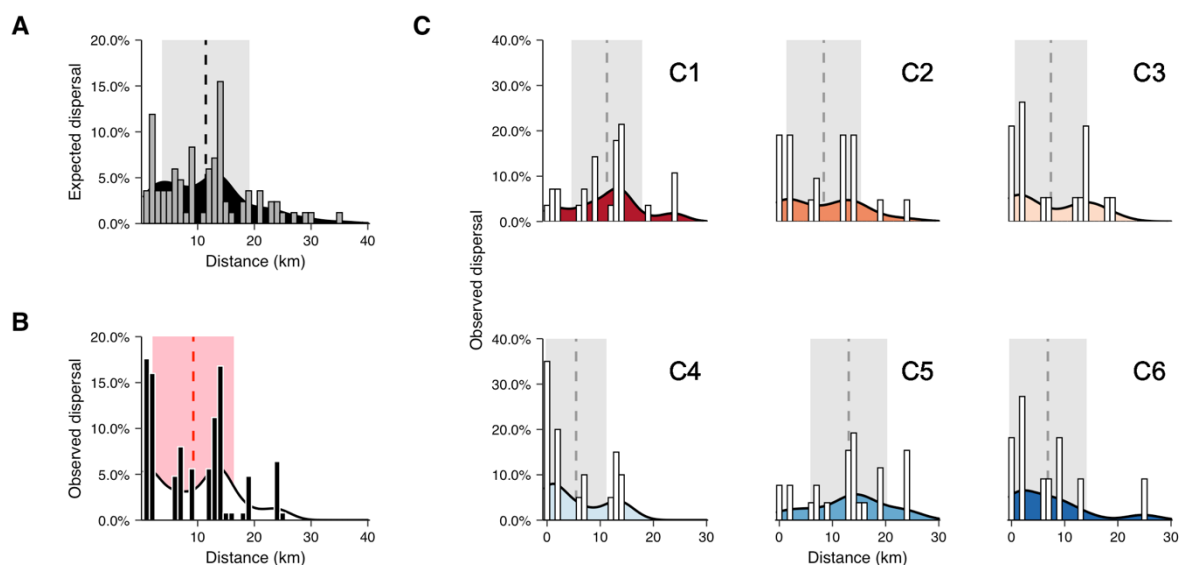


Fig. S2. Distributions of expected and observed dispersal distances of juvenile *P. maculatus* from four reserves in the Keppel Islands.

(A) The distribution of expected dispersal distances from reserves to all available recruitment habitats. A vertical dashed line and bounding box represent the mean expected dispersal distances and 1 standard deviation around the mean ($11.4 \text{ km} \pm 7.7 \text{ km S.D.}$). **(B)** Distributions of dispersal distances of

125 assigned juvenile *P. maculatus* from source reefs in the Keppel Islands between September 2007 to April 2013. A vertical red dot-dash line and bounding box represent the mean observed dispersal distances and 1 standard deviation around the mean ($9.2\text{km} \pm 7.2\text{km S.D.}$). (C) The distribution of observed dispersal distance in each of 6 recruitment cohorts (C1-C6). Vertical grey dashed line and bounding boxes represent the mean and 1 standard deviation for each cohort. Dispersal distances were measured as the Euclidian (straight line) distances between sampled adult and juvenile locations for each assigned parent-offspring pair.

The direction between all reefs in the Keppel Islands was measured to determine the distribution of all possible dispersal directions between reefs. We considered all reefs as possible sources and/or sinks so the resulting figures are naturally symmetric (Fig. S3A). The direction of dispersal events was measured between parent and juvenile collection points for all cohorts combined (Fig. S3B) and for each discrete cohort (Fig. S3C). The bearing between source and destination reefs were measured in the R package 'CircStats' (15) and plotted in 30° bins in 'ggplot2'. The directions of observed dispersal events were predominantly westward to northward (Fig. S3B), which broadly mirrored possible bearings between reserves and available settlement habitat ($\chi^2 = 69$, d.f. = 64, $P = 0.312$).

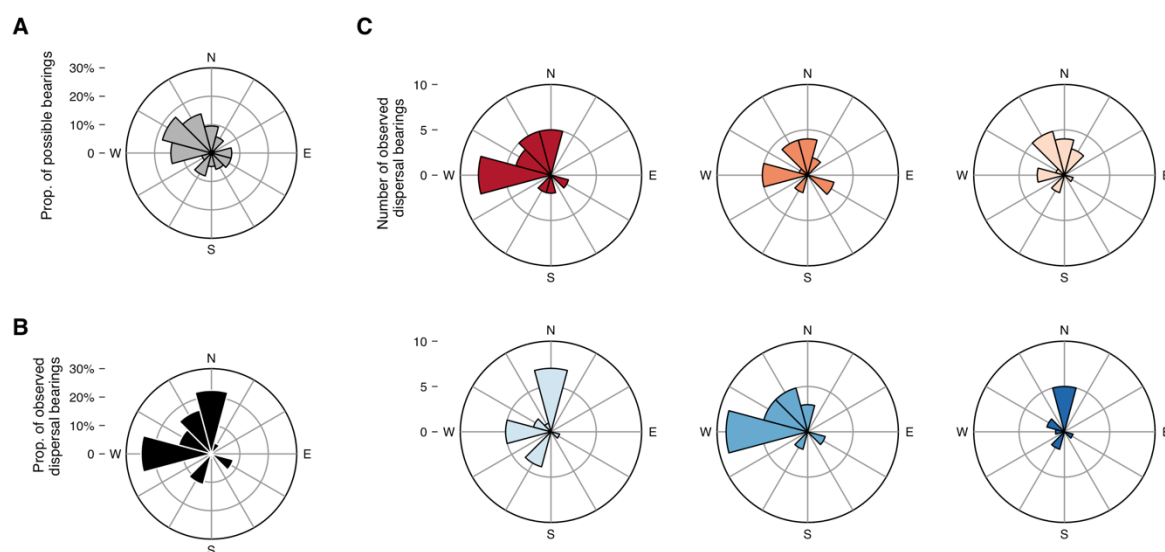


Fig. S3. Distributions of expected and observed dispersal directions of juvenile *P. maculatus* from four reserves in the Keppel Islands. (A) The distribution of expected dispersal directions from reserves to available recruitment habitats. (B) Distributions of dispersal distances of 125 assigned juvenile *P. maculatus* from source reefs in the Keppel Islands between September 2007 to April 2013. (C) The distribution of observed dispersal directions in each of 6 recruitment cohorts (C1-C6). Dispersal directions were measured as the bearing between sampled adult and juvenile locations for each assigned parent-offspring pair.

Data and code availability

Files attached to this supplementary information contain data and R code to measure the portfolio effect and reproduce figures in the manuscript.

Data and code are also available at: <https://github.com/HugoBH/CPE>

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References

1. Ferreira B (1993) Reproduction of the inshore coral trout *Plectropomus maculatus* (Perciformes: Serranidae) from the central Great Barrier Reef, Australia. *J Fish Biol* 42(6):831–844.
2. Ferreira BP (1995) Reproduction of the common coral trout *Plectropomus leopardus* (Serranidae: Epinephelinae) from the central and northern Great Barrier Reef, Australia. *Bull Mar Sci* 56(2):653–669.
3. Haemstra PC, Randall JE (1993) FAO Species Catalogue. Vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. *FAO Fish Synop* 125(16):382.
4. Samoily MA, Squire LC (1994) Preliminary observations on the spawning behavior of coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. *Bull Mar Sci* 54(1):332–342.
5. Sadovy de Mitcheson Y, et al. (2013) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish Fish* 14(2):119–136.
6. Campbell A, Leigh G, Bessel-Brown P, Lovett R (2019) Stock assessment of the Queensland east coast common coral trout (*Plectropomus leopardus*) fishery. *Department of Agriculture and Fisheries, Fisheries Queensland, Queensland Government, Brisbane Australia*.
7. Harrison HB, et al. (2014) Validation of microsatellite multiplexes for parentage analysis and species discrimination in two hybridizing species of coral reef fish (*Plectropomus spp.*, Serranidae). *Ecol Evol* 4(11):2046–2057.
8. Gerber S, Chabrier P, Kremer A (2003) FAMOZ: a software for parentage analysis using dominant, codominant and uniparentally inherited markers. *Mol Ecol Notes* 3(3):479–481.
9. Marshall T, Slate J, Kruuk L, Pemberton J (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol* 7(5):639–655.
10. Harrison HB, Saenz-Agudelo P, Planes S, Jones GP, Berumen ML (2013) Relative accuracy of three common methods of parentage analysis in natural populations. *Mol Ecol* 22(4):1158–1170.
11. Harrison HB, Saenz-Agudelo P, Planes S, Jones GP, Berumen ML (2013) On minimizing assignment errors and the trade-off between false positives and negatives in parentage analysis. *Mol Ecol* 22(23):5738–5742.
12. Csardi G, Nepusz T (2006) The igraph software package for complex network research. *Interjournal, Complex Systems* 1695.

13. Hijmans RJ (2016) *geosphere: Spherical Trigonometry*.
14. Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag, New York).
15. Agostinelli C (2001) *CircStats: Circular Statistics*, from “*Topics in Circular Statistics*.”