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Report

Larval Export from Marine Reserves and the Recruitment Benefit for Fish and Fisheries

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Summary

Marine reserves, areas closed to all forms of fishing, continue to be advocated and implemented to supplement fisheries and conserve populations [1–4]. However, although the reproductive potential of important fishery species can dramatically increase inside reserves [5–8], the extent to which larval offspring are exported and the relative contribution of reserves to recruitment in fished and protected populations are unknown [4, 9–11]. Using genetic parentage analyses, we resolve patterns of larval dispersal for two species of exploited coral reef fish within a network of marine reserves on the Great Barrier Reef. In a 1,000 km^2 study area, populations resident in three reserves exported 83% (coral trout, *Plectropomus maculatus*) and 55% (stripey snapper, *Lutjanus carponotatus*) of assigned offspring to fished reefs, with the remainder having recruited to natal reserves or other reserves in the region. We estimate that reserves, which account for just 28% of the local reef area, produced approximately half of all juvenile recruitment to both reserve and fished reefs within 30 km. Our results provide compelling evidence that adequately protected reserve networks can make a significant contribution to the replenishment of populations on both reserve and fished reefs at a scale that benefits local stakeholders.

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Results and Discussion

Coastal marine ecosystems have been subjected to a long history of human impacts that are predicted to escalate over the next century [12, 13]. Although there is no single solution to alleviate such impacts, no-take marine reserves represent one management action that can deliver tangible and rapid benefits [1–4]. Thousands of marine reserves have been implemented globally in the hope of restoring and sustaining fisheries and conserving biodiversity [14, 15]. Hundreds of studies have demonstrated that exploited species have higher abundance, biomass, and reproductive potential within adequately protected reserves [5–8]. In theory, the elevated populations in reserves can simultaneously provide both fisheries and conservation benefits, as long as there is both substantial larval export from reserves to fished areas and either self-recruitment within or dispersal among reserves [4, 9–11, 16]. In practice, there is little concrete evidence that reserves provide recruitment benefits beyond their immediate boundaries [2, 9, 17]. Recent breakthroughs in larval tagging and genetics have shown that it is possible to track the dispersal trajectories of larvae for small marine fishes over relatively short distances [18–26]. However, for large exploited fishes, it has been seemingly impossible to determine where the larvae from populations within reserves go or to assess the relative importance of the supply of juveniles from reserves. These are critical knowledge gaps that limit our understanding of the wider benefits of marine reserve networks for fish conservation and fisheries management.

We applied DNA parentage analysis to provide a unique assessment of the importance of reserves as a source of juveniles to both fished and protected populations in a coastal archipelago of the Great Barrier Reef (GBR). Here, 28% of coral reefs are protected in a network of six no-take marine reserves (Keppel Island group; Figure 1). Our field study focused on two commercially and recreationally targeted fish species: the coral trout, *Plectropomus maculatus* (Serranidae), and stripey snapper, *Lutjanus carponotatus* (Lutjanidae), for which the mean biomass of reproductive adults was approximately twice as high on no-take reserve reefs than on surrounding fished reefs (see Figure S2 and Supplemental Experimental Procedures available online). Over 4 weeks during the peak reproductive season (Austral summer), we collected tissue samples from 466 adult *P. maculatus* and 1,154 adult *L. carponotatus* within three focal reserves (Figure 1) representing 26.9% ± 8.3% SEM and 35.7% ± 7.1% SEM of focal populations, respectively. During the following 15 months, juveniles of both species were collected from 19 protected and fished locations up to 30 km from the focal reserves (Figure S1; Table S1). By recording the sampling locations of all adult and juvenile fishes and assigning offspring to one or both parents, we were able to establish the dispersal distance and direction of juveniles spawned in the focal reserves.

Dispersal Trajectories from Reserves

Our study revealed that adult fishes in reserves exported a significant proportion of their offspring to fished areas outside reserve boundaries. We identified 58 juvenile coral

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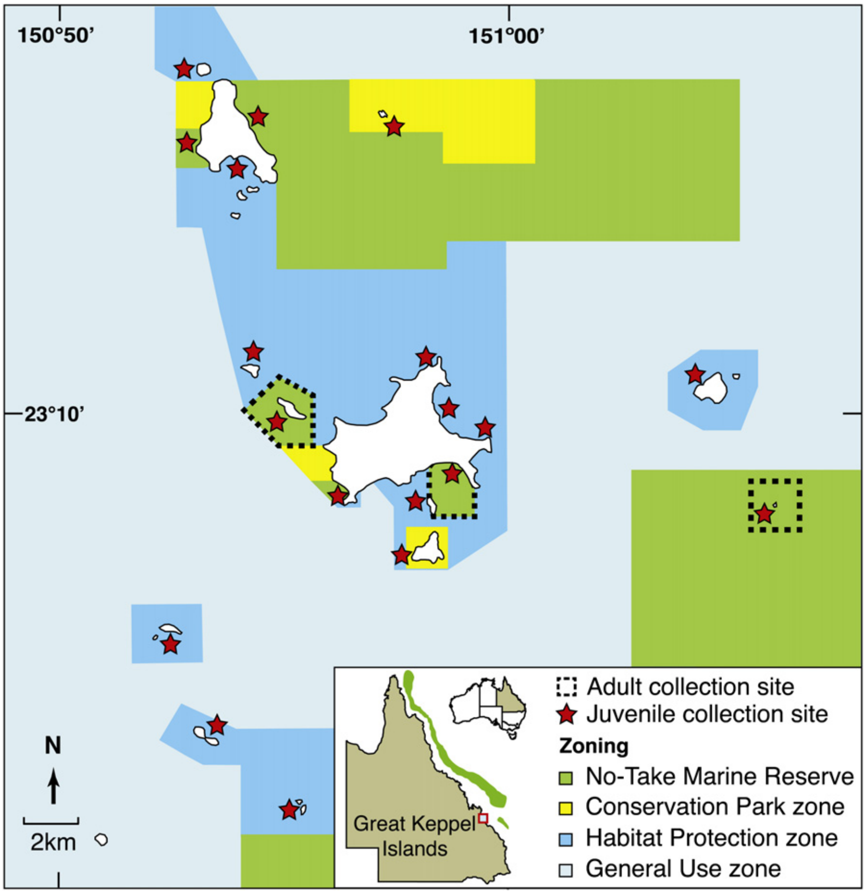

Figure 1. Sampling Locations of Adult and Juvenile Fish

The Keppel Islands includes six no-take marine reserves (Marine National Park zones, shaded green) protecting 28% of coral reefs. Adult *P. maculatus* and *L. carponotatus* were sampled within three no-take reserves (dashed line borders), and juveniles were sampled from 19 locations (red stars) within both reserves and areas open to fishing (see also Figure S1 and Table S1). Conservation Park zones (yellow) permit limited recreational hook-and-line and spear fishing. Habitat Protection zones (dark blue) exclude demersal trawling but permit hook-and-line and spear fishing. General Use zones (light blue) allow all types of fishing.

trout (Figure 2; Table S2) and 74 juvenile stripey snapper (Figure 2; Table S3) as the progeny of adults sampled within the three focal reserves. Overall, 83% (48 of 58) of assigned coral trout juveniles and 55% (41 of 74) of assigned stripey snapper juveniles were collected from reefs that were open to fishing, representing a clear demonstration of larval export from reserves (Figures 2A and 2B). For coral trout, 7% (4 of 58) of assigned juveniles were retained in natal reserves (self-recruitment) and 10% (6 of 58) were exchanged among reserves, whereas for stripey snapper, 22% (16 of 74) were retained in natal reserves and 23% (17 of 74) were exchanged between reserves (Figures 2C and 2D). Hence, for these two species, adults in reserve populations were not only exporting substantial numbers of offspring to nearby fished areas, but they were also contributing to population replenishment within the reserve network.

The observed frequency distribution of dispersal distances within 30 km of sampled reserves was remarkably similar for the two species (Figures 3A and 3B). Approximately 30% of assigned juveniles were collected within 1–2 km of their parents, and it is evident that the different modes in dispersal distance reflected the geographic distance between reefs (Figure 3C). For both species, the shortest dispersal mode (1–2 km) was predominantly associated with an area of retention at the largest of the islands (Great Keppel), whereas longer dispersal modes were associated with dispersal among islands (Figure 2). Across the entire 1,000 km^2 sampling area, over 90% of reefs that are open to fishing were within the mean observed dispersal range of both species, suggesting that the spacing of reserves is small enough to benefit most fished areas (Figure 3C). Clearly, successful dispersal may also have extended to unsampled reefs beyond the Keppel Island group, and the full spatial extent of the benefits of larval export from reserves remains to be determined.

Recruitment Contribution of the Reserve Network

We estimated that the six reserves in the Keppel Islands, which represent ~28% of the reef habitat in the Keppel Islands, supplied ~50% of the total recruitment in the region. This estimate accounted for both the expected contribution of unsampled adults in the three focal reserves and the additional reef area within the three other unsampled reserves. We assigned 11.8% (58 of 493) of juvenile coral trout and 15.6% (74 of 474) of juvenile stripey snapper to known parents in the focal reserves. However, given that we sampled ~26.9% of adult coral trout and ~35.7% of adult stripey snapper within the focal reserves, a significant number of the unassigned juveniles would have been the progeny of unsampled adults within those reserves (see Supplemental Experimental Procedures, equation 1). Taking these additional adult fish into consideration, we estimate that the three focal reserves accounted for ~25% of juvenile coral trout and ~27% of juvenile stripey snapper in our samples. Furthermore, if we also consider that the three focal reserves represented ~51.3% of total coral reef habitat within all six reserves and assume that the three unsampled reserves made the same proportional contribution to recruitment per unit area as the sampled reserves, then the six reserves would have accounted for ~49% of coral trout and ~52% of stripey snapper recruitment in the region (see Supplemental Experimental Procedures, equation 2).

The contribution of reserves to total regional recruitment for the two species was further subdivided to estimate the relative contribution to both fished areas and reserves (Figure 4). Applying the same calculations as above, our findings indicate that adults in reserves were making a large contribution to the replenishment of populations on both reserve and fished reefs in the Keppel Islands. Of the 353 juvenile coral trout and 303 juvenile stripey snapper that were collected from reefs that are open to fishing, we estimate that the six reserves accounted for ~57% of coral trout and ~46% of stripey snapper

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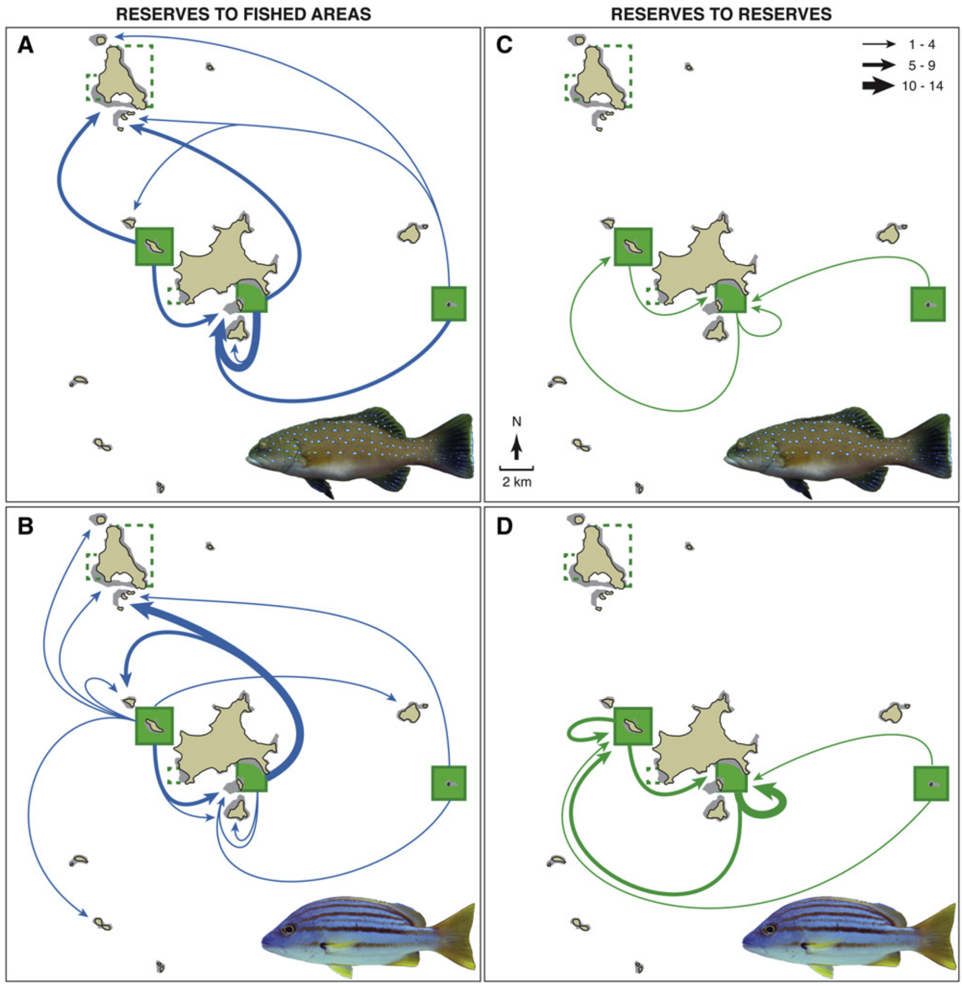

Figure 2. Realized Dispersal Patterns of Juvenile Fish from a Network of Marine Reserves

(A and B) The three focal marine reserves (green boxes) were an important source of juvenile recruitment for local fished areas. Forty-eight juvenile *P. maculatus* (A) and 41 juvenile *L. carponotatus* (B) that had recruited to fished areas were assigned to adults from one of three focal reserves (see also Tables S2 and S3). Coral reef areas are represented in gray, and arrow thickness is relative to the number of juveniles that were assigned to each focal reserve.

(C and D) Local retention within focal reserves and connectivity between reserves (dotted green boxes) also made an important contribution to juvenile recruitment in reserves. Ten juvenile *P. maculatus* (C) and 33 juvenile *L. carponotatus* (D) that had recruited in reserves were assigned to adults from one of three focal reserves (see also Tables S2 and S3).

recruitment (Figure 4). Similarly, we estimate that within reserves, ~30% of coral trout recruitment and ~64% of stripey snapper recruitment was supplied through self-recruitment to natal reserves or through larval exchange between reserves (Figure 4). The remaining juveniles were likely to be the progeny of unsampled adults within fished areas of the Keppel Island group or immigrants from distant reefs outside the island group.

Conclusions

Our study confirms that effective reserve networks can provide a significant source of recruitment to populations in both fished and protected areas on a regional scale. Not only were adults in reserves exporting a high proportion of their offspring to adjacent fished areas, there was also significant larval retention within natal reserves and connectivity among neighboring reserves. Furthermore, the proportion of observed dispersal trajectories less than 30 km is consistent with recent studies demonstrating that coral reef fish larvae may disperse relatively short distances despite spending several weeks in the pelagic environment [21].

The estimate that reserves contribute about half of the total recruitment in the Keppel Islands is clearly important, given that only 28% of reef area in the region is protected. This represents a ~1.8-fold increase in recruitment over that expected based simply on the area of reef within reserves. The significant role of reserves as sources of juvenile recruits in both fished areas and in reserves is likely due to the approximately 2-fold greater adult biomass inside reserves (Figure S2), the larger average adult size inside reserves, and, as a consequence, greater per capita and per unit area fecundity relative to adjacent fished populations [27].

Theoretical considerations highlight the importance of both self-recruitment and connectivity in ensuring metapopulation persistence in reserve networks [10, 11, 17, 28]. It is therefore encouraging that our study documented both self-recruitment to natal reefs and connectivity among reserves. Although the observed magnitude of the reserve contribution to recruitment

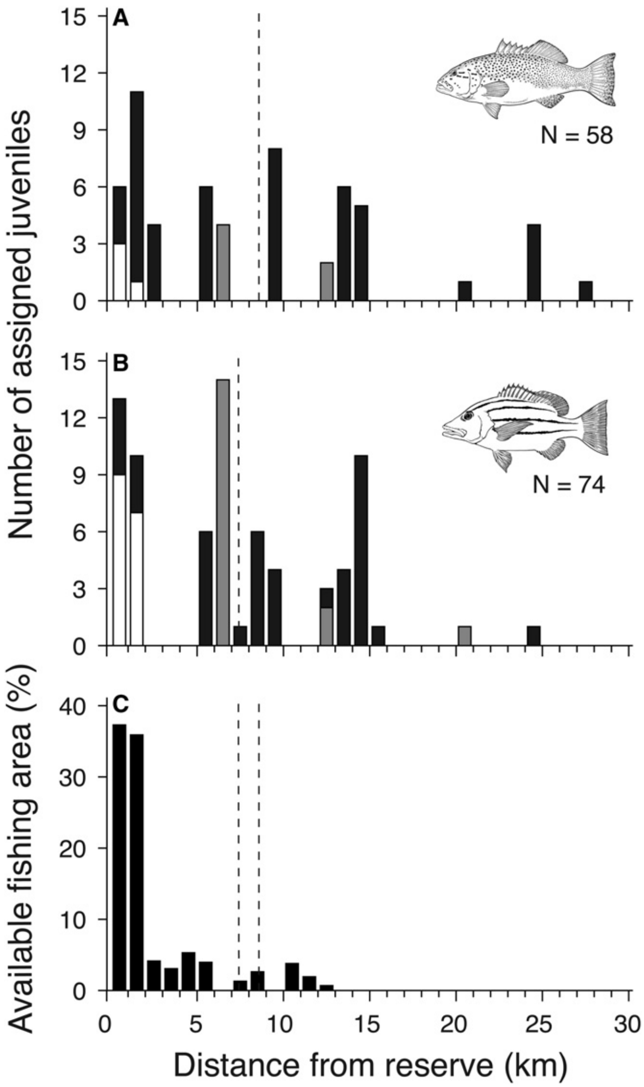

Figure 3. Dispersal Distance of Assigned Juvenile from Natal Reserves

(A and B) The frequency distributions of realized dispersal distances indicate that within the Keppel Islands, assigned juvenile *P. maculatus* (A) and *L. carponotatus* (B) were collected between hundreds of meters and 28 km from the location where their parents were sampled (average observed dispersal distance is indicated by the dashed vertical lines: 8.6 ± 1.0 km SEM for *P. maculatus* and 7.4 ± 0.6 km SEM for *L. carponotatus*). Each histogram bar is divided according to the number of assigned juveniles that returned to natal reserves (white), the number that dispersed from one reserve to another reserve (gray), and the number that dispersed from reserves to fished areas (black).

(C) The distribution of available reef area open to fishing that surrounds each of the six marine reserves is within the mean dispersal range of both species (dashed vertical lines).

in fished areas is consistent with modeling scenarios [16], the magnitude of larval supply from reserves may not be sufficient to offset a substantial increase in fishing pressure outside reserves [29]. We recommend that reserves continue to be coupled with traditional harvest restrictions, including fish size and catch limits, and seasonal spawning closures [30] to ensure that current yields for these fishes are sustainable.

Although the proportion of coral reef habitat in our GBR study area designated as no-take reserve is comparatively high in global terms [14, 15, 30], it is important to note that our results clearly demonstrate that reserves can provide significant fishery and conservation benefits on a scale as small as 10 km. In many places where people rely heavily on coral reefs for their livelihoods, this scale is typical of reef tenure areas and the only scale at which marine reserves can realistically be applied [31]. The fact that stakeholder communities can directly benefit from a source of recruitment from their local reserves is the strongest support yet that reserve networks can be an effective tool for sustaining future generations of both fish and fishers.

Experimental Procedures

Study Location and Sample Collection

This study was carried out in the Keppel Island group (23°10′ S, 150°57′ E) within the Great Barrier Reef Marine Park, Australia (Figure 1). There are six no-take marine reserves in the island group, which had been protected for between 3 and 19 years at the time of the present study (Figure S1; Table S1). Adults were sampled between November 2007 and February 2008 from four coral reefs in three focal marine reserves (Figure S1; Table S1). A total of 466 adult coral trout and 1,154 adult stripey snapper were sampled from the three focal marine reserves (Table S2; Table S3), and all individuals were released alive at the capture site. Juveniles were sampled in May 2008 and February 2009 from 19 locations scattered throughout the study area (Figure S1; Table S1). A total of 493 juvenile coral trout and 474 juvenile stripey snapper were collected, with slightly fewer samples collected in fished areas compared to reserves relative to the available reef area (*P. maculatus*, 1:1.04; *L. carponotatus*, 1:1.52).

Parentage Assignments

All adult and juvenile *P. maculatus* and *L. carponotatus* were genotyped with a panel of 11 and 13 microsatellite markers, respectively, resulting in unique genotype profiles for each individual (Table S4; Supplemental Experimental Procedures). Categorical allocation of parent-offspring relationships was assessed based on a maximum likelihood approach implemented in the software program Famoz [32] (see Supplemental Experimental Procedures). All collected juveniles were screened against the total pool of adult samples to identify parent-offspring relationships. By recording the sampling locations of all adult and juvenile fishes and assigning offspring to one or both parents, we were able to establish the dispersal distance and direction of juveniles sourced from the focal reserves.

Accession Numbers

The GenBank accession numbers for the 11 sequences reported in this paper are JN222545–JN222555.

Supplemental Information

Supplemental Information includes two figures, four tables, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2012.04.008.

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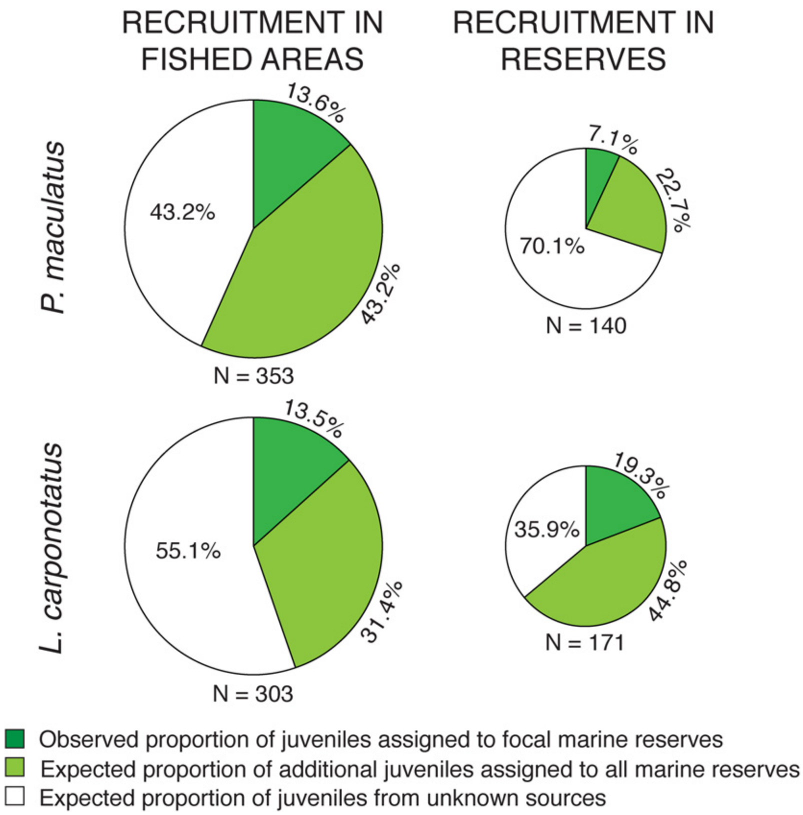

Figure 4. Local Recruitment Contribution from the Reserve Network

Observed (dark green) and estimated (light green) contribution of six marine reserves to local recruitment of coral trout and stripey snapper in fished and protected areas of the Keppel Islands. Proportions are based on the number of assigned juveniles relative to the total number of juveniles (*N*) collected in reserves and fished area. The estimated proportion of additional recruitment accounts for both unsampled adults in the three focal reserves and the three unsampled reserves. Pie charts are scaled relative to the size of available coral reef habitat in reserves (28%) and fished areas (72%).

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