Current Biology *23*, 626–630, April 8, 2013 ©2013 Elsevier Ltd All rights reserved http://dx.doi.org/10.1016/j.cub.2013.03.006

Report

# Dispersal of Grouper Larvae Drives Local Resource Sharing in a Coral Reef Fishery

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## Summary

**In many tropical nations, fisheries management requires a community-based approach because small customary marine tenure areas define the spatial scale of management [1]. However, the fate of larvae originating from a community's tenure is unknown, and thus the degree to which a community can expect their management actions to replenish the fisheries within their tenure is unclear [2, 3]. Furthermore, whether and how much larval dispersal links tenure areas can provide a strong basis for cooperative management [4, 5]. Using genetic parentage analysis, we measured larval dispersal from a single, managed spawning aggregation of squaretail coral grouper (*Plectropomus areolatus*) and determined its contribution to fisheries replenishment within five community tenure areas up to 33 km from the aggregation at Manus Island, Papua New Guinea. Within the community tenure area containing the aggregation, 17%–25% of juveniles were produced by the aggregation. In four adjacent tenure areas, 6%–17% of juveniles were from the aggregation. Larval dispersal kernels predict that 50% of larvae settled within 14 km of the aggregation. These results strongly suggest that both local and cooperative management actions can provide fisheries benefits to communities over small spatial scales.**

## Results and Discussion

To rebuild and sustain coastal fisheries in developing nations, nongovernmental and intergovernmental organizations have advocated the use of a range of small-scale initiatives, including marine protected areas (MPAs) [6, 7]. Incentives for adopting and complying with such initiatives are naturally greatest when people are likely to benefit from their actions. For example, if fishers agree to protect a portion of their fishing grounds, will they benefit and/or will benefits flow to other groups (i.e., positive externalities)? Logically, the key benefit of concern to fishers is the degree to which their actions can contribute to the replenishment of their own fish stock. Fisheries replenishment depends on juvenile recruitment, and fishes produce planktonic larvae that have the potential to disperse widely before recruiting to benthic habitats. Thus, understanding the spatial scale of larval dispersal—the dispersal kernel—plays a critical role in determining which management strategies are viable, who benefits from management, and the degree of cooperation necessary among neighbors for the fishery to be sustainable [3–5, 8–11]. If most larvae disperse far from a MPA, few will return to replenish the local fishery, and fishers therefore have little incentive to adopt or comply with restrictions [8]. The likelihood of this undesired outcome increases as the spatial scale of larval dispersal increases relative to the size of the local fishing ground. This fact is particularly worrying for the many tropical nations where fisheries management occurs at the spatial scale of small customary marine tenure (CMT) areas, which often consist of just a few hundred hectares of habitat [1, 12–14]. Recent advances are providing the first direct measurements of larval dispersal [15–17] and the first direct estimates of how the probability of larval dispersal varies as a function of distance [18, 19] in small coral reef fishes, but we know little about larval dispersal in larger fishery species [but see 20]. Thus, whether and at what spatial scale communities can benefit from management are unknown.

We used genetic parentage analysis to measure larval dispersal from a single fish spawning aggregation (FSA) of squaretail coral grouper (*Plectropomus areolatus*, Serranidae) at Manus, Papua New Guinea. In 2004, to replenish local fish stocks, fishers within a single CMT area established a MPA protecting 13% of their fishing grounds, including the studied FSA. We sampled this FSA over 2 weeks in May 2010 and collected tissue samples from, and externally tagged, 416 adult coral grouper (235 females, 180 males, and 1 sex undetermined), which represented an estimated 43% (95% confidence interval [CI]: 32%–53%) of the FSA population (see the Supplemental Experimental Procedures available online).

Over 6 weeks (November–December 2010), we collected 782 juvenile coral grouper from 66 reefs located within five CMT areas up to 33 km from the sampled FSA (Figure 1).

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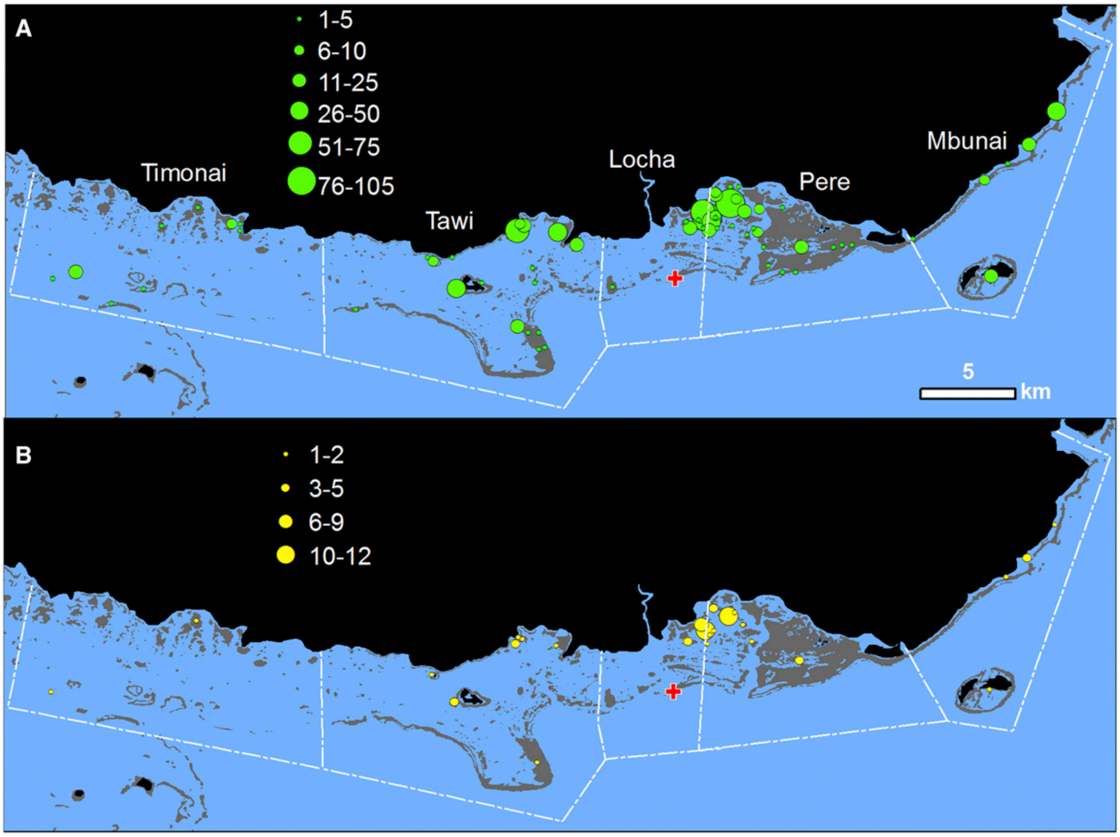

Figure 1. Location and Abundance of Sampled and Assigned Juveniles

Spatial patterns of coral grouper (*Plectropomus areolatus*) (A) juvenile sample collection and (B) juvenile parentage assignments. Green (A) and yellow (B) circles are scaled to the number of juveniles. Adults were sampled from a single fish spawning aggregation (red cross), and juveniles were collected from 66 individual reefs (green circles in A). White dashed lines are customary marine tenure boundaries of the five communities, with the name of each community in white above in (A). Land is black, coral reefs are gray, and water is blue. See also Figures S1 and S2.

Parentage analysis identified 76 juveniles that were the offspring of adults sampled at the FSA (see the Supplemental Experimental Procedures), and these 76 juveniles came from 25 reefs (Figure 1). Assigned juveniles ranged in size from 62–288 mm total length and were between 94 and 394 days old (see the Supplemental Experimental Procedures). The proportion of the juvenile sample collected from each CMT area that was assigned to adults sampled from the FSA was significantly higher for Locha (the tenure area containing the FSA) than for any other CMT area ($p < 0.02$ from a permutation test) and lowest for Timonai, the CMT that is the most distant from Locha (Table 1). We estimated the number of parentage assignments missed due to incomplete adult sampling (see the Supplemental Experimental Procedures), and the expected mean percent of recruitment derived from the sampled FSA in each CMT area was as follows: Mbunai, 13.1%; Pere, 13.9%; Locha, 19.6%; Tawi, 12.1%; and Timonai, 6.9% (Table 1).

Juvenile samples were collected from 66 reefs with known locations, and we calculated the Euclidean distance between each reef and the sampled FSA. We used the proportion of juveniles at each reef assigned by parentage analysis to sampled FSA adults to estimate the shape of the larval dispersal kernel. Assigned juveniles came from 25 of the 66 reefs sampled, and assignment proportions from all 66 reefs were used to estimate the dispersal kernel. We fit five functional forms to these data, and we found that Ribbens and Gaussain kernels provided the best fit, with AIC weights of approximately 0.3. Randomization tests of goodness of fit indicated that both models describe trends that would occur by chance with a probability of less than 8% (see the Supplemental Experimental Procedures). These two kernels agreed that at least 50% of larvae settle within 14 km of the FSA (Figures S1 and S2). A Ribbens kernel [21] provided the best fit and predicted that 50% and 95% of larvae settled within 13 km and 33 km, respectively, of the FSA (Figure 2). The mean dispersal distance calculated from the Ribbens kernel was 14.4 km (see the Supplemental Experimental Procedures).

Understanding whether, how much, and at what spatial scale human communities can benefit from management actions is key to designing effective strategies, obtaining and sustaining support for management, and providing greater incentives for compliance. Our results suggest that communities on Manus can indeed benefit from management, both independently and collectively. Exactly how recruitment benefits are distributed among communities will depend on the locations of CMT boundaries relative to larval dispersal patterns and spawning aggregations, but the shape of the larval dispersal kernel in the present study suggests that the greatest recruitment benefits are retained within several kilometers of the larval source. Whether recruitment translates directly to fisheries benefits requires further study, focusing

Table 1. Observed and Expected Parentage Assignments in Each Customary Marine Tenure Area

| | Observed | | | Expected | |
|---|---|---|---|---|---|
| Tenure Area | Juvenile Samples | Parentage Assignments | % Assignment | Parentage Assignments | % Assignment (95% CI) |
| Mbunai | 79 | 7 | 8.9 | 10.4 | 13.1 (11.4–16.5) |
| Pere | 235 | 22 | 9.4 | 32.6 | 13.9 (12.1–17.4) |
| Locha | 204 | 27 | 13.2 | 40.1 | 19.6 (17.1–24.7) |
| Tawi | 221 | 18 | 8.1 | 26.7 | 12.1 (10.5–15.2) |
| Timonai | 43 | 2 | 4.7 | 3.0 | 6.9 (6.0–8.7) |
| Total | 782 | 76 | 9.7 | 112.7 | 14.4 (12.5–18.1) |

Adults were sampled from a single *Plectropomus areolatus* spawning aggregation located in the Locha tenure area. Expected parentage assignments were calculated by correcting for incomplete sampling of adults (see the Supplemental Experimental Procedures).

particularly on the relationship between successful recruitment and subsequent adult densities. However, because the 76 juveniles assigned to adults sampled from the FSA were 94–394 days old and mortality is greatest within the first few days after larvae settle from the plankton and declines dramatically thereafter [22, 23], the recruitment resulting from larval dispersal from the FSA as measured in this study likely translates directly to fisheries benefits.

There are eight other known coral grouper FSAs within the five CMT areas we studied. Oceanographic conditions across the 75 km of coastline encompassing these five CMT areas are likely similar, and we predict that larval dispersal patterns from the eight unsampled FSAs fall within the 95% confidence interval of the maximum likelihood fit of the dispersal kernel observed from the sampled FSA (Figure 2). If this is true, (1) each CMT area will have a high level of self-recruitment, (2) the five CMT areas will be connected to each other by larval dispersal, and (3) the strength of connectivity between CMT areas will decline as a function of the distance between them. As a result, actions by one community will influence its neighbors, and cooperation among the five communities in managing the coral grouper fishery is likely to enhance both fisheries sustainability and the long-term persistence of the coral grouper metapopulation. Studies that resolve larval dispersal patterns and their relationship to recruitment can provide a compelling argument for cooperative management. Indeed, after presenting the results of the present study to communities in the five CMT areas in November 2011, these communities formed the Titan MWANUS Endras Cooperative Society to collectively manage the coral grouper fishery and other marine resources. Prior to the Society's formation, each community had managed its CMT area independently.

Encouragingly, coral grouper larval dispersal patterns are qualitatively consistent with results from studies on small, nonfishery species [17, 24–27] and the only other study on fishery species [20]: larvae often settle within 30 km from their parents. Our estimate of a mean larval dispersal distance for coral grouper (14.4 km for *Plectropomus areolatus*) is similar to mean dispersal estimates from parentage analysis for two other fishery species from the Great Barrier Reef (8.6 km for *Plectropomus maculatus* and 7.4 km for *Lutjanus carponotatus*) [20]. Furthermore, two studies that used genetic isolation-by-distance theory, and sampled over much greater spatial scales than the aforementioned studies, provide similar estimates of mean dispersal distance: 8.8 km for yellowtail clownfish (*Amphiprion clarkii*) in Philippines [25] and 2–14 km for barred hamlet (*Hypoplectrus puella*) in the Caribbean [26]. The observation that mean dispersal distance varies only 2-fold among species studied to date, rather than by an order of magnitude, suggests that localized larval dispersal is common in coral reef fishes [17]. This improves the likelihood that fisheries management decisions, such as choices about the size and spacing of marine protected areas, could provide robust benefits to a range of species simultaneously [28].

We quantified how larvae dispersing from a coral grouper FSA contribute to recruitment to five CMT areas. We found that (1) 17%–25% of recruitment to the CMT area that contains the sampled FSA came from that same FSA and that (2) in each of the four adjacent CMT areas, 6%–17% of recruitment was from the sampled FSA. Finally, (3) the two best-fit dispersal kernels based on these data predict that 50% of larvae settled within 14 km of the FSA. Our study highlights how restricted larval dispersal could allow communities to benefit from efforts to protect spawning stock, even when management units are small. Our results therefore suggest that use of small MPAs to protect critical areas such as spawning aggregations can be defensibly justified on the basis of direct local benefits [29]. Ultimately, our results can empower and incentivize communities to take proactive management actions, both independently and in coordination with their neighbors.

## Experimental Procedures

### Study Area, Study Species, and Sample Collection

Fieldwork was conducted in partnership with The Nature Conservancy and five communities on the south coast of Manus Island (2°04′S, 147°00′E), Papua New Guinea [30]. CMT boundaries and the local name of each reef (or part of a reef) were recorded during discussions with clan leaders and fishers in each community during examination of satellite imagery of the study area (GeoEye 1, 1 m resolution, image acquisition date October 14, 2009). Reefs were digitized across the entire study area at a scale of 1:4,000 with ArcGIS [31].

Squaretail coral grouper (*P. areolatus*) support subsistence, artisanal, and commercial fisheries throughout the Indo-Pacific, form transient FSAs at predictable times and locations and are a key target of the southeast-Asia-based Live Reef Food Fish Trade [32]. Coral grouper are most often targeted and extremely vulnerable to fishing while at their FSA [33]. During nonaggregating periods, adults occupy small home ranges typically located within 10 km of their FSA [34]. Larvae likely spend approximately 4 weeks in the pelagic environment before settling to reefs; larvae of the congeneric *P. leopardus* spend 19–31 days in the plankton [35].

Adult coral grouper were sampled April 29–May 14, 2010 by 20 local fishers. Each adult was measured (total length, TL), its sex was determined by examination of a sample of gametes, and a 1 cm × 1 cm piece of the dorsal fin was preserved in 85% ethanol. Each adult was tagged with a uniquely numbered 100-mm-long plastic dart tag (Hallprint, Australia; PDS type) inserted into the dorsal musculature and released at the point of capture. Juveniles were collected November 4–December 15, 2010 by ~100 total fishers from the five communities. Juveniles were defined as individuals smaller than the smallest coral grouper captured at the FSA (320 mm TL) and were thus assumed to be reproductively inactive. Juveniles were measured to the nearest millimeter (TL) and a 1 cm × 1 cm section of the dorsal fin was preserved in 85% ethanol for parentage analysis.

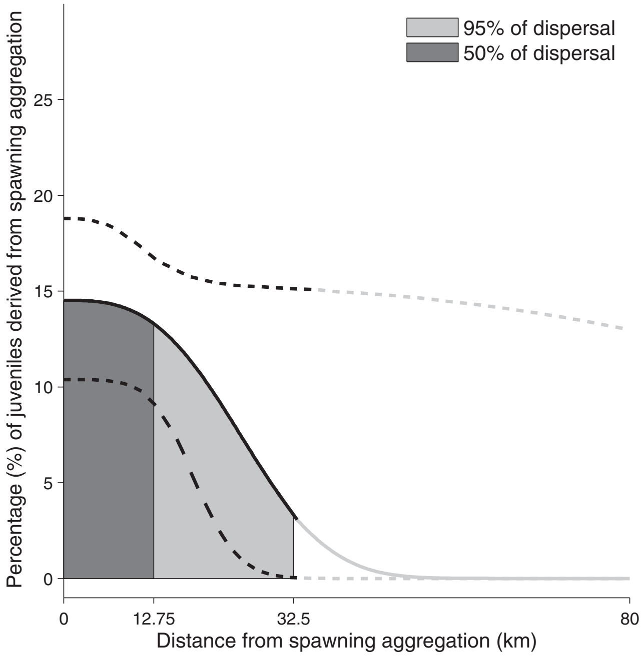

Figure 2. Dispersal Kernel of Larval Coral Grouper

Dispersal kernel of larval coral grouper (*Plectropomus areolatus*) produced by the fish spawning aggregation estimated with the Ribbens function, $f(d) = A\,exp(-Bd^3)$. The solid black line is the maximum likelihood fit ($A = 0.15$; $B = 4.2 \times 10^{-5}$), with vertical lines demarcating the distances within which 50% and 95% of larvae are predicted to settle. Dashed lines show 95% bootstrap confidence intervals (see the Supplemental Experimental Procedures and Figures S1 and S2). Juveniles were collected a maximum of 33 km from the FSA, and the shape of the kernel from 33–80 km (indicated by gray lines) is therefore an extrapolation to the scale of management in our study area. See also Figures S1 and S2.

### Genetic and Parentage Analyses

All adult and juvenile *P. areolatus* were genotyped with a panel of 23 polymorphic microsatellites. Categorical allocation of parent-offspring relationships was assessed using a maximum likelihood approach in FAMOZ [36] (see the Supplemental Experimental Procedures). Recent work has shown that FAMOZ performs well and provides similar results as other parentage assignment methods when 20 or more polymorphic microsatellite loci are used [37]. Juveniles were tested against the total pool of sampled adults. Type I and type II assignment error rates of 0.01% and 1.4%, respectively, were calculated from test simulations [38].

### Accession Numbers

The GenBank accession numbers for the 19 new microsatellite sequences reported in Table S1 are KC602414–KC602432.

### Supplemental Information

Supplemental Information includes two figures, two tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.03.006.

### Acknowledgments

We thank the communities of Timonai, Tawi, Locha, Pere, and Mbunai for their assistance and permission to work on their reefs; C. Costello for field assistance; N. Tolou and S. Baksay for genetic analysis; D.C. Lou for otolith analysis; R.H. Kuiter and J.E. Randall for photographs; and S.R. Connolly, A. Green, T.P. Hughes, K. McLeod, M.S. Webster, and R. Weeks for comments on drafts. Funding was provided by the Australian Research Council (ARC), ARC Centre of Excellence for Coral Reef Studies, The Nature Conservancy's Rodney Johnson/Katherine Ordway Stewardship Endowment, National Fish and Wildlife Foundation, and The David and Lucille Packard Foundation. This work was conducted in accordance with James Cook University's ethics guidelines for research involving animal subjects and human participation.

Received: December 18, 2012
Revised: February 12, 2013
Accepted: March 1, 2013
Published: March 28, 2013

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