

# Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park

DAVID H. WILLIAMSON,\*† HUGO B. HARRISON,\* GLENN R. ALMANY,\*‡ MICHAEL L. BERUMEN,§ MICHAEL BODE,\*¶ MARY C. BONIN,\*† SEVERINE CHOUKROUN,\*\* PETER J. DOHERTY,†† ASHLEY J. FRISCH,\*‡‡ PABLO SAENZ-AGUDELO‡‡‡§§ and GEOFFREY P. JONES\*†

\*Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld 4811, Australia, †Marine Biology and Aquaculture, College of Science and Engineering, James Cook University, Townsville, Qld 4811, Australia, ‡National Center for Scientific Research (CNRS), USR 3278 CNRS-EPHE CRIOBE, University of Perpignan, 66860 Perpignan Cedex, France, §Red Sea Research Center, King Abdullah University of Science and Technology, 23955-6900 Thuwal, Kingdom of Saudi Arabia, ¶ARC Centre of Excellence for Environmental Decisions, School of BioSciences, University of Melbourne, Parkville, Melbourne, Vic. 3010, Australia, \*\*Physical Sciences, College of Science, Technology and Engineering, James Cook University, Townsville, Qld 4811, Australia, ††Australian Institute of Marine Science, PMB#3, Townsville MC, Qld 4810, Australia, ‡‡Reef HQ, Great Barrier Reef Marine Park Authority, Townsville, Qld 4810, Australia, §§Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile

## Abstract

Larval dispersal is the key process by which populations of most marine fishes and invertebrates are connected and replenished. Advances in larval tagging and genetics have enhanced our capacity to track larval dispersal, assess scales of population connectivity, and quantify larval exchange among no-take marine reserves and fished areas. Recent studies have found that reserves can be a significant source of recruits for populations up to 40 km away, but the scale and direction of larval connectivity across larger seascapes remain unknown. Here, we apply genetic parentage analysis to investigate larval dispersal patterns for two exploited coral reef groupers (*Plectropomus maculatus* and *Plectropomus leopardus*) within and among three clusters of reefs separated by 60–220 km within the Great Barrier Reef Marine Park, Australia. A total of 69 juvenile *P. maculatus* and 17 juvenile *P. leopardus* (representing 6% and 9% of the total juveniles sampled, respectively) were genetically assigned to parent individuals on reefs within the study area. We identified both short-distance larval dispersal within regions (200 m to 50 km) and long-distance, multidirectional dispersal of up to ~250 km among regions. Dispersal strength declined significantly with distance, with best-fit dispersal kernels estimating median dispersal distances of ~110 km for *P. maculatus* and ~190 km for *P. leopardus*. Larval exchange among reefs demonstrates that established reserves form a highly connected network and contribute larvae for the replenishment of fished reefs at multiple spatial scales. Our findings highlight the potential for long-distance dispersal in an important group of reef fishes, and provide further evidence that effectively protected reserves can yield recruitment and sustainability benefits for exploited fish populations.

**Keywords:** coral trout (*Plectropomus* spp.), Great Barrier Reef Marine Park, larval connectivity, no-take marine reserves, parentage analysis, recruitment

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Correspondence: David H. Williamson, Fax: +61 7 4725 5043;  
E-mail: david.williamson@jcu.edu.au

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## Introduction

Marine populations and the ecosystems that support them are subject to a vast array of anthropogenic impacts, from overharvesting and destructive fishing practices to coastal habitat degradation, pollution and the escalating effects of climate change (Pauly *et al.* 1998; Myers & Worm 2003; Brodie *et al.* 2012). Networks of no-take marine reserves are increasingly established in coastal seascapes with the primary goals of conserving biodiversity and/or enhancing the sustainability of exploited fish populations (Roberts *et al.* 2005; Mora *et al.* 2006; Levin & Lubchenco 2008; Wood *et al.* 2008; Gaines *et al.* 2010; Green *et al.* 2014). There are now numerous examples of increased abundance, mean size, age and per-capita fecundity of exploited species within adequately protected reserves (Lester *et al.* 2009; Graham *et al.* 2011; Edgar *et al.* 2014; Baskett & Barnett 2015). These effects can also extend to entire assemblages, with increasing evidence that reserves can contribute to the restoration of biodiversity and community trophic structure (Lester *et al.* 2009; Babcock *et al.* 2010; Graham *et al.* 2011, 2015). However, for the full potential of reserves to be realized, these ecological improvements need to be exported beyond the boundaries of individual protected areas.

Several studies have demonstrated that reserves can provide adult 'spillover' that contributes to local fishery production in reef habitat that is contiguous with reserves (McClanahan & Mangi 2000; Russ *et al.* 2004; Abesamis & Russ 2005; Goni *et al.* 2010; Kerwath *et al.* 2013). Demonstrating reserve effects over broader seascapes has proved more challenging however, primarily due to the difficulty of resolving patterns of larval dispersal, the key process by which populations of most marine organisms are connected and replenished (Cowen *et al.* 2000; Jones *et al.* 2007). Most inferences about larval dispersal patterns and the spatial scales over which reserves may contribute to population replenishment come from biophysical models. Many advanced models can predict dispersal patterns by integrating high-resolution physical oceanographic data with biological information such as the timing of spawning and the pelagic larval duration (PLD) of focal species (Cowen *et al.* 2006; Paris *et al.* 2007; Pelc *et al.* 2010). However, there are few empirical data that can be used to ground-truth these predictions or independently verify that reserve networks can contribute to regional conservation and fishery management initiatives (Sale *et al.* 2005; Gaines *et al.* 2010; McCook *et al.* 2010).

The development of transgenerational isotope labeling and genetic parentage analyses have provided a means to track the dispersal of reef fish larvae that

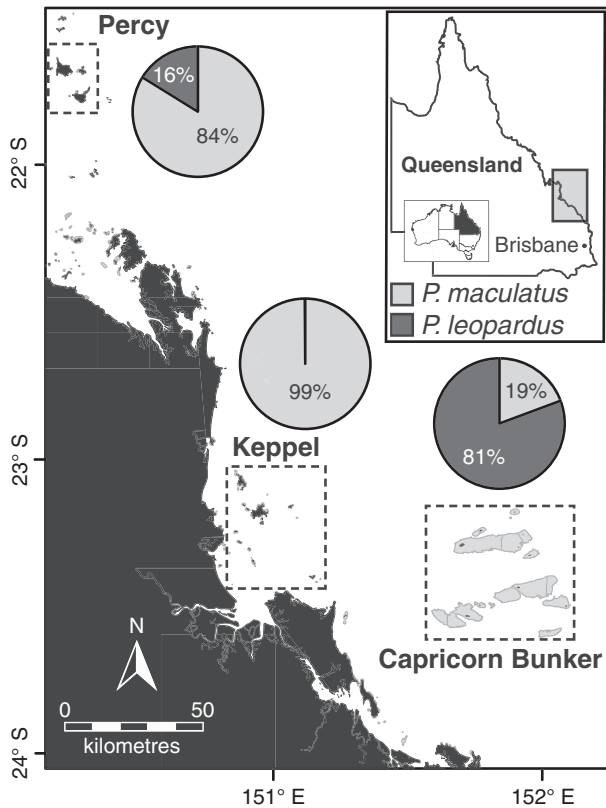
settle either on or in close proximity to their natal reef (Jones *et al.* 2005; Almany *et al.* 2007, 2013; Berumen *et al.* 2012; Buston *et al.* 2012; Saenz-Agudelo *et al.* 2012; D'Aloia *et al.* 2014). These approaches have also been used to quantify connectivity in small reserve networks (Planes *et al.* 2009) and the contribution of reserves to recruitment in adjacent fished areas (Planes *et al.* 2009; Harrison *et al.* 2012). The vast majority of these empirical studies have been limited to tracking larval dispersal over distances of <40 km, much smaller than the potential dispersal distances of most marine fishes and invertebrates, and smaller than the scales of many existing reserve networks. Several empirical studies have demonstrated that coral reef fish larvae may successfully disperse over hundreds of kilometres (Bay *et al.* 2004; Christie *et al.* 2010; Gaither *et al.* 2011; Simpson *et al.* 2014); however, the pattern and relative strength of connectivity across large networks of reserves have not been quantified.

The principal objective of this study was to describe patterns of larval dispersal for two species of grouper (Serranidae), the bar-cheek coral trout (*Plectropomus maculatus*) and the leopard coral trout (*Plectropomus leopardus*), among coral reefs distributed across a broad seascape in the southern Great Barrier Reef Marine Park (GBRMP). To begin, underwater visual censuses (UVC) were undertaken to document the distribution and abundance of the two grouper species in the region and differences in abundance on reserve and nonreserve reefs. We then collected a large number of DNA samples from adults and juveniles of each species, and used genetic parentage analysis to identify juvenile fish that were the progeny of adults sampled in three clusters of reefs that are separated by distances up to 220 km. Assigned juveniles were used to assess the spatial scale and directionality of larval dispersal trajectories among reefs, and fit dispersal kernels. We also aimed to document occurrences of larval exchange among reserve and nonreserve reefs within and among regional reef clusters.

## Methods

### Study locations

This study was conducted in the Keppel Islands (23°10'S, 150°57'E), the Percy Islands (21°42'S, 150°18'E) and the Capricorn Bunker reefs (23°25'S, 151°46'E) in the southern section of GBRMP, Australia (Fig. 1). The Keppel and Percy Island groups are archipelagos of high continental islands surrounded by fringing coral reefs, while the Capricorn Bunker group comprises emergent platform reefs located on the outer margin of the continental shelf. The vast majority of the seafloor



**Fig. 1** Study location map and coral trout species composition. Tissue samples were collected from adult and juvenile coral trout (*Plectropomus maculatus* and *Plectropomus leopardus*) on reefs in the Keppel, Percy and Capricorn Bunker regions in the Great Barrier Reef Marine Park. Pie charts illustrate the proportional composition of the two coral trout species within each focal region.

surrounding the three focal reef clusters is dominated by open sand habitat, and apart from several deep-water shoals to the north of the Capricorn Bunker group, there are no other significant coral reef habitats within the study domain (Fig. 1).

At the Keppel Islands, fringing coral reefs cover ~700 ha, of which 196 ha (~28%) is protected within a network of no-take marine reserves. Three reefs (Middle Island, Halfway Island and Egg Rock) have been reserves since 1987, while four additional reefs (Clam Bay, Monkey Bay and North Keppel Island) were designated as reserves in July 2004. Aside from one no-entry (preservation zone) reef at Peak Island, the remaining reefs in the Keppel Islands are nonreserve areas that are open to fishing. The three main islands that comprise the Percy Island group (Middle Percy, South Percy and Northeast Percy) are located ~80 km from the mainland and are more remote and less frequently visited by fishers than are the Keppel Islands. The Percy Islands are surrounded by ~1870 ha of fringing coral reefs, all of

which are open to fishing. The Capricorn Bunker group comprises a vast area of platform reefs, many of which have extensive reef flat and lagoon habitats. This study focused on eleven reefs in the northern section of the Capricorn Bunker group, bound by Polmaise Reef (southwest), Northwest Reef (northwest), North Reef (northeast) and One Tree Reef (southeast). The eleven focal reefs have a total reef area of nearly 25 700 ha, of which ~14 700 ha (~57%) is designated as no-take marine reserve and 11 000 ha (~43%) is open to fishing.

#### Study species

Two closely related species of grouper (Serranidae) were examined in this study, the bar-cheek coral trout (*Plectropomus maculatus*) and the leopard coral trout (*Plectropomus leopardus*). Both species inhabit coral reefs throughout the central Indo-Pacific region. Within the GBRMP, *P. maculatus* are generally most abundant on inner shelf and fringing reefs, while *P. leopardus* are the most abundant coral trout species on mid- and outer shelf reefs (Mapstone *et al.* 1998). Both species are heavily exploited throughout their geographic ranges, and in the GBRMP, they are highly targeted by both commercial and recreational fishers (Sadovy de Mitcheson *et al.* 2013). Rapid and sustained increases in mean density, body size and biomass of coral trout have been recorded on reserve reefs throughout the GBRMP, while populations on nonreserve reefs have remained relatively stable (Williamson *et al.* 2004; Russ *et al.* 2008; McCook *et al.* 2010; Emslie *et al.* 2015) (see Supplementary Material for further information on coral trout biology, ecology and fishery status).

#### Estimation of coral trout density, population size and the effects of reserves

Underwater visual census (UVC) were conducted on focal reserve and nonreserve reefs within the three study regions to assess the effects of reserves on *Plectropomus* spp. population densities and to provide a baseline for estimating total population sizes. A towed-GPS UVC method was used, with replicated 10-min UVC tracks surveyed within reef slope, reef crest, reef flat and lagoon habitats on each focal reef. Observers recorded the number and estimated the total length (5 cm categories) of all *P. maculatus* and *P. leopardus* sighted on each UVC track. Mean densities of adult coral trout (*P. maculatus* and *P. leopardus* pooled) were calculated for reserves and nonreserves in each region, and two-factor analysis of variance (ANOVA) was used to test the significance of density differences among management zones and regions (see Supplementary Material for further detail on the UVC method and the

estimation of coral trout densities and total population sizes).

### Sampling of coral trout populations

Adult and juvenile coral trout were sampled from reefs in the Keppel, Percy and Capricorn Bunker regions between September 2011 and August 2013. At the Keppel Islands, intensive sampling of adults for DNA profiling was concentrated in, but not exclusive to, focal no-take reserves. Sampling of juveniles at the Keppel Islands was undertaken on all reserve and nonreserve reefs with effort proportional to the relative area of each reef. At the Percy Islands and Capricorn Bunker reefs, sampling of adults and juveniles was opportunistic, but included as many reserve and nonreserve reefs as possible.

Adult fish were sampled using either hook-and-line or modified tissue biopsy probes (PneuDart, USA). Coral trout captured using hook-and-line were visually identified as *P. maculatus* or *P. leopardus*, measured for TL, 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 was estimated to the nearest 5 cm category. Juvenile coral trout were collected by divers using various methods including low-calibre spear guns, hand spears, clove oil and small fence nets.

Densities of juveniles of both species were found to be highest on reef flats and in shallow lagoons with patch reefs dispersed within expanses of coral rubble and sand. Lower densities of juveniles were encountered in rubble-dominated habitats at the base of reef slopes, particularly in the vicinity of small patch reefs. All collected juvenile coral trout were measured for TL, and sagittal otoliths were removed for age determination, and to define the spawning date and larval dispersal period for any parentage-assigned juveniles. All tissue samples were preserved in 95% high-grade ethanol. Juvenile *P. maculatus* and *P. leopardus* have very similar morphology and colour patterns such that many of the collected juveniles in the smallest size-class (<5 cm TL) could not be identified to species in the field. As a result, juvenile coral trout were later identified to species level using the genetic analyses methods defined in Harrison *et al.* (2014).

A total of 880 adult and 1190 juvenile *P. maculatus*, and 659 adult and 199 juvenile *P. leopardus* were sampled across the three study regions (Tables 1 and S1). For *P. maculatus*, 61% of the adult samples and 38% of the juvenile samples were collected from reserve reefs,

while for *P. leopardus*, 65% of the adult samples and 52% of the juvenile samples were collected from reserve reefs. All other samples were collected from nonreserve reefs. The proportion of the adult coral trout populations sampled on focal reefs ranged from ~1% to 21% for *P. maculatus*, and from <1% to 41% for *P. leopardus* (see Table S1).

### Genetic parentage analyses

Genomic DNA was extracted from ~2 mm<sup>2</sup> of fin or muscle tissue and screened at 25 microsatellite loci following the protocol described in Harrison *et al.* (2014). One locus in *P. maculatus* (*Pma112*) and four loci in *P. leopardus* (*Pma036*, *Pma097*, *Pma109*, *Pma112*) presented significant departure from Hardy–Weinberg expectations and were excluded from subsequent analyses. In addition, locus *Pma036* was removed from the *P. maculatus* data set due to the presence of a large number of rare alleles that may have skewed the parentage analyses. The genetic diversity of sampled *P. maculatus* and *P. leopardus* populations among reef clusters was estimated from the entire sample of individuals for each species using an analysis of molecular variance (AMOVA) with significance tested over 9999 permutations in GenoDive v2.0 (Meirmans & Van Tien-deren 2004). There was no evidence of genetic structure among regional reef clusters for *P. leopardus* ( $F_{ST} = 0.000$ ,  $P = 0.458$ ), and while there was some variation in genetic diversity of *P. maculatus* populations among regions ( $F_{ST} = 0.001$ ,  $P < 0.001$ ), it was not considered ecologically significant.

All collected juveniles were screened against the total pool of adult samples to reveal parent–offspring relationships, which were identified using a maximum-likelihood approach implemented in the software program FAMOZ (Marshall *et al.* 1998; Gerber *et al.* 2003). 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 Monte Carlo simulated LOD scores from 50 000 known parent–offspring pairs and 50 000 unrelated pairs. These were identified as 4.0 for *P. maculatus*, 5.0 for *P. leopardus* and 15.0 for the assignment to parent pairs in both species. 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 LOD thresholds. 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 0.63% (false positive – type I error) in *P. maculatus* and 0.9%

**Table 1** Summary of sampled and parentage-assigned juvenile *Plectropomus maculatus* and *Plectropomus leopardus*. The three right-hand columns list the proportion of assigned juveniles that self-recruited back to their natal reefs, the proportion that were sourced from reefs within the natal region (including natal reef) and the proportion of that were sourced from reefs beyond the natal region. Values in bold type represent the overall pooled totals

Species	Region	No. Juv. sampled	No. Juv. assigned	Prop. Juv. assigned	Proportion of assigned juveniles from source		
					Natal reef	Natal region	Other region
<i>P. maculatus</i>	Keppel	454	31	0.07	0.03	0.52	0.48
	Percy	425	22	0.05	0.14	0.14	0.86
	Capricorn Bunker	319	16	0.05	0.25	0.44	0.56
	<b>Total</b>	<b>1190</b>	<b>69</b>	<b>0.06</b>	<b>0.12</b>	<b>0.38</b>	<b>0.62</b>
<i>P. leopardus</i>	Keppel	3	0	0	0	0	0
	Percy	2	1	0.50	0	0	1.00
	Capricorn Bunker	194	16	0.08	0.19	0.88	0.12
	<b>Total</b>	<b>199</b>	<b>17</b>	<b>0.09</b>	<b>0.18</b>	<b>0.82</b>	<b>0.18</b>

in *P. leopardus*. Conversely, the probability of a true parent-offspring pair not being identified knowing that the true parent was sampled was <0.01% (false negative – type II error) in both species. Any identified parent-offspring pairs that presented over three confirmed mismatches between parent and offspring genotypes were excluded from the final list of assigned pairs (see Harrison *et al.* 2014 for further detail).

#### Larval dispersal scale and direction

Observed larval dispersal distances and directions were assessed by plotting the GPS coordinates of the sampling locations of each parentage-assigned adult and juvenile fish onto a 15 m × 15 m geographic grid overlaid onto high-resolution satellite imagery. The sampling location coordinates of each assigned adult and juvenile fish were subsequently adjusted to the nearest geographic grid centre. A straight line between the two grid centres was defined as the minimum Euclidean distance and angular direction of dispersal between the natal (adult) location and the settlement (juvenile) location. Dispersal trajectory distributions were generated by pooling the observed dispersal distances and directions of each parentage-assigned juvenile *P. maculatus* and *P. leopardus* into 5 km distance bins and 10° direction bins.

Digitized maps of available reef habitat were generated from high-resolution satellite imagery for each of the sampled reefs, and these maps were overlaid with the 15 m × 15 m geographic grid.

The distance and direction between all sampled coral reef habitats within and among the three focal regions were quantified using GIS, and distributions of habitat distance (within 5-km bins) and direction (10° bins)

were generated for all possible connections that could have been identified by our sampling regime. Due to differences in the distribution and sampling locations of *P. maculatus* and *P. leopardus*, the habitat distance and direction distributions were species-specific. Chi-square tests of independence were used to examine whether the observed larval dispersal distance, and direction distributions were independent of the expected distributions of distance and direction among all sampled reef habitats for both species. All GIS spatial analyses were conducted using ArcGIS (ESRI, Redlands, CA, USA).

#### Fitting dispersal kernels

Larval dispersal kernels were fitted to the observed parentage assignments using maximum-likelihood methods. Dispersal kernels estimate the rate at which the strength of dispersal connections decays with distance from the natal population, and are commonly used in both ecological and conservation theory (Botsford *et al.* 2009; Bode *et al.* 2011). Each candidate kernel  $\rho_i(\theta, d)$  calculates the amount of dispersal between two reefs relative to local retention (i.e. the amount of dispersal back to the natal reef), based on the kernel's functional form  $i$ , its parameterization  $\theta$  and the distance  $d$  between two reefs. The likelihood that a particular kernel described the juveniles (assigned and unassigned) sampled at a given reef was calculated using the multinomial distribution, on the assumption that the genotyped juveniles are an unbiased sample from the settling cohort. Note that for a given dispersal kernel, the settling cohort (and therefore the likelihood) is calculated using: (i) sampled adults on sampled reefs, (ii) unsampled adults on sampled reefs and (iii)

unsampled adults on unsampled reefs. We compared the best-fit parameters and maximum likelihood of four alternative functional forms for the kernel: three exponential distributions (the Laplacian, Gaussian and Ribbens) and one fat-tailed distribution (the Cauchy). For the best-fit kernel shape and parameterization, we calculated 95% confidence intervals using bootstrap resampling of the reef units, as well as the median dispersal distance and the distance within which 50% and 95% of dispersal occurred. Finally, we assessed how well the best dispersal kernel explained the variation in the data, using a parametric bootstrap goodness-of-fit test. Full details of the fitting processes are provided in Bode *et al.* (2016).

## Results

### Coral trout distribution and abundance

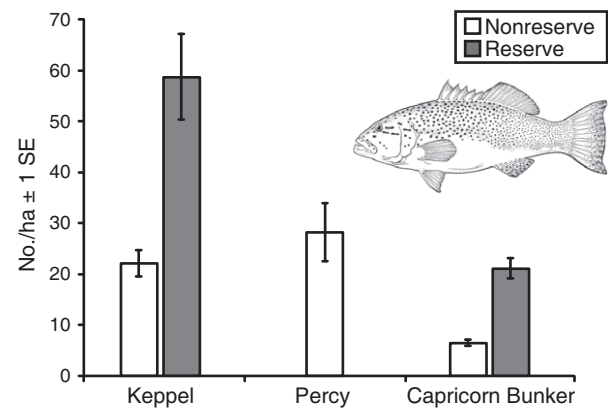
In the Keppel and Percy Islands, between 84% and 99% of all sighted adult coral trout were *Plectropomus maculatus*, while *Plectropomus leopardus* represented 81% of coral trout sighted on reefs in the Capricorn Bunker region (Fig. 1). Over 50% of the *P. maculatus* sighted in the Capricorn Bunker region were recorded on Polmaise Reef and Northwest Reef, which are located at the inner shelf (western) margin of the reef system. Lower numbers of *P. maculatus* were recorded on the more seaward (eastern) Capricorn Bunker reefs, where almost all sighted coral trout were identified as *P. leopardus*.

Adult coral trout densities were more than twice as high on reserve reefs than on nonreserve reefs in the Keppel Islands (ANOVA;  $F_{2,195}$  d.f. = 10.4,  $P < 0.001$ ) and approximately three times higher on reserve reefs than on nonreserve reefs in the Capricorn Bunker region (ANOVA;  $F_{2,298}$  d.f. = 27.4,  $P < 0.001$ ) (Fig. 2). All sampled reefs in the Percy Islands were open to fishing (nonreserve).

### Parent–offspring assignments

Approximately 6% of sampled *P. maculatus* juveniles (69 of 1190) and 9% of sampled *P. leopardus* juveniles (17 of 199) were genetically assigned to a single sampled parent (Table 1). No juveniles of either species were assigned to both parents. For *P. maculatus*, the mean LOD ( $\pm$  SD) score across all parent–offspring assignments was  $6.8 \pm 3.1$  (range, 4.0–25.6), while for *P. leopardus* it was  $7.5 \pm 2.3$  (range, 5.2–15.2).

Of the 69 parentage-assigned juvenile *P. maculatus*, 45% were collected from reefs in the Keppel Islands, 32% were collected in the Percy Islands and 23% were collected from the Capricorn Bunker reefs. The vast



**Fig. 2** Mean density (No./ha  $\pm$  1 SE) of adult ( $\geq 30$  cm TL) coral trout (*Plectropomus maculatus* and *Plectropomus leopardus* pooled) on no-take marine reserve and nonreserve reefs in the Keppel, Percy and Capricorn Bunker regions during the sampling period (2011–2013).

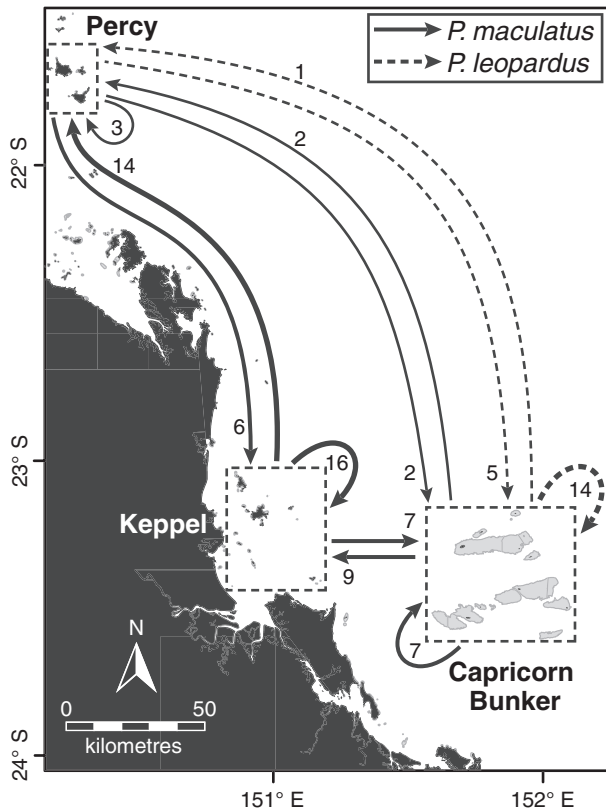
majority (94%) of the 17 assigned *P. leopardus* juveniles were collected from reefs in Capricorn Bunker group. Only three *P. leopardus* juveniles were collected in the Keppel Islands and none were assigned to a parent, while one of the two juvenile *P. leopardus* collected in the Percy Islands was assigned (Table 1).

Otolith age analyses revealed that the 69 assigned *P. maculatus* juveniles ranged in age from 49 to 255 days at the time of collection and that the 17 assigned *P. leopardus* juveniles ranged in age from 72 to 300 days. The mean pelagic larval duration (PLD), identified using the ‘settlement-mark’ on otoliths, was 26 days ( $\pm 2$  days SD) for both species.

### Larval connectivity at local and regional scales

Parentage analysis indicated substantial larval connectivity of *P. maculatus* and *P. leopardus* populations at both local and regional scales. Both species exhibited retention of larvae to natal reefs, larval exchange among local reefs within regions, and long-distance, multidirectional larval dispersal among regions (Fig. 3). Of the assigned juveniles, 38% of *P. maculatus* (26 of 69) and 82% of *P. leopardus* (14 of 17) recruited either to their natal reef or to reefs within their natal region, while all other assigned juveniles had dispersed between the regions (Fig. 3, Table 2).

Finer scale patterns of retention and dispersal of *P. maculatus* and *P. leopardus* within regions indicated both self-recruitment to natal reefs and connectivity among local reefs (Fig. 4). At the Keppel Islands, most *P. maculatus* juveniles sourced from four focal reserves dispersed throughout the island group, while one juvenile self-recruited to Clam Bay on the southern side of Great Keppel Island (Fig. 4A). The seven assigned



**Fig. 3** Regional-scale dispersal patterns of coral trout larvae. Arrows depict realized larval connectivity from natal to settlement reefs for 69 parentage-assigned juvenile *Plectropomus maculatus* (solid arrows) and 17 assigned *Plectropomus leopardus* juveniles (dashed arrows). Numbers adjoining each arrow are the number of assigned juveniles that dispersed from natal regions to settlement regions.

*P. maculatus* juveniles from the Capricorn Bunker region were all collected at Polmaise Reef, and they had either self-recruited or dispersed from Northwest Reef (Fig. 4B). Assigned *P. leopardus* juveniles had dispersed among reefs throughout the Capricorn Bunker region, with some self-recruitment at Tryon reef (Fig. 4B).

#### Larval dispersal distance

Observed dispersal distances of parentage-assigned juvenile coral trout ranged from <200 m to a maximum of ~250 km (Fig. 5). Larval dispersal among reefs within regions covered linear distances of up to ~50 km, while dispersal among regions involved minimum dispersal distances of at least 70 km and up to ~250 km (Fig. 5). For *P. maculatus*, 9.4% of assigned juveniles had dispersed to reefs within 5 km of their natal reef, 29.6% had dispersed within 50 km, and 71.9% had dispersed <100 km. For *P. leopardus*, 15.9% of

assigned juveniles dispersed <5 km, 83.7% dispersed <50 km and 84.2% dispersed <100 km. The distributions of dispersal distances for both species exhibited distinct modes corresponding with the availability of suitable reef habitat and the spatial distribution of population sampling (Fig. 5). For *P. maculatus*, the distribution of observed dispersal distances was independent of the spatial distribution of sampled reef habitats ( $\chi^2 = 118.2$ , d.f. = 60,  $P < 0.001$ ). For *P. leopardus*, observed dispersal distances were significantly influenced by the distribution of sampled habitats ( $\chi^2 = 27.4$ , d.f. = 60,  $P > 0.05$ ).

#### Dispersal kernels

Dispersal strength declined with distance from the natal population, with the sampled dispersal distances for both species best represented by Laplacian dispersal kernels (Fig. 6). The AIC weights of the Laplacian kernels were 78% for *P. maculatus* and 60% for *P. leopardus*, with the remainder of the support for the fat-tailed Cauchy kernel (22% for *P. maculatus* and 40% for *P. leopardus*). The kernels predicted that *P. leopardus* larvae dispersed substantially longer distances than *P. maculatus*, with 50% of *P. leopardus* settlement within 185 km and 95% of within 811 km, compared with 50% of settlement within 110 km and 95% within 480 km for *P. maculatus* (Fig. 6). The kernel-estimated median dispersal distance was ~190 km for *P. leopardus* and ~110 km for *P. maculatus*.

The estimates of dispersal scale for *P. leopardus* were more uncertain, reflecting the smaller data set and fewer parent-offspring assignments (Fig. 6). Given this uncertainty, the dispersal kernels for *P. leopardus* failed to explain a substantial amount of the dispersal variation, and did no better than the assumption of a well-mixed larval pool (as evidenced by the horizontal 95% upper confidence bound on the kernel). In contrast, the best-fit kernel for *P. maculatus* described the data significantly better than an uninformative null ( $P < 0.001$ ), but the observed maximum log-likelihood was significantly lower than we would expect if dispersal strictly conformed to the kernel dynamics (i.e. the fit is worse;  $P < 0.001$ ). Comparable fit outcomes were found when applying the Cauchy kernel to both species.

#### Larval dispersal direction

Both species exhibited multidirectional dispersal, with the long-distance trajectories reflecting the alignment of the coast and GBR (Fig. 7). Realized dispersal directions for *P. maculatus* larvae were predominantly in a north-westerly direction, with 56.5% of larvae dispersing to

**Table 2** Summary matrix for realized larval connectivity of parentage-assigned juvenile *Plectropomus maculatus* ( $n = 69$ ) and *Plectropomus leopardus* ( $n = 17$ ) among natal reefs (source) and settlement reefs (sink) within both nonreserve and no-take marine reserve management zones in the Keppel, Percy and Capricorn Bunker regions

	Settlement reefs (Juveniles)						Total
	Keppel		Percy Nonreserve	Capricorn Bunker			
	Nonreserve	Reserve		Nonreserve	Reserve		
Natal reefs (Adults)							
<i>P. maculatus</i>							
Keppel							
Nonreserve	0	1	0	0	1	2	
Reserve	8	7	14	1	5	35	
Percy							
Nonreserve	4	2	3	0	2	11	
Capricorn Bunker							
Nonreserve	1	1	0	0	2	4	
Reserve	6	1	5	0	5	17	
69							
<i>P. leopardus</i>							
Percy							
Nonreserve	—	—	0	2	0	2	
Capricorn Bunker							
Nonreserve	—	—	0	3	0	3	
Reserve	—	—	1	2	9	12	
17							

reefs on trajectories of between 270° and 360° from natal reefs (Fig. 7A). For *P. leopardus*, approximately equal numbers of assigned juveniles had dispersed in either a generally northward or southward direction (Fig. 7C). The distributions of observed larval dispersal directions were independent of the distributions of possible directions from all natal reefs to all settlement reefs sampled for both *P. maculatus* ( $\chi^2 = 444.7$ , d.f. = 35,  $P < 0.001$ ) and *P. leopardus* ( $\chi^2 = 180.2$ , d.f. = 35,  $P < 0.001$ ) (Fig. 7).

#### Larval exchange among management zones

Parentage assignments indicated extensive larval exchange between reserve and nonreserve reefs for *P. maculatus* and *P. leopardus*, both at relatively fine scales within regions (Keppel and Capricorn Bunker) and at broader inter-regional scales (Fig. 4). Three-quarters (~75%) of all parentage-assigned juveniles of both species were the progeny of adults on reserve reefs that had either self-recruited to their natal reef (12%), dispersed to another reserve reef (30%) or dispersed to a nonreserve reef (58%). One-quarter (~25%) of the parentage-assigned juveniles were sourced from adults on nonreserve reefs. Of those, ~59% had dispersed among nonreserve reefs while 41% had dispersed from nonreserve to reserve reefs (Table 2).

## Discussion

Resolving patterns of larval dispersal and determining the scales of connectivity in marine metapopulations continues to be recognized as an important challenge in marine ecology, conservation and bioeconomics (Cowen *et al.* 2000; Sale *et al.* 2005; Jones *et al.* 2007; Jones 2015). It has been theorized that metapopulation persistence is reliant on both short-distance dispersal, including the local retention of juvenile offspring, as well as longer distance dispersal that provides connectivity among distinct habitat patches (Hastings & Botsford 2006; Burgess *et al.* 2014). In recent years, the application of larval tagging studies and genetic parentage analyses has successfully determined larval dispersal trajectories over relatively small spatial scales (Almany *et al.* 2007, 2013; Planes *et al.* 2009; Saenz-Agudelo *et al.* 2011; Berumen *et al.* 2012; Harrison *et al.* 2012). The challenge has been to scale-up these approaches to explore dispersal patterns over a broader range of possible dispersal distances and to provide connectivity information that is relevant to large-scale spatial management objectives.

#### Seascape-scale larval connectivity

Here, we have begun to resolve seascape-scale larval dispersal patterns for two iconic and high-value fishery-



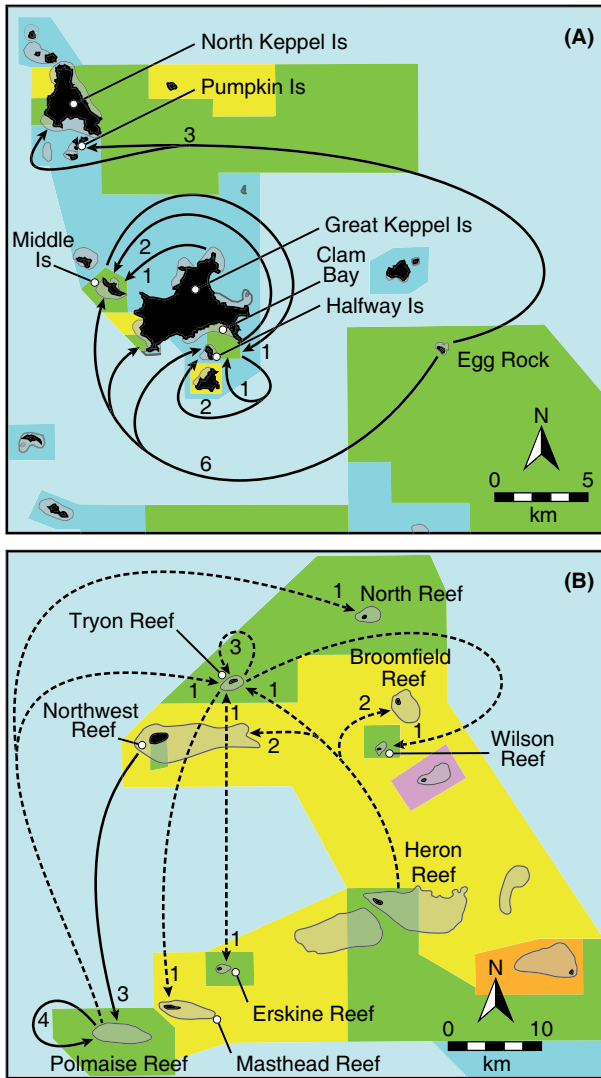


Fig. 4 Local-scale dispersal patterns of coral trout larvae. Arrows depict realized larval connectivity from natal to settlement reefs for each parentage-assigned juvenile *Plectropomus maculatus* (solid arrows) and *Plectropomus leopardus* (dashed arrows). Numbers adjoining each arrow are the number of assigned juveniles that dispersed from natal reefs to settlement reefs. Map colours depict management zones: Marine National Park zones (green) are no-take marine reserves; Conservation Park zones (yellow) permit limited hook-and-line and spear fishing; Habitat Protection zones (dark blue) permit hook-and-line and spear fishing. Other zones were not sampled in this study. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

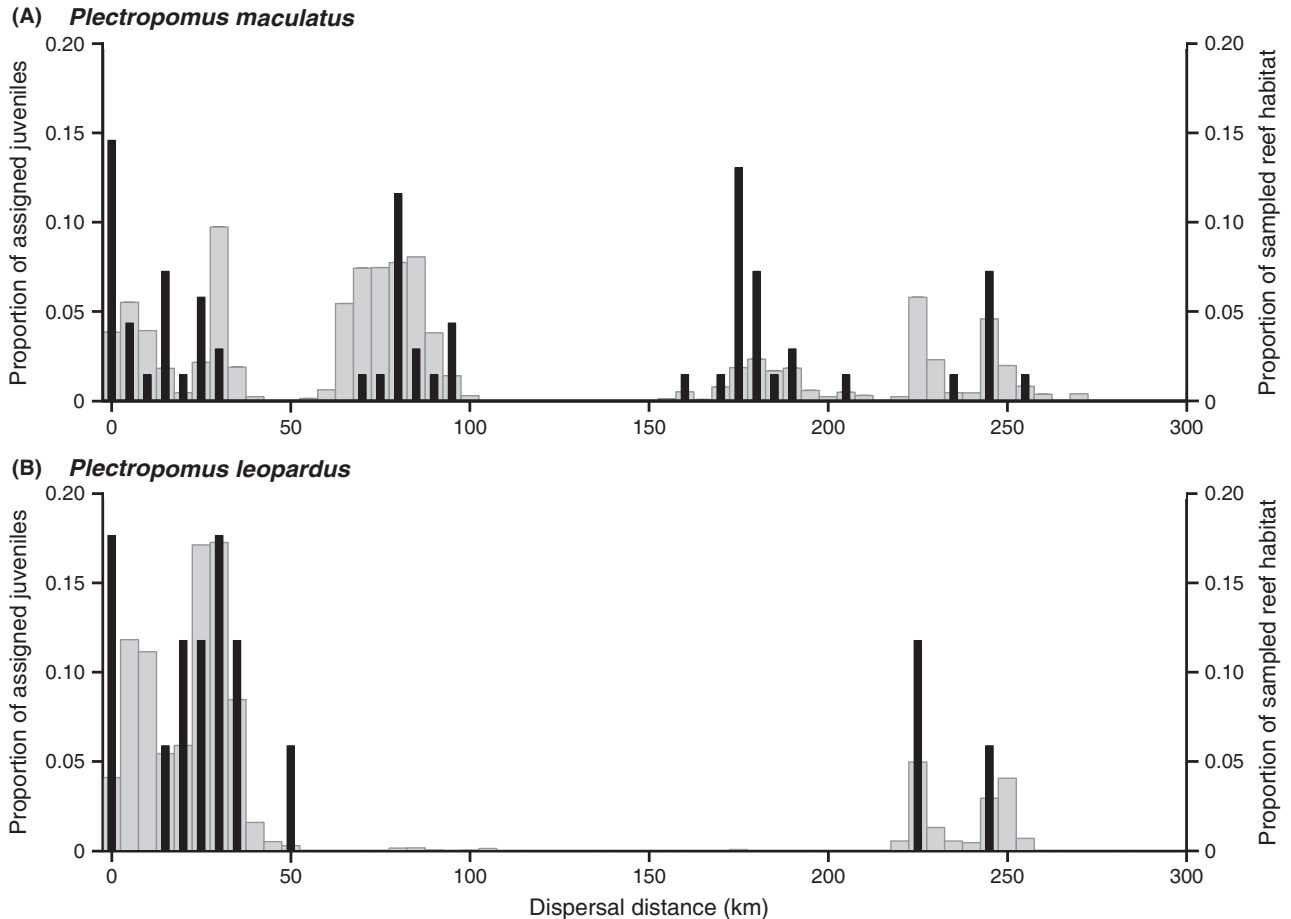
targeted species. Parentage analysis revealed dispersal distances that ranged from 200 m to ~250 km. We identified seven *Plectropomus maculatus* (~10% of assigned juveniles) and three *Plectropomus leopardus* (~17% of assigned juveniles) that had dispersed between 220 and 250 km from their natal reefs. Both *P. maculatus* and *P. leopardus* also exhibited self-recruitment of larvae to

natal reefs and larval exchange among neighbouring reefs within regional clusters. This study adds to growing evidence that larval dispersal in marine fishes may be spread across broad seascapes (Cowen *et al.* 2006; Christie *et al.* 2010; Simpson *et al.* 2014), with both local recruitment and long-distance dispersal contributing to the demography of metapopulations. The large scale of the observed dispersal provides encouraging evidence that marine reserves can provide mutually reinforcing demographic benefits over regional seascapes. However, it also complicates the design of the resulting reserve networks, and the empirical evidence required to understand their performance, given that the population dynamics of an individual reef reflect processes, human activities and conservation decisions over hundreds of kilometres of surrounding reef.

The frequency distribution of observed dispersal distances for *P. leopardus* larvae closely matched the spatial distribution of sampled reef habitats; however, the dispersal distances recorded for *P. maculatus* larvae were less strongly linked to habitat spacing. Furthermore, it was evident that the observed dispersal directions of both species were essentially independent of the directions from natal reefs to available settlement reefs. Despite these findings, there is little doubt that the geographic arrangement of suitable habitat patches can significantly influence realized larval dispersal patterns (Jones *et al.* 2009; Saenz-Agudelo *et al.* 2011; Harrison *et al.* 2012; Pinsky *et al.* 2012; D'Aloia *et al.* 2014). Oceanographic currents and the spacing of reefs together may not necessarily account for the full range of dispersal trajectories observed here. Indeed, coral trout larvae have well-developed auditory and olfactory capabilities, and they are excellent swimmers (Leis & Carson-Ewart 1999; Wright *et al.* 2008). Behavioural attributes of coral trout larvae, including directional or depth-stratified swimming preferences, direction orientation and reef homing abilities, are likely to have influenced the observed dispersal patterns (Kingsford *et al.* 2002; Gerlach *et al.* 2007; Leis *et al.* 2007).

### Dispersal kernels

Potential dispersal patterns are described by larval dispersal kernels, which predict the amount of dispersal that may occur at a given distance from the natal patch, if suitable habitat is available. Both species' dispersal data were best fit by Laplacian distributions, with a decline in dispersal intensity with distance from the natal reef. The kernels predicted that 50% of *P. maculatus* larvae would attempt to settle within 110 km (185 km for *P. leopardus*) of their natal reef and that 95% of larvae would settle onto reefs within 480 km (811 km for *P. leopardus*). The stronger support for the



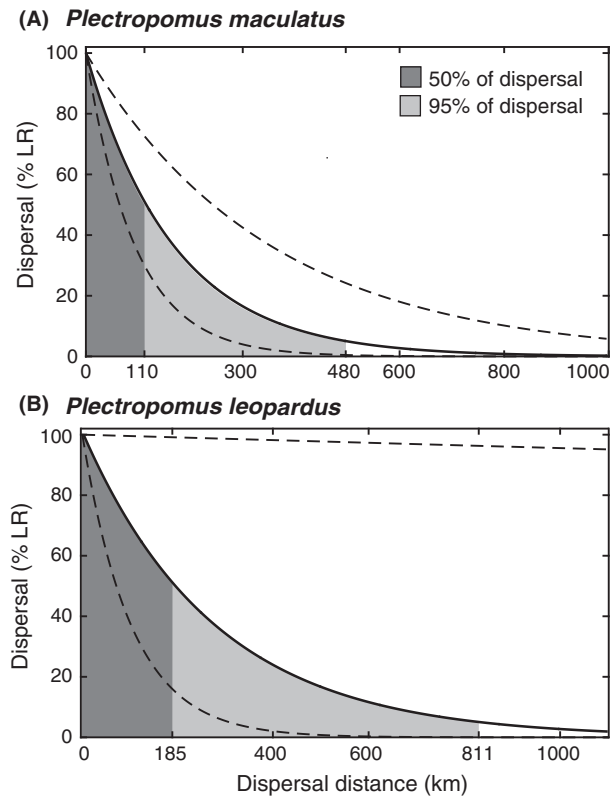
**Fig. 5** Realized dispersal distances of larval coral trout. Frequency distributions of realized linear dispersal distances of assigned juvenile (A) *Plectropomus maculatus* and (B) *Plectropomus leopardus* within 5 km distance categories (black bars). Grey bars define the proportional area of reef habitat available for each species within 5 km distance bins. Blank areas between the habitat distribution clusters are the distance ranges within which sampling was not conducted and/or where there was no known reef habitat supporting either *P. maculatus* or *P. leopardus* populations.

thin-tailed Laplacian fit was somewhat surprising given that the data set contains a substantial number of long-distance dispersers, but it is consistent with other reef fishes (D'Aloia *et al.* 2014). The bootstrap goodness-of-fit tests indicated that the best-fit kernel for *P. maculatus* contains useful information about the scale of larval dispersal; however, it could not account for a large proportion of the observed dispersal variation. This outcome is not unexpected since, as we have discussed, a set of biological and oceanographic factors operate in the southern GBR that are not effectively described by dispersal kernels, such as directional advective currents and the sensory and locomotive behaviour of the larvae. Perhaps most importantly, dispersal within reef groups (e.g. between reefs in the Keppel Islands region) is likely to be driven by an oceanographic regime characterized by shallow-water bathymetry, tidal forcing and decreased mixing (Andutta *et al.* 2012). In contrast, broader scale dispersal among reef groups will

predominantly be influenced by prevailing winds, currents and mesoscale circulation features. A statistical kernel that offers insights into larval dispersal distances at broad, inter-regional scales will likely have difficulty explaining the fine-scale patterns within reef groups, and vice versa. In some cases, mixture models that combine both broad-scale kernels for inter-regional dispersal and fine-scale kernels for within region dispersal may yield superior fit. However, given the increasing sophistication of coupled biophysical models, the observed variation will best be explained and larval dispersal predicted by direct comparisons between genetic parentage data and these mechanistic models.

#### *Dispersal directionality*

Multidirectional dispersal of coral trout larvae was recorded both within, and among all three focal regions across a range of distances up to ~250 km.



**Fig. 6** Dispersal kernels of larval coral trout. Dispersal kernels of larval coral trout (A) *Plectropomus maculatus* and (B) *Plectropomus leopardus*, sourced from reefs in the Keppel, Percy and Capricorn Bunker regions. Kernels were estimated using the Laplacian function ( $\rho(k,d) = \exp[-kd]$ ). Solid black lines are the maximum-likelihood fit, while dashed lines show 95% bootstrap confidence intervals. Grey-shaded areas indicate the distances within which 50% and 95% of larvae are predicted to settle. Juvenile coral trout were sampled at a maximum distance of ~250 km from sampled adult source populations, and the shape of the kernel beyond 250 km is therefore an extrapolation to the maximum scale of 1000 km.

Hydrodynamic models of the Keppel Bay region, and of the southern Great Barrier Reef (GBR) lagoon more broadly, have shown both complex circulation patterns and net current flow from south to north (Luick *et al.* 2007; Lambrechts *et al.* 2008). Although the East Australian Current (EAC) is the dominant oceanographic feature flowing north to south along the continental shelf margin, southeast trade winds force the predominant current flow within the GBR lagoon from south to north for much of the year (Lambrechts *et al.* 2008). The observed skew towards northwesterly dispersal trajectories of *P. maculatus* larvae observed here may be closely linked to the net hydrodynamic flow in the study region. Additionally, the transient 'Capricorn Eddy' circulation feature within the study region may at least partially explain the observed bidirectional dispersal

patterns between the three regions, particularly if the eddy was operational during the spring–summer peak spawning periods of 2011–2012 and 2012–2013 (Weeks *et al.* 2010).

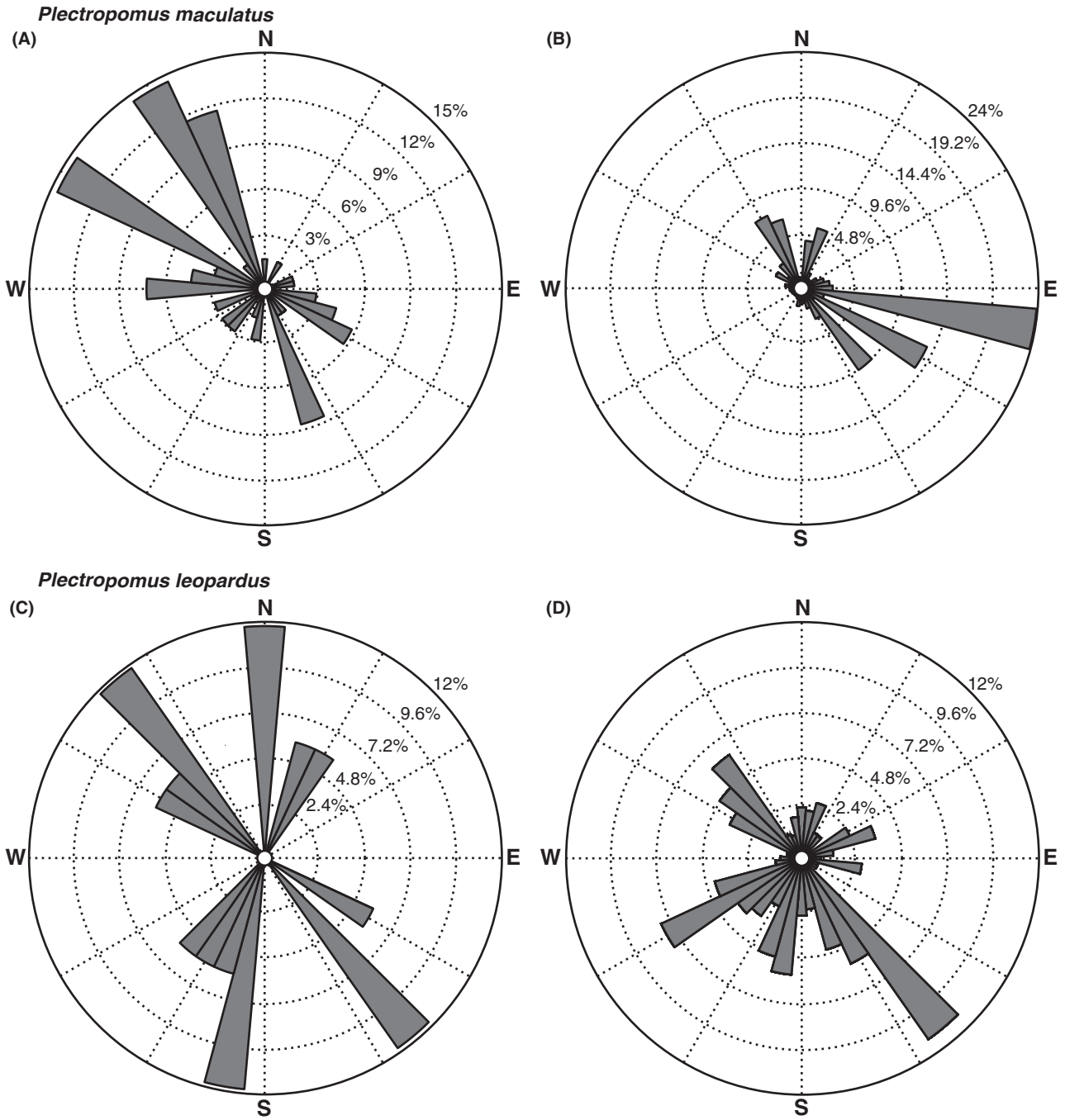
The development and expansion of coupled biophysical larval dispersal models will continue to refine estimates of dispersal distance and directionality. Given that empirical larval connectivity studies are invariably geographically and temporally constrained, improved models should facilitate scaling up of connectivity information for an expanded range of focal species. Broader utilization of empirical data such as those presented here will play an important role in the validation of such models.

#### *Connectivity among reserve and nonreserve reefs*

This study provides further evidence that no-take reserves can provide valuable sources of larvae for the replenishment of populations on surrounding reefs. Approximately 75% of assigned coral trout juveniles were identified as the progeny of adults in reserves, while 25% were sourced from nonreserve reefs. Although our findings provide clear evidence of larval export from reserve to nonreserve reefs, sampling of adult coral trout populations was skewed towards reserve reefs (61% of adult *P. maculatus* samples, 65% of *P. leopardus* samples) and this must be taken into account when interpreting the findings. Despite extensive population sampling and UVC effort, the vast area of reef habitat in the study region meant that the proportions of adult fish sampled at each reef could not be accurately estimated, and a number of reefs within the study region could not be adequately sampled. As such, specific estimates of the contributions of reserve and nonreserve reefs to total coral trout recruitment could not be established within the scope of the present study. Ultimately, empirical data such as those presented here must be incorporated into metapopulation models that can be used to estimate the contribution of reserve networks to population persistence and fishery productivity (Burgess *et al.* 2014).

#### *Implications for postdisturbance recovery of coral trout populations*

Reefs in the Keppel Islands were severely impacted by a series of major climatic disturbance events between 2006 and 2013, with significant loss of live hard coral and subsequent declines in the abundance of most fish species, including coral trout (*P. maculatus*) (Williamson *et al.* 2014). Williamson *et al.* (2014) identified several reefs in the Keppel Islands that provided postdisturbance refuges for *P. maculatus*, all of which were within



**Fig. 7** Realized dispersal directions of larval coral trout. Realized dispersal direction trajectories of assigned juveniles pooled into 36 equal (10°) direction categories for (A) *Plectropomus maculatus* and (C) *Plectropomus leopardus*. Species-specific reef habitat direction trajectories among all sampled locations for (B). *P. maculatus* and (D). *P. leopardus*. The length of the dispersal direction vectors corresponds to the proportion of assigned juveniles that dispersed along each direction trajectory (as defined by the annotated concentric circles).

reserves. The findings presented here, and those of Harrison *et al.* (2012), suggest that reserve reefs in the Keppel Islands provide important local sources of coral trout recruitment that should contribute to population recovery. Our new findings demonstrate that the

Keppel Islands coral trout metapopulation is also being replenished by larval supply from the Percy Islands and the Capricorn Bunker reefs. Two reserve reefs in the Capricorn Bunker group, Northwest Reef and Polmaise Reef, were identified as sources for assigned

juvenile *P. maculatus* collected in the Keppel Islands. This suggests that these two reefs may provide a critical offshore source of larvae for the recovery and long-term persistence of the inshore Keppel Islands *P. maculatus* population. Conversely, our findings also demonstrate that reserve reefs in the Keppel Islands that have escaped the worst effects of disturbances should continue to provide a source of *P. maculatus* larvae for reefs in the Percy and Capricorn Bunker regions.

## Conclusions

This study has provided valuable insights into the larval dispersal patterns of two iconic and economically important coral reef fish species, resolving dispersal at scales up to ~250 km. It documents the largest scale of larval connections between reserve and nonreserve areas recorded to date, suggesting large-scale mixing of populations among management zones within the GBRMP. The findings are highly relevant to the management of exploited fish populations in Australia and globally. Most large reef fishes are heavily targeted wherever fishers can access them, and in many areas, populations of species such as coral trout have been heavily depleted (Sadovy de Mitcheson *et al.* 2013). The implementation of marine reserve networks that aim to protect habitats and restore populations of exploited species is slowly gaining momentum throughout many coastal seascapes (Mora *et al.* 2006; Hamilton *et al.* 2011; Green *et al.* 2014). Furthermore, estimates of larval connectivity are increasingly being used to inform the design of spatial management systems that aim to establish effectively connected reserve networks that can yield both biodiversity conservation and fishery sustainability benefits (Jackson *et al.* 2015; Eastwood *et al.* 2016; Stockwell *et al.* 2016).

The findings presented here build upon those of two previous studies that tracked dispersal of coral trout (*Plectropomus* spp.) larvae and demonstrated recruitment subsidies from reserves at local scales (Harrison *et al.* 2012; Almany *et al.* 2013). These new findings suggest that recruitment subsidies from reserves can also be expected at broader, regional scales. This study has provided further evidence that the combination of effective reserve networks and direct controls on fishery catch and effort can provide a powerful dual approach for enhancing the sustainability and persistence of exploited reef fish populations.

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## Data accessibility

Microsatellite data sets for *Plectropomus leopardus* and *Plectropomus maculatus* are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4m67g>.

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### Supporting information

Additional supporting information may be found in the online version of this article.

### Appendix S1 Methods.

**Table S1** Summary of locations, sample sizes, and population estimates of adult *Plectropomus maculatus* and *Plectropomus leopardus*.