Seascape genomics reveals fine-scale patterns of dispersal for a reef fish along the ecologically divergent coast of Northwestern Australia

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Abstract
Understanding the drivers of dispersal among populations is a central topic in marine ecology and fundamental for spatially explicit management of marine resources. The extensive coast of Northwestern Australia provides an emerging frontier for implementing new genomic tools to comparatively identify patterns of dispersal across diverse and extreme environmental conditions. Here, we focused on the stripey snapper (Lutjanus carponotatus), which is important to recreational, charter-based and customary fishers throughout the Indo-West Pacific. We collected 1,016 L. carponotatus samples at 51 locations in the coastal waters of Northwestern Australia ranging from the Northern Territory to Shark Bay and adopted a genotype-by-sequencing approach to test whether realized connectivity (via larval dispersal) was related to extreme gradients in coastal hydrodynamics. Hydrodynamic simulations using CONNIE and a more detailed treatment in the Kimberley Bioregion provided null models for comparison. Based on 4,402 polymorphic single nucleotide polymorphism loci shared across all individuals, we demonstrated significant genetic subdivision between the Shark Bay Bioregion in the south and all locations within the remaining, more northern bioregions. More importantly, we identified a zone of admixture spanning a distance of 180 km at the border of the Kimberley and Canning bioregions, which collectively experiences the largest tropical tidal range and some of the fastest tidal
1 | INTRODUCTION

Coastal ecosystems contain some of the most productive, diverse and valuable environments on the planet but are also exposed to high anthropogenic stressors such as fishing, tourism, mineral and petrochemical industries, and coastal development (Moore et al., 2016). A robust understanding of the ecological drivers that underpin population regulation in marine systems is pivotal for the effective management of coastal aquatic resources. Larval dispersal is one such driver with particular relevance to coastal management because it has the potential to link the demographic fates of distant populations, as well as provide the genetic diversity necessary for evolutionary adaptation.

Many coastal marine species have restricted home ranges as adults (Cowen & Sponaugle, 2009), and so it is their dispersive planktonic larval stages that promote demographic and genetic connectivity between suitable habitats. Marine larvae exhibit diverse life histories, but typically they are small and have at least some capacity to determine their precise destination (Leis, 2015). The magnitude of larval dispersal is determined by a combination of the physical environment such as ocean currents, habitat distributions and coastal topography, as well as larval attributes such as swimming speed, sensory capabilities and pelagic larval duration (PLD; Leis, 2015; Treml, Ford, Black, & Swearer, 2015). Some species will therefore operate as closed demographic units on small spatial scales (within a few kilometres), whereas others may remain connected over hundreds of kilometres (Almany et al., 2017; Berumen et al., 2012; Saenz-Aguadelo, Jones, Thorrold, & Planes, 2011). Coastal ecosystems can also be topographically complex, which makes correct predictions of connectivity among the network of populations elusive given the environmental variability among sites (Burgess et al., 2014). Even though connectivity may dictate the resilience of entire ecosystems (Selkoe et al., 2016), it is often context dependent, variable among resident taxa (Drew & Barber, 2012) and difficult to directly measure (Krueck et al., 2016). In the light of these challenges, we apply an indirect genomic approach (i.e., proxy) to measure connectivity (Riginos, Crandall, Liggins, Bongaerts, & Treml, 2016).

Single nucleotide polymorphism (SNP) discovery and genotyping (Andrews, Good, Miller, Luikart, & Hohenlohe, 2016) via next-generation sequencing (NGS) provide a means to quantify connectivity within coastal ecosystems with high resolution (Riginos et al., 2016). The high genomic coverage provided by thousands of SNPs means that it is possible to detect signatures of differential natural selection between different environments (Nosil, Funk, & Ortiz-Barrientos, 2009; Rellstab, Gugerli, Eckert, Hancock, & Holderegger, 2015). Access to remotely sensed environmental data such as sea surface temperature and nutrient proxies (e.g., chlorophyll-a) from satellites also provides opportunities to identify the geographic and environmental determinants of genetic structure (Balkenhol, Waits, & Dezani, 2009; Wang & Bradburd, 2014).

The globally unique Northwestern Australian (NWA) marine environment and the Kimberley Bioregion in particular (Chin et al., 2008; Halpern et al., 2015; Wilkinson, 2008) are likely to be subject to proposed increases in industrial developments, fishing and tourist activities (Wood & Mills, 2008). In recognition of the potential for increased anthropogenic stressors in NWA, there has recently been a growth in management activity, including the formation of major marine reserves (e.g., Department of Parks and Wildlife 2016). In some cases, management strategies have been implemented in the absence of basic knowledge of ecological processes operating within these ecosystems (Moore et al., 2016). Most marine ecological enquiry in NWA has focused on characterizing biodiversity, community assemblages and species distributions (Harvey et al., 2012; Hutchins, 2001; McKinnon, Duggan, Holloway, & Brinkman, 2015; McLean et al., 2016; Moore & Morrison, 2009; Moore, Morrison, Hutchins, Allen, & Sampey, 2014; Poore & O’Hara, 2007; Travers, Newman, & Potter, 2006; Travers, Potter, Clarke, & Newman, 2012; Travers, Potter, Clarke, Newman, & Hutchins, 2010; Wilson, 2013). A limited number of studies have investigated connectivity among the distinct but ecologically and economically important Australian coastal ecosystems (Broderick et al., 2011; Horne, Momiglio, van Herwerden, & Newman, 2013; Horne, Momiglio, Welch, Newman, & van Herwerden, 2011, 2012; Johnson, Hebbert, & Moran, 1993; Johnson & Joll, 1993; Ovenden, Lloyd, Newman, Keenan, & Slater, 2002; Taillebois et al., 2017; Veilleux, van Herwerden, Evans, Travers, & Newman, 2011), and none have focused on inshore fishes with a comprehensive sample coverage across substantial environmental gradients. This emerging frontier in NWA therefore provides the ideal model system to increase our understanding of larval dispersal and connectivity in a management context.

Herein, we evaluate genetic connectivity of the Spanish flag snapper or stripey snapper, Lutjanus carponotatus (Richardson, 1842), across the entire NWA region using a genotyping-by-sequencing approach. Lutjanus carponotatus is abundant on tropical inshore reefs across the coast of Australia north of latitude −27°S, but also occurs in coastal waters from India through to the Indo-West Pacific.
This species is of significant recreational fishing importance across NWA, comprising 14% of the boat-based recreational catch in the North Coast Management Bioregion during 2013 and 2014 (Ryan et al., 2015). We also focus on *L. carponotatus* as a “model species” because its larval settlement behaviour and ecology are similar to other predatory species of commercial importance in NWA (e.g., *Lethrinus* spp., Fisher, Leis, Clark, & Wilson, 2005). A recent genetic investigation of *L. carponotatus* on the Great Barrier Reef (GBR) in eastern Australia using mitochondrial DNA markers found complete panmixia within and between inshore islands at a scale of 400 km (Evans, Van Herwerden, Russ, & Frisch, 2010). A companion study based on the same species and molecular markers in Western Australia (WA), identified a comparable scenario of panmixia in this region at a scale of 800 km, although it was strongly differentiated from the GBR populations (Veilleux et al., 2011). We have significantly improved on and extended these studies by performing a genome-wide survey of *L. carponotatus* at 51 sites along the extensive ~2,500 km coast of NWA to compare broadscale patterns of genomic divergence among bioregions that differ in reef composition as well as oceanographic, tidal and current regimes. In our seascape genomic analysis, we include Euclidean distance, oce
cinic-derived distance, biophysical modelling, environmental variables and management boundaries to understand drivers of resistance to
gene flow over an extensive and globally significant coastline.

## MATERIALS AND METHODS

### 2.1 | Study region

The remote coast of NWA between ~13°S and 27°S is largely unpopulated and geologically ancient, with low productivity, and is characterized by limited accessibility and extreme marine conditions (Molony, Newman, Joll, Lenanton, & Wise, 2011; Wilson, 2013). This coastline contains nearly 3,000 islands, two World Heritage sites (Ningaloo Reef and Shark Bay), four National Heritage areas of outstanding natural and indigenous significance, several marine reserves, and hosts a diverse assemblage of fishes and corals (McLean et al., 2016; Moore et al., 2014; Richards, Garcia, Wallace, Rosser, & Muir, 2015; Richards & O’Leary, 2015; Travers et al., 2006, 2010, 2012). Environmental conditions vary significantly across this coast but the most extreme are the tides that range from ~12 m in the Kimberley Bioregion, the highest tropical tidal range in the world, down to 1 m at Shark Bay, with maximum monthly water temperatures ranging from ~32°C in the Kimberley to 24°C in Shark Bay (Lowe, Pivan, Falker, Symonds, & Gruber, 2016; Wilson, 2013).

Existing biogeographic data, along with information on environmental attributes including ocean currents, geology and marine sediments has formed the foundation of bioregional classifications such as the provinces and ecoregions of Spalding et al. (2007), as well as the provincial and mesoscale bioregions of the Integrated Marine and Coastal Regionalisation of Australia (IMCRA). Indeed, the NWA coast spans seven IMCRA mesoscale marine bioregions (Table 1: sensu Commonwealth of Australia, 2006).

### 2.2 | Sample collection

Tissue samples of *L. carponotatus* (Figure 1, Tables 1, and S1) were collected from 51 coastal sites across NWA from the Anson Beagle in the Northern Territory (hereafter referred to as NT) through the Kimberley, Canning, Pilbara, Ningaloo and Shark Bay bioregions of WA. In total, 1,016 samples were collected across 13° of latitude and 17° of longitude of the tropical Australian coastline (also see Tables 1 and S1) and immediately preserved in 95% ethanol. Most sampling was undertaken in 2014 and 2015; however, muscle tissue collected in 2002 and frozen at ~80°C was obtained from four sites (Cape Bossut, Cape Keraudren, Cape Preston, Locker Point).

### 2.3 | Reduced representation SNP genotyping

DNA was extracted from tissue samples using 96-well plates and the salt extraction method described by Cawthorn, Steinman, and Wittthuhn (2011), followed by purification with Zymo ZR-96 DNA Clean and Concentrator kits (Zymo Research, California, USA). Downstream SNP genotyping was undertaken using a modified DA'Tseq™ protocol (Grewe et al., 2015), which is a proprietary method for reduced representation genomic library preparation and NGS (Cruz, Kilian, & Dierig, 2013; Kilian et al., 2012), where select loci at high coverage vs. the entire genome at low coverage are sequenced for individual samples. In our case, genomic DNA was digested with two restriction enzymes (*Pst*I-SphI and *Pst*I-NspI) instead of one to generate more SNP loci. PCR conditions consisted of an initial denaturation step at 94°C for 1 min followed by 30 cycles of 94°C for 20 s, 58°C for 30 s and 72°C for 45 s, with a final extension step at 72°C for 7 min. After PCR, equimolar amplification products from each sample were pooled and applied to a cBot bridge PCR system followed by sequencing on an Illumina Hiseq2500. The sequencing (single read) was run for 77 cycles.

Read assembly, quality control (QC) and SNP calling were undertaken using DArT PLD’s software DArTsoft14, a program that produces scoring consistency derived from technical sample replicates (i.e., samples processed twice, from DNA library preparation to SNP calling). Testing for Mendelian distribution of alleles in these populations facilitated selection of technical parameters discriminating true allelic variants from paralogous sequences. A total of 17,007 SNP loci were identified during this process.

### 2.4 | Quality filtering

Following SNP genotyping, additional QC steps were performed to the 17,007 loci identified prior to genetic analyses: (i) rare alleles (frequency <0.05) and highly variable loci (heterozygosity >0.75) were removed, (ii) loci with coverage less than 20× and greater than 200× were removed and (iii) individuals with more than 1% missing data were removed as suggested by thresholds within the R package dartR (https://github.com/green-striped-gecko/dartR). Following these filtering steps, we were left with 5,094 loci. We tested for departures from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium
**Table 1** Site. IMCRA classification, sample size (N) and molecular metrics (N_a = number of alleles; H_o = observed heterozygosity; H_e = expected heterozygosity; F_IS = inbreeding coefficient) for Lutjanus carponotatus based on 4,402 SNP loci. IMCRA mesoscale bioregions are derived from the Commonwealth of Australia (2006).

<table>
<thead>
<tr>
<th>Site</th>
<th>IMCRA bioregion</th>
<th>N</th>
<th>N_a</th>
<th>H_o</th>
<th>H_e</th>
<th>F_IS</th>
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(Continues)
Descriptive statistics, genetic subdivision and outlier detection

$F_{ST}$, $F_{IS}$ and genetic diversity metrics (percentage of polymorphic loci, average number of alleles, observed and expected heterozygosity) were estimated using Genodive version 2.0 (Meirmans & Van Tienderen, 2004); the significance of pairwise $F_{ST}$ values was tested by 10,000 permutations via bootstrapping. To identify SNPs that may be under divergent selection, we performed outlier scans between all pairs of sites using Outflank version 0.1 (Whitlock & Lotterhos, 2015). The approach implemented in Outflank is based on an improved method for deriving the null distribution of population differentiation for neutral loci and results in fewer false positives than other outlier tests (Lotterhos & Whitlock, 2015). We ran Outflank with 5% left and right trim for the null distribution of $F_{ST}$, minimum heterozygosity for loci of 0.1% and a 5% false discovery rate ($q$-value). Sixty-six SNPs under putative directional selection were identified. These loci were included in all downstream analyses, unless otherwise noted, given that they had a marginal effect on the outcome of these tests.

Model-based clustering analysis

To explore genetic structure across sampling sites, a model-based clustering analysis was performed with STRUCTURE version 2.3.4 (Pritchard, Stephens, & Donnelly, 2000) with a priori information on the geographic origin of each sample. The analyses were run on the CSIRO Accelerator Cluster “Bragg” under the admixture model with correlated allele frequencies, a burn-in of 200,000 MCMC iterations, followed by 500,000 iterations for each run (Falush, Stephens, & Pritchard, 2003). The number of $K$ (putative populations) ranged from 1 to 8, and 20 replicate analyses were run for each value of $K$. The number of clusters was inferred by comparing the $\ln Pr (X|K)$ among different values of $K$; the value that was highest or reached a plateau was selected as the most parsimonious number of populations in our sample. The ad hoc statistic $\Delta K$ (Evanno, Regnaut, &
Goudet, 2005) was also considered. The outcome was no different when no a priori information on geographic origin of each sample was included, and so we only present results with a priori information. To objectively assess whether geographic origin correlates with the ancestry profiles from STRUCTURE, we estimated a correlation coefficient (R^2) statistic using the program ObStruct version 1.0 (Gayevsky, Klaere, Knight, & Goddard, 2014) and a default of 10,000 permutations.

2.7 Discriminant analysis of principle components

We employed discriminant analysis of principle components (DArC) implemented in the R package Adegenet to further describe genetic groups present within our data. Initially, the k-means algorithm was employed to evaluate all potential clusters (K) in the data. For this analysis, we retained all principle components and then evaluated the Bayesian information content for all values of K. A linear discriminant analysis was then conducted based on 338 retained principle components (N individuals divided by 3) identified as optimal based on the optim.a.score command, and 50 discriminant functions retained (N – 1 populations) to describe the clusters evident in the data. For this analysis, we did not restrict the number of clusters to the number identified in the find.clusters analysis. All analyses were run on all loci as well as only on the outlier loci.

2.8 Spatial autocorrelation and isolation by distance

GenALEx version 6.502 (Peakall & Smouse, 2006) was used to quantify spatial autocorrelation based on all sites with N > 6. Calculations were made separately for the three distinct “clusters” identified in model-based clustering (see above). Within the Kimberley cluster, distances were 0–256 km (N = 266); within the Pilbara cluster, distances were 0–426 km (N = 391); and within the “transition zone” between the Kimberley and Pilbara clusters, distances were 0–148 km (N = 193). We conducted multiple distance-class spatial autocorrelations rather than conventional correlograms to accommodate uneven sample sizes and distances typical of reef topography (Peakall, Ruibal, & Lindenmayer, 2003). Geographic distances between sites were calculated based on the shortest across-water distance with a minimum low tide water depth of 1 m. These estimates were calculated with the Marmap R package (Pante & Simon-Bouhet, 2013) and based on the GEBCO 2014 30-s bathymetry available from the British Oceanographic Data Centre.

We applied Mantel tests to evaluate the relationship between linearized FST (FST/(1 – FST)) and distance (isolation by distance, IBD). This analysis was based on 9,999 permutations of the data calculated with the vegan R package (Oksanen et al., 2007). Mantel tests were applied to the entire data set, as well as the Kimberley and Pilbara bioregions separately. A generalized linear model (GLM) implemented in R was used to test for regional isolation-by-distance effects in the Pilbara and Kimberley bioregions.

2.9 Determinants of genetic differentiation

We used an information-theoretic approach (Anderson, 2008) to determine the geographic and oceanographic variables that best explain the observed genetic subdivision (FST) in L. carponotatus throughout NWA. This method ranks alternative models per their relative empirical support (Correa & Hendry, 2012). Sample sites with N < 20 individuals were excluded from the analysis given uncertainty in FST estimates when based on low sample sizes (Willing, Dreyer, & Van Oosterhout, 2012). Geographic variables were included in the model selection process, and each model was ranked based on their AIC score, evidence ratio and posterior probability. Geographic factors included the Euclidean distance between sites (geo) and the presence of three putative barriers to larval dispersal based on the regional designations described below. We also calculated hydrodynamic distance between sites (hyd; see details below). Although the northern and western coasts of Australia have been classified and reclassified according to a number of marine biogeographic boundaries (Fox & Beckley, 2005; Spalding et al., 2007; Thackway, 1998), we follow the marine ecoregions of the world (MEOW) of Spalding et al. (2007), as it utilizes the most recent quantitative data on marine fish distributions in this area. The ecoregional units we specifically test (and thus the barriers between them) are the Bonaparte Coast, Exmouth to Broome and Ningaloo Reef to Shark Bay. The NT ecoregion was not included in this analysis due to a limited sample size.

It should be noted that the marine ecoregional units differ from the management bioregions used for the purposes of fisheries management. To examine potential connectivity across management bioregion boundaries, we also specifically explored the following divisions: NT (all NT sites), Kimberley (Long Reef to Cape Bossut), Pilbara (Cape Keraudren to Paroo Shoal) and Gascoyne (Locke Point to Dorre Island), in addition to the MEOW ecoregional units as outlined above. Indeed, these management bioregions most closely align with the bioregional boundaries developed by IMCRA (Commonwealth of Australia, 2006) rather than MEOW (Spalding et al., 2007).

The common feature of the various bioregional classifications and other quantitative fish assemblage studies is the pronounced faunal break in the Cape Leveque region at the northern tip of the Dampier Peninsula (Figure 1; Spalding et al., 2007; Thackway, 1998; Travers et al., 2010; Wilson, 2013). Barriers were modelled as a factor with values of 0–3 (or 0–2), where sites compared on the same side of the barrier received a score of 0 and sites compared on different sides of a barrier received a score of 1–3 (or 1–2) depending on the number of barriers in between.

Overall, 15 models were fitted using both linear models (lm) and linear mixed effects models (lmer). Linear mixed effects models included site ID as a random effect to compensate for the fact that pairwise FST values are not independent among sites. For each model, the sample size-corrected Akaike information criterion (AICc) was calculated. Models were then ranked based on increasing AICc and further interpretation based on model probabilities (w) and evidence ratios (Anderson, 2008).
2.10 | Broadscale hydrodynamic model and connectivity calculations

Null connectivity of L. carponotatus was modelled using CONNIE, the engine behind the CONNIE3 web interface (www.csiro.au/con nie). This tool combines currents from oceanographic models, particle tracking techniques and simple behavioural models to estimate connectivity statistics (Condie, Hepburn, & Mansbridge, 2012). Estimates of the oceanographic conditions along the WA coast were based on an output of the 10 km resolution BlueLink Ocean ReANalyis (BRAN2.1) model (Schiller et al., 2008). Although finer resolution models do exist, none include the entire geographic span of the 51 L. carponotatus sampling sites. Particles were released from each of the 51 sites, and the parameterization of the particles was selected to resemble the behaviour of L. carponotatus larvae; particles were released in the final quarter (1 October to 31 December) of each year from 2003 to 2008. Over the course of each day, 100 particles were released randomly within a 0.2 degree square around the latitude and longitude of each sampling site. Individual particles were then tracked as they were dispersed by the horizontal component of modelled ocean currents over a total dispersal time of 40 days. For the first 5 days, particles remained at a depth of 5 m. From day 5 onwards, each particle underwent diel vertical migration, spending the day at 15 m and the night at 5 m, where the length of day depends on the time of the year.

The number of particles in a simulation released from a source site that arrive at a destination site here represents the potential connectivity between sites (Hock, Wolff, Condie, Anthony, & Mumby, 2014). The particle trajectories were used to calculate the potential connectivity between each pair of sites \((i, j)\) and this was combined to create a combined connectivity matrix for the region. The particles were only allowed to “settle” (and contribute to the connectivity matrix) 33–40 days from their release. If a particle moved within 0.1 degree of a potential settlement site, that particle was assumed to have settled and would not move onwards to any other potential settlement sites. The connectivity value between any two sites \((i, j)\) is the percentage of particles released from site \(i\) that “settled” at site \(j\). Self-recruitment \((i, i)\) was also estimated.

2.11 | Fine-scale biophysical dispersal model: Effects in the Kimberley Bioregion

The biophysical dispersal model was based on the regional ocean modelling system hydrodynamic model with 2 km resolution (M. Feng, unpublished data) to construct a pairwise matrix of larval connectivity among sampling sites. We used only a subset of sites based on: (i) the quality (i.e., resolution) of available data and (ii) our interest in larval dispersal within the oceanographically complex Kimberley Bioregion. The hydrodynamic model, which included fine-scale tidal data, was nested within the Ocean Forecasting for Australia Model 3 (OFAM3) simulation (Zhang et al., 2016) and forced by three hourly meteorological measures derived from Kobayashi et al. (2015). The simulation was carried out over the 2011 time period, with hourly sea surface current velocities (0–5 m) extracted from the model output and used for particle tracking. A total of 100 particles were seeded at sampling sites during the austral spring-summer period (September–January), at 3-day intervals with a PLD of 40 days. This particle release period was chosen to capture all possible spawning periods for L. carponotatus (Kritzer, 2004; R. Evans et al., unpublished data). A fourth-order Runge-Kutta sub-time-stepping scheme was used to update the particle locations every hour. Using the random walk effect of 1 m²/s, particles were tracked for 35 days based on the potential PLD of this species (33–38 days; Quéré & Leis, 2010). The settlement of the particles was set to be within 500 m of a particular site. Connectivity among sampling sites was estimated as the average number of particles released from site \(i\) that were tracked to be in site \(j\), this ranged from 0 to 7.49 per release period, based on 48 simulation replicates. The oceanographic connectivity matrix was visualized using the package agraph (Epskamp, Cramer, Waldorp, Schmittmann, & Borsboom, 2012).

For the purposes of comparison to genetic data, the output matrix was converted into a distance matrix by dividing by the number of released particles and subtracting from 1 and averaging the genetic connectivity between pairwise sites. To increase the confidence in the FST results for correlation purposes, we used only sites with \(N > 7\) samples (see Willing et al., 2012), resulting in 18 sites for the Mantel test comparing pairwise FST to larval particle tracking results and the oceanographic distance in the Kimberley Bioregion. Mantel tests with 10,000 repetitions were run in the R package vegan.

3 | RESULTS

3.1 | Genetic diversity

A summary of the principal statistics (number of individuals per site, percentage of polymorphic loci, average number of alleles, observed and expected heterozygosity and \(F_{IS}\)) obtained for 1,016 individual samples from 51 locations in NWA is presented in Tables 1 and S1. Observed heterozygosity was significantly higher in the southwestern bioregions (combined Canning, Pilbara and Shark Bay) than the northeastern bioregions (NT and Kimberley; \(t\) test: \(t = −4.19\) and \(p < .001\)). Observed heterozygosity was weakly correlated with the latitude of each site \((r = .159)\), suggesting a bioregional effect rather than a direct effect of latitude. \(F_{IS}\) values were mostly positive in the southwestern bioregions, whereas in the northeastern bioregions they were mostly negative (\(t\) test: \(t = −3.17\) and \(p = .0026\)). \(F_{IS}\) values were similarly weakly correlated with the latitude of each site \((r = .137)\). We also identified 66 outlier loci using Outflank; analyses based on the outlier loci were, in most cases, no different from the same analyses based on all 4,402 SNP loci.

3.2 | Genetic subdivision

Patterns of pairwise genetic differentiation revealed small but significant genetic differences among most sampling sites (i.e., 424 of 496...
tests were significant in Figure 2 and Table S2), which suggests restrictions in gene flow between adjacent sites and geographically distant ones (e.g., NT and Shark Bay). The historical samples collected from sites in the Pilbara in 2002 exhibited higher levels of genetic differentiation than those collected in 2014 and 2015 (Figure 2 and Table S2). Pairwise differentiation was more often significantly greater than zero in the Kimberley (92% pairwise comparisons significant) than in the Pilbara (63% pairwise comparisons significant; Figure 2 and Table S2).

3.3 | Model-based clustering analysis

Bayesian clustering analysis suggested $K = 3$ populations as the most parsimonious partitioning of individuals based on the $\Delta K$ metric (Evanno et al., 2005; also see Fig. S1, $\Delta K = 1.233$). Inspection of the STRUCTURE ancestry profiles revealed that at $K = 3$, there was a clear distinction between the sites in Shark Bay and the remaining sites to the north (ObStruct analysis: $r^2 = .96$, $p < .0001$), and at $K = 4$ ($\Delta K = 0.179$), a further distinction between the Kimberley and Pilbara sites was evident (ObStruct analysis: $r^2 = .98$, $p < .0001$; also see Figure 3a). In addition, several sites spanning the Canning-Kimberley bioregional boundary exhibited ancestry profiles that transitioned between those typical of other Pilbara and Kimberley sites (i.e., from Dugong Bay to Emeriau Point). In all such results, $q$ values of 0.5 to 0.7 were attributed to an uninformative common cluster in all individuals.

When applied to the outlier loci data set (66 loci), STRUCTURE analysis revealed the same pattern of three clear genetic clusters plus a transition zone between the Canning-Kimberley bioregional boundary, but with greater clarity since the uninformative cluster across all individuals was no longer evident (Figure 3b). For the outlier loci, the optimum $K$ was 2 ($\Delta K = 416.427$), which was further supported by the ObStruct analysis ($r^2 = .93$, $p < .0001$; $\Delta K$ was markedly higher at $K = 3$ ($\Delta K = 0.773$) and $K = 4$ ($\Delta K = 2.096$).

3.4 | Discriminant analysis of principle components

The k-means clustering algorithm was optimized at $K = 2$ in both the neutral and outlier data sets. Linear discriminant analysis of principal components revealed that for the neutral data set these groups corresponded to the Shark Bay Bioregion vs. all remaining sites to the north (Figure 4a). The DAPC analysis of the outlier data set revealed

![Heatmap](image)

**FIGURE 2** Heatmap of pairwise $F_{ST}$ values for *Lutjanus carponotatus* populations with 20 or more individuals in Northwestern Australia based on 4,402 SNP loci. *Indicates significant difference after Narum correction ($p < .0074$). The four historical sample sites (i.e., 2002) are indicated by small, red arrows. SNP, single nucleotide polymorphism
a similar pattern (Figure 4b); however, Shark Bay sites were less differentiated. Sites spanning the Canning–Kimberley bioregional boundary appeared intermediate between clusters composed of remaining Pilbara and Kimberley sites in both the analysis of neutral and outlier loci.

### 3.5 | Determinants of genetic differentiation

For analyses based on all 4,402 SNP loci, four models outperformed all the others, which included the variables geo, hyd, the presence of all three barriers, as well as an interaction between the terms (Table S3). We repeated this analysis with outlier loci only and got the same result. These outcomes did not change when the MEOWs or fisheries management divisions for outlining barriers to dispersal were considered across all sites. Thus, modelling the effects of barriers to dispersal, hydrodynamic distance (i.e., connectivity) and geographic distance on genetic differentiation in this species revealed strong effects for all three factors, but in most cases, these effects could not be distinguished from each other. Indeed, sites that are far apart geographically are more likely to be separated by multiple barriers and less connected via prevailing currents. Further, this analysis reinforces the IBD effect, with the slope of IBD changing within different bioregions as outlined below. It should also be noted that hydrodynamic distance was an order of magnitude higher on average within all 51 sites (0.053 ± 0.063 SD) relative to between all 51 sites (0.003 ± 0.010 SD), a potential indicator of strong self-recruitment in this system (Table S4).

### 3.6 | Spatial autocorrelation and IBD

Spatial autocorrelation analysis revealed modest ($r = .0025$), but significant local-scale genetic structure that dropped away from its initial plateau (Figure 5) to cross the x-axis at approximately 300 km in all regions, except in the transition zone (i.e., Dugong Bay to Emeriau Point), where the axis was crossed at 80 km. This crossing point indicates the distance where the random effects of genetic drift, not gene flow, are the primary determinants of genetic composition. A Mantel test revealed that when considering all data,
distance was significantly correlated with genetic differentiation between sites ($r = .25$, $p < .001$; Figure 6). Distance was not a significant correlate with genetic differentiation when considering sites in the Kimberley only ($r = .08$, $p = .23$), but was significantly correlated for the sites in the Pilbara only ($r = .50$, $p = .01$). Supporting these results, a GLM showed that pairwise $F_{ST}$ was on average significantly higher in the Kimberley than the Pilbara after removing the effect of distance ($p < .0001$), but also provided a significant interaction term, indicating that the relationship between distance and $F_{ST}$ differed significantly between these regions ($p < .001$).

### 3.7 Hydrodynamic models

As outlined above, hydrodynamic distance in the CONNIE model correlated with genetic differentiation across all sampling sites (Shark Bay to Kimberley) but this could not be distinguished from other factors (geographic distance and barriers to dispersal; Table S3). In contrast, the custom fine-scale modelling analysis did not predict the observed genetic structure in the Kimberley Bioregion. Indeed, a Mantel test with linearized $F_{ST}$ found no correlation between particle tracking outputs from fine-scale hydrodynamic models ($r = .1044$, ...)
This study is one of the first to investigate coastal connectivity within the remote Kimberley Bioregion of WA and includes extensive sampling across ~2,500 km covering all of the major marine bioregions in NWA. We provide evidence of restricted connectivity between geographically distant sites and, in some cases, neighbouring sites within bioregions separated by a few kilometres. These results support earlier observations of restricted connectivity in fishes and corals between the Pilbara, Ningaloo Reef and Shark Bay bioregions (Johnson et al., 1993; Thomas, Kennington, Evans, Kendrick, & Stat, 2017; Underwood, 2009; Whitaker, 2006). In addition, we identified a localized region of admixture within the Buccaneer Archipelago and adjacent waters between the otherwise genetically distinct Kimberley and Canning bioregions. This region of admixture corresponds to a well-defined biogeographic boundary based on shifts in faunal composition for several taxa, including fishes (Hutchins, 2001; Travers et al., 2010), mangroves and molluscs (Wilson, 2013), and experiences the most extreme tidal fluctuations of tropical waters globally.

4 | DISCUSSION

This study is one of the first to investigate coastal connectivity within the remote Kimberley Bioregion of WA and includes extensive sampling across ~2,500 km covering all of the major marine bioregions in NWA. We provide evidence of restricted connectivity between geographically distant sites and, in some cases, neighbouring sites within bioregions separated by a few kilometres. These results support earlier observations of restricted connectivity in fishes and corals between the Pilbara, Ningaloo Reef and Shark Bay bioregions (Johnson et al., 1993; Thomas, Kennington, Evans, Kendrick, & Stat, 2017; Underwood, 2009; Whitaker, 2006). In addition, we identified a localized region of admixture within the Buccaneer Archipelago and adjacent waters between the otherwise genetically distinct Kimberley and Canning bioregions. This region of admixture corresponds to a well-defined biogeographic boundary based on shifts in faunal composition for several taxa, including fishes (Hutchins, 2001; Travers et al., 2010), mangroves and molluscs (Wilson, 2013), and experiences the most extreme tidal fluctuations of tropical waters globally.

4.1 | Genetic diversity and broadscale subdivision across NWA

Levels of genetic diversity were similar throughout the sampling range of L. carponotatus (Tables 1 and S1), which may be due to the relatively long PLD of this species (33–38 days; Quéré & Leis, 2010) and large genetic neighbourhoods that we observed (i.e., positive spatial autocorrelation up to 450 km; Figure 5). In contrast, two dominant patterns of genetic subdivision were evident from the SNP genotyping of L. carponotatus. The first was an IBD effect, where on average sampling sites were genetically most similar to their closest neighbours and least similar to distant sites (Figure 6). By implication, dispersal is limited on the scale of this investigation (~2,500 km) and proceeds in a stepping-stone manner. This pattern is likely also true for other species in the region from the Lutjanidae or Lethrinidae families with similar life histories, although, like L. carponotatus, we would expect this correlation to be weak due to the abundance and fecundity of these species in addition to their larval dispersal capabilities (Berry, England, Marriott, Burridge, & Newman, 2012; Kritzer, 2004; Marriott et al., 2010; Newman, Cappo, & Williams, 2000; Travers et al., 2006).

In addition to the IBD effect, several pronounced genetic discontinuities were evident among samples of L. carponotatus from across NWA. One of the obvious genetic breaks was between the Shark Bay Bioregion and all locations of the northwest continental shelf (Ningaloo Reef, Pilbara, Canning and Kimberley) including the NT. This genetic break coincides with a well-recognized biogeographic boundary and oceanographic features at North West Cape near Ningaloo Reef (Commonwealth of Australia, 2006; Hutchins, 2001; Spalding et al., 2007; Woo, Pattiaratchi, & Schroeder, 2006). Wilson (2013) suggested that the effect of the poleward flowing Leeuwin Current across this region, the most dominant boundary current of the western coast of Australia (Figure 1; Godfrey & Ridgway, 1985), may not be effective in preventing exchange for species with planktotrophic larvae (such as L. carponotatus). Some studies have suggested that this barrier is gradual rather than abrupt (Johnson et al., 1993; Thomas et al., 2014, 2017; Whitaker, 2006), and potentially results from a mesoscale eddy that advects larvae offshore (Woo et al., 2006).

A second apparent boundary was observed between the Kimberley and Canning bioregions (Figures 2–4). This pattern was most evident in the STRUCTURE analysis of outlier SNPs as a region of progressive admixture between two apparently homogenous genetic clusters representing the Kimberley and NT, and the combined Pilbara and Canning bioregions (Figure 3). The result was also reflected in the DAPC analysis of both neutral and outlier SNPs (Figure 4), but again it was not as clear for the neutral data set. These results, supported by a distinctive pattern of low spatial autocorrelation in this region (Figure 5), indicate that it likely represents restricted dispersal over ~180 km near the tip of the Dampier Peninsula and Buccaneer Archipelago (Figure 1). This is consistent with a recognized biogeographic break in marine communities (Wilson, 2013) that parallels a change in the underlying coastal geology (e.g., from Proterozoic sandstone and basic intrusive rock in the north to Mesozoic sandstone with diverse sedimentary structures in the south) and associated dominant benthic habitat (e.g., from coral reefs in the north to soft substrate communities in the south). This break also corresponds with an abrupt change of coastal geomorphology from the ria coast of the Kimberley with its numerous islands and embayments to the Canning coast comprised of coastal dunes and tidal flats (Brocx & Semeniuk, 2010). As discussed below, a change in tidal regimes across this region is also a likely driver of this dispersal pattern.

This study is the first example of an investigation of a coastal fish in this region using SNPs. Studies on several other marine taxa from this region including a brooding reef fish Pomacentrus milleri (Berry, Travers, Evans, Moore, & Hernawan, 2017) and a mangrove Avicennia marina (R. M. Binks, unpublished data) show similar broadscale genetic structure with the use of SNPs. The genetic discontinuities between broadscale bioregions evident in the coastal L. carponotatus samples contrast to the widespread connectivity observed in deep-water and epipelagic species with similar PLDs. Studies using nuclear microsatellite markers and mitochondrial DNA found evidence for weak genetic structure between sites along the edge of the continental shelf in this region (Bentley et al., 2014; Gaither et al., 2011; Johnson et al., 1993; Kennington et al., 2017), suggesting that the processes operating offshore and across continental shelves and islands may differ significantly from those processes influencing dispersal in coastal species. Alternatively, the genetic structure detected
among coastal sites in the current study, relative to the offshore and deepwater studies, may be a function of the higher resolution markers that we used. Veilleux et al. (2011) found no genetic structure in *L. carponotatus* at similar coastal sampling sites spread across the Kimberley to the Pilbara bioregions, albeit with only one mitochondrial marker. Although connectivity estimated using the different markers is not directly comparable between the overlapping studies given their different rates of evolution and mode of inheritance, as well as a focus on fine-scale vs. broadscale information, comparisons with the offshore studies highlight the need to incorporate NGS approaches into stock assessments.

### 4.2 Fine-scale connectivity across NWA

The broadscale genetic discontinuities between bioregions were overlaid by subtle genetic differentiation within each bioregion. Genetic patterns also differed between the bioregions, indicating that *L. carponotatus* dispersal behaviour may be variable across its range. On average, genetic differentiation between sites was higher in the Kimberley than the Pilbara bioregions (Figure 2 and Table S2), implying that dispersal is more restricted in the Kimberley. A moderate IBD effect was evident among Pilbara samples, yet not in the Kimberley (Figure 6). This also suggests greater restriction to gene flow in the Kimberley than the Pilbara, and the more idiosyncratic patterning likely reflects the more powerful tidal regime (e.g., tidal pumping at the mouth of King Sound) and complex coastal topography (e.g., numerous islands, rocky islets and bays) present in the Kimberley in contrast to the more linear current flow along the Canning and Pilbara coasts (Feng, Colberg, Slawinski, Berry, & Babcock, 2016). Larval *L. carponotatus* on the GBR are capable of actively influencing their dispersal and settlement through swimming and sensory capabilities (Quéré & Leis, 2010). However, the maximum larval swimming speed recorded for this species is ~33 cm/s, which is considerably less than the maximum tidal velocity in the vicinity of the transition zone identified here (100 cm/s; Lowe, Leon, Symonds, Falter, & Gruber, 2015; Wolanski & Spagnol, 2003). Although spawning probably occurs during neap tides (Quéré & Leis, 2010), *L. carponotatus* have a relatively long PLD (33–38 days; Quéré & Leis, 2010), which would expose them to the full spectrum of tidally driven water movement in this region. Tidal currents and their interactions with complex coastal topography may thus play an active role in larval retention by limiting the opportunities for net larval transport to periods of slack water in the ebb/flood tidal cycle and during neap tides known as selective tidal-stream transport (Forward & Tankersley, 2001), when the swimming speed of larvae exceeds the speed of tidal currents.

### 4.3 Seascape genomics

The integration of geographic and oceanographic variables to explain genetic signals of differentiation, often referred to as seascape genomics, is a growing field (Selkoe et al., 2016). Although we explored hydrodynamic distance across the entire sampling range of *L. carponotatus*, in most cases, linear distance provided a comparable explanation for the observed patterns of genetic structure (Table S3). This reflects the fact that the hydrodynamic distance and number of barriers almost exactly tracked linear distance (i.e., collinearity: \( r = -0.25, p < 0.001 \)), due in part to the large spatial scale of the study. That is, large distances between sampling sites (up to hundreds of kilometres) over a gradual latitudinal gradient lend itself to other forms of change relative to that gradient.

Fine-scale genetic partitioning in the Kimberley Bioregion was not predicted by the custom particle tracking model used in this study nor the oceanographic distance. This highlights the complex biological and physical characteristics of larval dispersal in the Kimberley. First, the 2-km scale of this model likely does not account for the fine-scale eddy effects of the large tides in the Kimberley Bioregion, although on the whole it is considered well mixed; this disconnect may affect the signal-to-noise ratio in our custom model. Second, late-stage larval *L. carponotatus* are capable of swimming speeds up to 33 cm/s and may be able to limit their dispersal by swimming to larval retention zones near reefs (Quéré & Leis, 2010) or via vertical migration by interacting with currents at different depths (Stephenson, Power, Laffan, & Suthers, 2015). Indeed, Wolanski and Kingsford (2014) demonstrated that coral reef fish larvae with directional swimming abilities using olfactory and auditory cues appear to self-recruit an order of magnitude more frequently than passive particles in their predictive model. The genetic results support the larval behaviour hypothesis given that greater retention or less dispersal of *L. carponotatus* in the Kimberley Bioregion was observed vs. elsewhere on the coast of NWA.

### 4.4 Caveats and future directions

Management of *L. carponotatus* in NWA is currently based in part on recognizing three overarching management units corresponding to: (i) the NT, (ii) combined Kimberley, Canning and Pilbara Bioregions and (iii) the Gascoyne Bioregion, which includes both Shark Bay and Ningaloo Reef in fisheries management arrangements. Our results indicate that the management boundaries of these stocks require re-evaluation or alternatively that the barriers to connectivity need to be considered within management arrangements. Moreover, this highlights the need for continuous improvement of adaptive management processes as new techniques arise. In this case, NGS and SNP genotyping has improved our ability to determine restrictions to gene flow over ecological timescales.

The distinctiveness of the Shark Bay samples from all other bioregions indicates that the Gascoyne management boundary is not supported because sites north of Shark Bay have greater affinities to sites in the Pilbara Bioregion. In addition, support for separate management of *L. carponotatus* from the NT is equivocal. NT samples were significantly, albeit weakly, genetically differentiated from all other samples (Figure 2), and appeared weakly divergent in both STRUCTURE and DAPC analyses. However, a large sampling gap exists between the Kimberley and NT sites despite available habitat, and so it is unclear whether the genetic differentiation of the NT samples reflects a genuine discontinuity, or a continuation of the
isolation-by-distance effect observed elsewhere in the range of *L. carponotatus*. Although unavoidable in this study due to the remoteness of the region, this gap in the data highlights the necessity to sample evenly across a species’ range (Meirmans, 2015).

The transition zone identified around the Dampier Peninsula that separates the Kimberley from the Pilbara/Canning populations may be uniquely influenced by the extreme tidal flushing and seasonal reductions in salinity (i.e., mean runoff $5.75 \times 10^9$ m$^3$ year$^{-1}$; Wolanski & Spagnol, 2003) at the mouth of King Sound. Fine-scale parentage analysis (Harrison et al., 2012; Pusack, Christie, Johnson, Stallings, & Hixon, 2014) coupled with larval dispersal models that include both tides and currents, explored over multiple lunar phases and spawning seasons, may be needed to understand the source-sink dynamics of larvae and successful recruitment in this zone. This investigation would be beneficial given its applicability to other harvested fish species occurring within the transition zone.

Samples included in this analysis were collected over a span of 15 years. Although older samples exhibited their closest affinity to newer samples from the same bioregion, in most cases they also exhibited a distinct genetic composition. Based on post hoc analyses, we were able to exclude at least one mechanism of DNA degradation, which could have accounted for this pattern (deamination or C/T transitions; Fig. S2), by comparing SNP type (i.e., transition vs. transversion) between samples. This result may instead represent a real shift in allele frequencies over time, indicating the potential for changing patterns of connectivity among sites, and in this case, an increase in connectivity.

The coastal-associated *L. carponotatus* is harvested by commercial, recreational, charter and indigenous fishers at various locations throughout its range. Currently, spatial partitioning based on genetic separation in the more northern bioregions largely conform to existing management boundaries. However, the genetic transition zone that spans a distance of ~180 km in the Buccaneer Archipelago and adjacent waters within the Kimberley Bioregion is unique. The identification of this transition zone was unique to the NGS and SNP genotyping approach; this pattern was absent in a study of Kimberley to Pilbara/Canning populations of *L. carponotatus* using mitochondrial markers (Veilleux et al., 2011). That said, it is still unclear whether these transition zones isolate populations on either side of them, and influence the evolution of life history traits such as reproduction, spawning dynamics and growth.

5 | CONCLUSION

The use of NGS and SNP genotyping in this population connectivity study has highlighted the advantages of adopting higher resolution genetic markers in a seascape genomics context to re-evaluate the potential for restrictions to gene flow in species that once were considered panmictic. Our study also highlights the benefits of collecting samples across an extensive and broad range of habitats and hydrodynamic regimes within a species range. Our model species, *L. carponotatus*, has a PLD of 33–38 days, which likely enables sufficient dispersal to limit any latitudinal effects on genetic diversity across the sampling range. Through multiple lines of evidence however, and despite an apparent stepping-stone process to dispersal, genetic connectivity was not homogeneous across the sampling range. Indeed, the bioregion with the most extreme hydrodynamic environment in our tropical oceans, the Kimberley, displayed less connectivity among sampling sites than did the Pilbara/Canning bioregion, which exhibits lower tidal flows and a less complex coastal topography. Thus, the spatial scale of sampling, hydrodynamic effects within the sampling range, genetic approach used and the biology of the study species are all important considerations when inferring patterns of dispersal under a management framework.

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DATA ACCESSIBILITY


AUTHOR CONTRIBUTIONS

O.B., M.T., G.M. and R.E. designed the study. M.T., G.M., R.E., S.N., S.M. and T.S. collected the samples. J.D. and O.B. executed the genetic analyses. M.F. and R.G. executed the oceanographic modelling analyses. J.D., O.B., M.T., G.M. and R.E. interpreted the data and led the writing of the manuscript. All authors contributed to the final draft of the manuscript.
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