



## Population connectivity of the Stripey Snapper *Lutjanus carponotatus* along the ecologically significant coast of northwestern Australia

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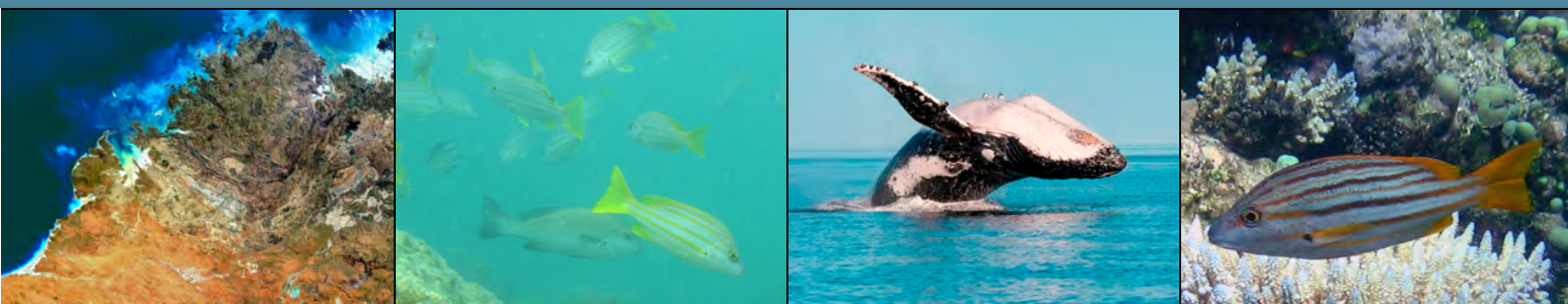
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## WAMSI Kimberley Marine Research Program

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## WAMSI Kimberley Marine Research Program

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

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Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Stripey snapper. (Image: DBCA)

Image 3: Humpback whale breaching (Image: Pam Osborn)

Image 4: Stripey snapper (Image: DBCA)

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## Executive Summary

This report focuses on the widespread and abundant Stripey Snapper (*Lutjanus carponotatus*), which is an important recreationally targeted lutjanid in coastal waters throughout the Central Indo-Pacific realm, including the coast of northwestern Australia (NWA) south to Shark Bay. This species was selected as a model to represent numerous broadcast pelagic spawning reef-associated fish species with relatively long pelagic larval durations (PLD for *L. carponotatus* ~ 37 days). The Stripey Snapper is among the top five targeted inshore fish species by recreational anglers in NWA and is managed according to a full Ecosystem Based Fisheries Management (EBFM) approach in which the sustainability of targeted fish species are assessed within the bioregional boundaries defined under the Integrated Marine and Coastal Regionalisation of Australia classification scheme (IMCRA, Commonwealth of Australia, 2006). The adoption of a widespread sampling regime in this study allowed us to explore the potential influences of extreme gradients in coastal hydrodynamics, such as tidal driven currents, water turbidity, and seasonal freshwater outflow from the Northern Territory (NT) southwards through the Kimberley, Canning, Pilbara, Ningaloo and Shark Bay Bioregions of Western Australia (WA). This study fills gaps in understanding of both broad-scale marine connectivity in NWA and fine-scale connectivity within the Kimberley Bioregion to be addressed against a background of rapid coastal development supporting the mineral and petrochemical industries. Such development has the potential to directly impact the biodiversity and productivity of nearshore marine ecosystems via dredging, construction, pollution, shipping, and other indirect pressures associated with increased human populations such as fishing.

One thousand and sixteen Stripey Snapper samples were collected from 3 locations in the NT, 29 locations in the coastal Kimberley Bioregion, 17 locations in the Pilbara and Canning bioregions, and 2 locations in the Shark Bay Bioregion (full dataset). In order to focus on only the best sampled populations ( $N \geq 20$ ), 895 Stripey Snapper individuals were considered from 1 location in the NT, 11 locations in the coastal Kimberley bioregion, 17 locations in the Pilbara and Canning bioregions and 2 locations in the Shark Bay Bioregion (reduced dataset). Samples were genotyped via a genotype-by-sequencing method which, after quality filtering, yielded 4,402 polymorphic Single Nucleotide Polymorphism (SNP) loci that met Hardy-Weinberg equilibrium and linkage equilibrium expectations. A number of genetic analyses were repeated with a subset of outlier loci ( $N = 66$  SNPs) that are putatively under directional selection.

### Insights into broad and fine-scale connectivity

Significant genetic sub-division was evident between the Shark Bay Bioregion and all locations of the North West Shelf, including northern Ningaloo, and NT in most cases. A significant genetic 'transition zone' was evident across a geographic distance of < 80km across the tip of the Dampier Peninsula, near the entrance to King Sound, which marks the border of the Kimberley and Canning marine bioregions. There was evidence for an isolation-by-distance (IBD) effect overall and within the Pilbara, but isolation-by-distance was not evident among samples from the Kimberley Bioregion. Northern Ningaloo and the Pilbara exchange few recruits with Shark Bay and are effectively demographically independent, while the regions north of Shark Bay probably exchange recruits through a stepping stone process. Some tests support the genetic sub-division between NT and the adjacent Kimberley bioregion (i.e. pairwise  $F_{st}$ , STRUCTURE), whereas with other tests the evidence is equivocal (i.e. DAPC). Modelling the effects of barriers to dispersal, environmental attributes, and geographic distance on genetic differentiation in this species revealed that all three factors had strong effects, but in most cases, these effects could not be distinguished from each other because of strong correlations among them.

The genetic 'transition zone' in the Kimberley coincides with the Sunday Strait, which experiences the largest tropical tidal range and fastest tidal currents in the world. Here dispersal and realised gene flow is more limited than elsewhere throughout the range of this species, suggesting a possible zone of retention based on local hydrodynamic effects. Results from the spatial autocorrelation analysis showed local scale dispersal within the coastal Kimberley is at a scale of 300 km, except in the transition zone where it was only 80 km. Two

hydrodynamic models for the area now highlight a degree of retention within King Sound, which will likely be relevant to identifying the underlying process that may explain the reduced gene flow northward or southward from the transition zone.

Only 63% of pairwise comparison between Pilbara sites were genetically differentiated, whereas in the Kimberley 92% of pairwise comparisons between sites were genetically differentiated. This suggests that the Kimberley is less connected than the Pilbara. These observations are consistent with more extensive movement occurring between reefs in the Pilbara than the Kimberley.

## **Implications for management at a broad- and fine-scale**

The level of inter-state genetic sub-division revealed in this study suggests that the current separate State and Territory based management arrangements for Stripey Snapper stocks in WA and the NT are likely to be appropriate, although there is a wide gap in sampling coverage between the Kimberley and the NT. The collection of additional samples between these two regions should be a priority. Based on this single broadcast spawning reef fish species, while the intra-state spatial genetic sub-division supports the separate fisheries management arrangements for the Gascoyne and North Coast bioregion stocks, the inclusion of the Ningaloo Bioregion within the Gascoyne coast of the State based fisheries management boundaries is not supported. The potential for demographic separation of Kimberley and Pilbara/Canning populations, including the genetic transition zone, should be taken into consideration for future management initiatives and reviews of management arrangements.

At a Kimberley Bioregional scale, management of Striper Snapper should be treated over this broad area as effectively being a single stock over the ecological timeframes relevant to harvest management. Samples collected from within the gazetted and proposed Kimberley marine parks suggest that at a fine scale, dispersal of Stripey Snapper between parks in the North Kimberley and the South-Western Kimberley is likely. However, the transition zone identified around the Dampier Peninsula that separates the Kimberley from the Pilbara/Canning populations should be recognised by managers of coastal resources along these coasts as a region of ecological significance.

## **Residual knowledge gaps**

Genetic differentiation between samples of Stripey Snapper from the Kimberley and NT may represent limited demographic exchange between these currently separately managed stocks. Further sampling from the intermediate region is needed to confirm this and potentially refine the area of transition.

Ocean currents are likely to play a significant role in distributing the larvae of Stripey Snapper. Models of hydrodynamic processes throughout NWA are available (see Condie & Andrewartha 2008), however it would be useful to evaluate how well these models predict the observed genetic structure in Stripey Snapper, since that would provide confidence that the models accurately reflect biological processes and therefore may be applied to other bioregions and/or species. This analysis is currently in development (O. Berry unpublished).

In contrast, the transition zone identified around the Dampier Peninsula that separates the Kimberley from the Pilbara/Canning populations is likely to be influenced by the extreme tidal flushing at the head of King Sound, rather than ocean currents. A fine-scale hydrodynamic model for this region was prepared by WAMSI Kimberley Project 2.2.7 (M. Feng, CSIRO, pers. comm). It would be useful to test whether this model can account for the observed genetic structure in this highly dynamic zone that supports harvest of numerous fishes.

Evidence for temporal variation in population structure was revealed through the analysis of historically collected samples. For these temporal samples we explored the reason for their observed divergence and were able to exclude at least one mechanism of DNA degradation (Appendix 1). This result may therefore represent a real shift in allele frequencies over time, potentially indicative of changing patterns of larval connectivity.

However, since we did not sample these exact locations again, it's unclear whether the pattern is wholly temporal or also has a spatial component. Additional sampling at these historical sites is required to resolve this question.

## 1 Introduction

Coastal ecosystems are some of the richest and most productive environments on the planet and yet are often at higher risk to anthropogenic threats (i.e. fishing, tourism, coastal development) than ecosystems further from shore. Many marine species inhabiting coastal ecosystems have restricted home ranges and do not migrate as adults (Cowen & Sponaugle 2009), it is therefore the free-living, dispersive larval stage that instead enables connection between sites. As a direct consequence of this larval stage, nearshore marine species exist in a system of interconnected populations influenced by the vagaries of currents, larval behaviour, and recruitment dynamics (e.g. Trembl *et al.* 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. Coastal ecosystems can also be topographically complex, which makes predicting connectivity among the network of populations difficult given the environmental variability among sites (for review see Burgess *et al.* 2014).

The proliferation of next-generation sequencing (NGS) approaches that enable high-throughput Single Nucleotide Polymorphism (SNP) discovery and genotyping (Andrews *et al.* 2016) now provides a means to quantify connectivity within coastal ecosystems with much greater resolution. The isolation of thousands of SNP markers across the genome can parse neutral processes, such as genetic drift (Riginos & Liggins 2013), from natural selection, which may drive phenotypic divergence between populations inhabiting different ecological environments (Nosil *et al.* 2009; also see Rellstab *et al.* 2015). Ease of access to environmental data derived from satellite imagery also provides a great opportunity to examine how geography and environment further influence genetic structure, including identifying shared barriers to larval dispersal and significant sources of larval recruits (Balkenhol *et al.* 2009; Wang & Bradburd 2014).

The coast of NWA provides an emerging frontier for implementing these new genomic tools under a management framework, given its diverse and extreme environmental conditions. There are several bioregional classifications for this coast including the Provinces and Ecoregions of Spalding *et al.* (2007) and the Provincial and Meso-scale Bioregions of the Integrated Marine and Coastal Regionalisation of Australia (IMCRA) of the Commonwealth of Australia (2006). As the fisheries resources along this coast are largely managed according to the IMCRA Meso-scale Bioregions, we follow these bioregions and highlight the potential implications of the results of our study in relation to bioregional and management boundaries (see Fig. 1 for overview). The NWA coast spans six marine bioregions (*sensu* Commonwealth of Australia 2006). The tropical Anson Beagle and Kimberley bioregions in particular hosts more than 2,633 islands (i.e. Buccaneer and Bonaparte Archipelagos), a diverse assemblage of fish and corals (Travers *et al.* 2010; Moore *et al.* 2014; Richards *et al.* 2015), highly turbid water, seagrass meadows and mangrove forests (e.g. Duke 2006), and a strong tidal regime (range ~11 meters) that likely impacts larval exchange (Thackway & Cresswell 1998; also see Wilson 2014). Reef faunal communities in the Kimberley display heterogeneous composition within the bioregion, as well as differentiation from adjacent bioregions (Travers *et al.* 2010; Wilson 2014); only a few studies have assessed genetic variation here (sea turtles: Waayers & Fitzpatrick 2013; fish: Horne *et al.* 2011, 2012, 2013; Veilleux *et al.* 2011). The Canning Bioregion to the west is characterized by moderately clear water that becomes turbid during spring tides and a tidal range up to 9m. This coast contains a wide variety of landforms with the shore principally composed of long sandy beaches (Thackway & Cresswell, 1998). The Pilbara Bioregion has tides from 1 to 5m, with water clarity ranging from highly turbid at inshore sites to clearer at offshore sites (i.e. Montebello Islands), with extensive seagrass and macroalgal meadows interspersed between the many islands in the region (Wilson *et al.* 2010; Evans *et al.* 2014, McLean *et al.* 2016). It also harbours a diverse and abundant fish and coral fauna (McLean *et al.* 2016; Travers *et al.* 2010; Hutchins 2001). The Ningaloo Bioregion to the southwest covers the entire Ningaloo Reef and is characterised by low tidal (~1m), fringing reefs adjacent to large lagoons with clear oligotrophic water regularly driven through the system by high-energy waves (Zhang *et al.* 2011). Shark Bay to the south has high cliffs, fringing reefs and low relief sandy shorelines (within Shark Bay), with intermittent but significant freshwater input from river outflows and the largest coverage of tropical and temperate seagrass meadows in WA (Walker 1990). 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 and at the Northwest Cape of Australia near Ningaloo Reef (Fig. 1A; Spalding *et al.* 2007; Travers *et al.* 2010, Thackway & Cresswell 1998). Few studies have investigated connectivity among these six distinct but ecologically important Australian coastal ecosystems (Johnson & Joll 1993; Johnson *et al.* 1993; Veilleux *et al.* 2011), and none to our knowledge focus on inshore fishes and include comprehensive sample coverage.

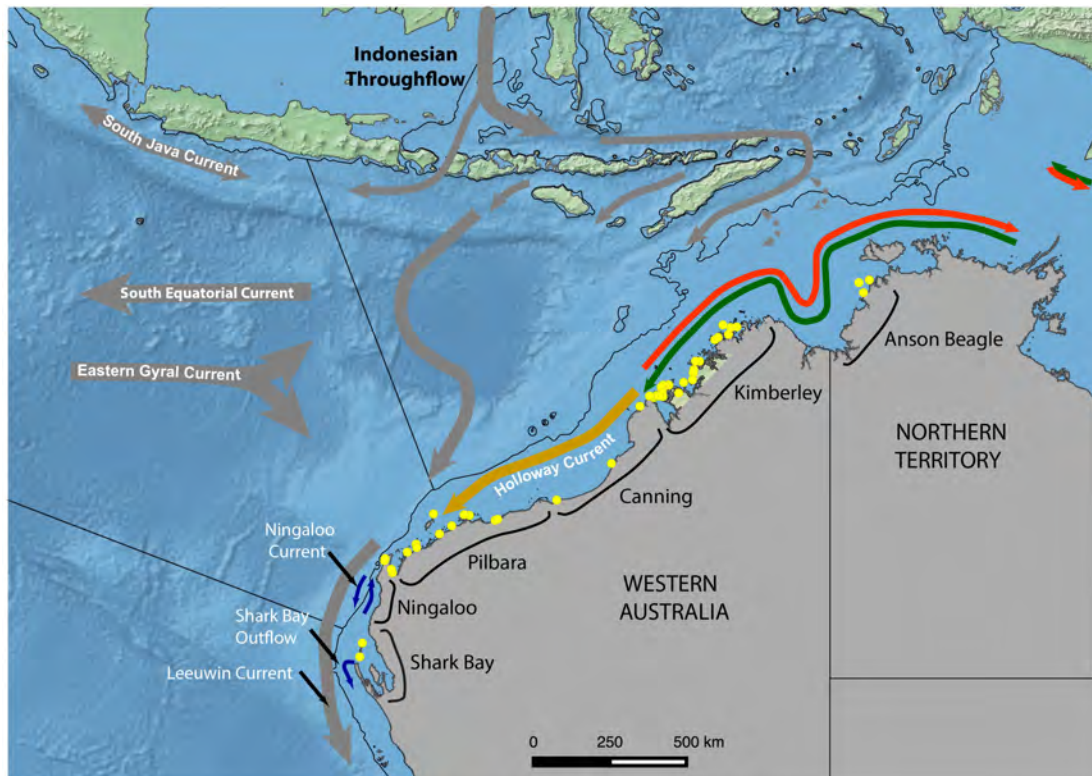
Here we evaluate genetic connectivity of the Stripey snapper, *Lutjanus carponotatus* (Richardson, 1842), across all six of the aforementioned bioregions using a genotyping-by-sequencing approach. *Lutjanus carponotatus* is abundant on inshore and mid-shelf reefs from Shark Bay to Bargara, Queensland, but also found more broadly in turbid waters from India through to the Indo-West Pacific. We here focus on this “indicator species” given its importance in recreational fisheries (Kritzer 2004), its ecological function as a macrofaunal predator, and the fact that its larval settlement behaviour is similar to other predatory species of commercial importance (e.g. *Plectropomus* sp.; Quéré and Leis 2010). A recent genetic survey of *L. carponotatus* on the Great Barrier Reef using mitochondrial markers found complete admixture within and between inshore islands at a scale of 800 km (Evans *et al.* 2010). A companion study based on the same species and molecular markers in WA identified a comparable scenario of complete admixture in this region, although it was strongly differentiated from the Great Barrier Reef populations (Veilleux *et al.* 2011). Both of these studies failed to separate evolutionary from ecological patterns of gene flow, which SNPs, applied here, may resolve.

We performed a genome-wide survey of *L. carponotatus* among 51 sites along the extensive ~3,000 km coast of NWA to compare broad-scale patterns of genomic divergence among bioregions that differ in reef composition, environmental conditions, and oceanographic current regimes. By using thousands of SNP loci as our proxy for realised dispersal we were able to further partition genetic divergence into the component that departs from neutral expectations (i.e. outlier loci) when comparing sites that are subject to different environmental conditions. We also performed a fine-scale investigation within the Kimberley Bioregion to identify barriers to larval dispersal.

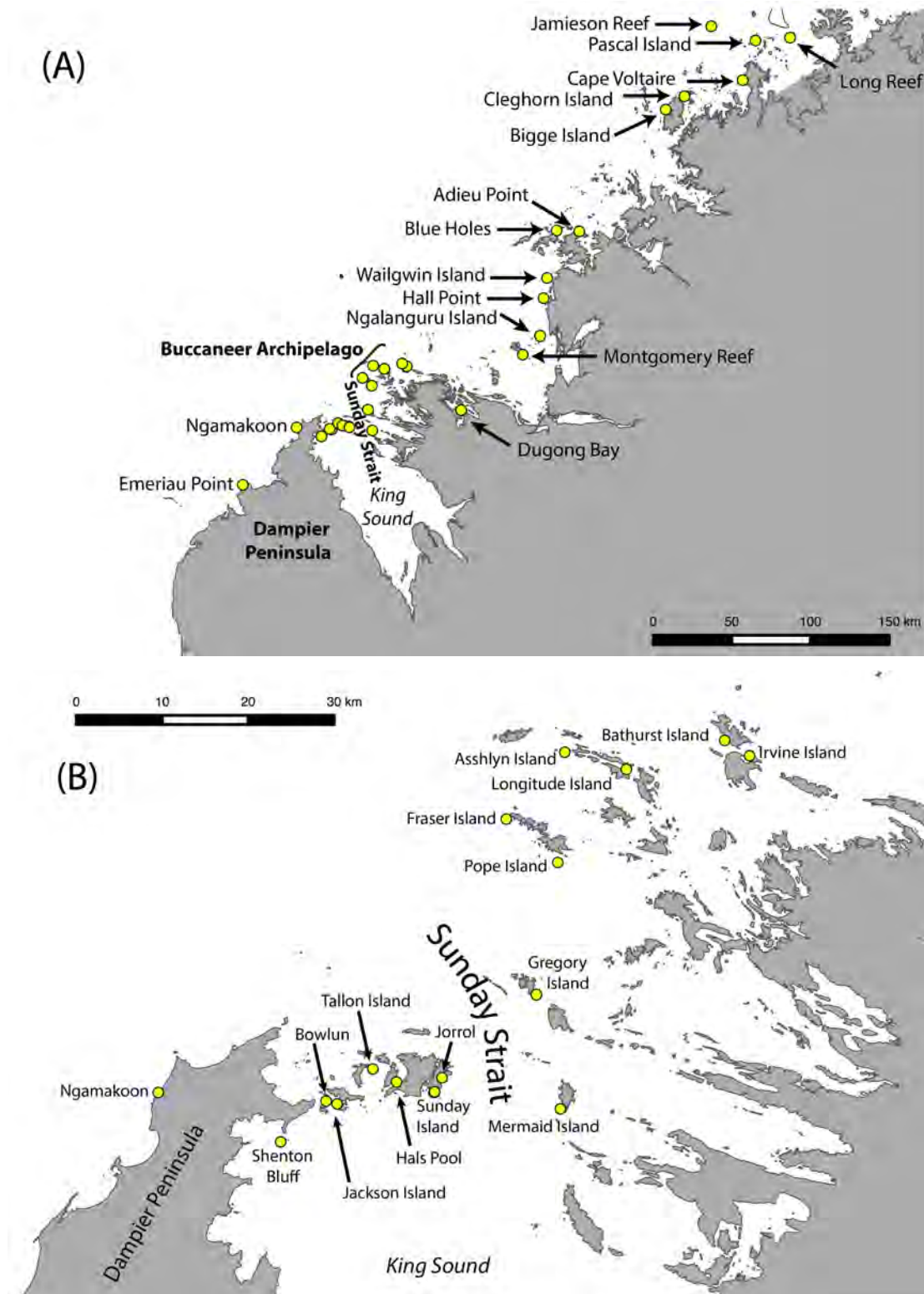
## 2 Materials and Methods

### 2.1 Study area and sample collection

Tissue samples of *L. carponotatus* (Fig. 1 and Fig. 2) were collected from 51 coastal sites across NWA from the Anson Beagle (now 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 tropical Australian coastline (also see Table 1) and immediately preserved in 95% ethanol. The majority of sampling was undertaken in 2014 and 2015, however, historic muscle tissue samples collected in 2002 and frozen at -80°C were obtained from four sites (Cape Bossut, Cape Keraudren, Cape Preston, Locker Point). An indirect test with these historical samples gave negative results for DNA degradation (see Appendix 1 and population genetic statistics methods for more details).



**Fig. 1** Map of sampling sites (yellow dots) for *L. carponotatus* in NWA. The dominant current affecting the outer shelf of the Kimberley, Canning and Pilbara Bioregions is the Holloway Current, which flows south-west along the shelf margin from May to September due to the prevailing winds. The dominant current affecting the Ningaloo and Shark Bay Bioregions is the Leeuwin Current (adapted from Sprintall *et al.* 2002; Domingues *et al.* 2007; D'Adamo *et al.* 2009; Schiller 2011). Red, green, and amber coloured lines indicate flow direction in summer, winter, and autumn, respectively. The 220 m isobath is indicated by the curved black line that follows the shoreline of NWA.



**Fig. 2** Sampling sites in the Kimberley management region (A) and sites surrounding the Sunday Strait and King Sound.

**Table 1.** Site, region, sample size (N), and molecular metrics (Na = number of alleles; Ho = observed heterozygosity; He = expected heterozygosity; Fis = Inbreeding coefficient) for *L. carponotatus* based on 4,402 SNP loci.

Site	Fisheries Management Area	MEOW Province	MEOW Ecoregion	IMCRA Bioregion	N	Na	Ho	He	Fis
Bass Reef	NT	Sahul Shelf	Bonaparte	Anson Beagle	13	1.833	0.208	0.219	0.034
Point Blaze	NT	Sahul Shelf	Bonaparte	Anson Beagle	10	1.784	0.205	0.218	0.040
Sail City	NT	Sahul Shelf	Bonaparte	Anson Beagle	2	1.385	0.195	0.158	-0.246
Long Reef	Kimberley	Sahul Shelf	Bonaparte	Kimberley	28	1.939	0.224	0.229	0.023
Pascal Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	15	1.868	0.217	0.224	0.024
Jamieson Reef	Kimberley	Sahul Shelf	Bonaparte	Kimberley	12	1.829	0.205	0.218	0.041
Cape Voltaire	Kimberley	Sahul Shelf	Bonaparte	Kimberley	49	1.970	0.214	0.229	0.058
Cleghorn Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	9	1.763	0.243	0.225	-0.071
Bigge Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	43	1.968	0.222	0.231	0.037
Blue Holes	Kimberley	Sahul Shelf	Bonaparte	Kimberley	30	1.938	0.200	0.222	0.081
Adieu Point	Kimberley	Sahul Shelf	Bonaparte	Kimberley	22	1.912	0.211	0.224	0.046
Wailgwin Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	19	1.892	0.207	0.220	0.045
Hall Point	Kimberley	Sahul Shelf	Bonaparte	Kimberley	22	1.921	0.207	0.224	0.059
Ngalanguru Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	17	1.877	0.225	0.227	0.004
Montgomery Reef	Kimberley	Sahul Shelf	Bonaparte	Kimberley	4	1.580	0.216	0.198	-0.100
Dugong Bay	Kimberley	Sahul Shelf	Bonaparte	Kimberley	21	1.905	0.207	0.223	0.056
Bathurst Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	3	1.495	0.221	0.183	-0.203
Irvine Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	8	1.845	0.348	0.262	-0.256
Fraser Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	7	1.711	0.207	0.210	-0.006
Longitude Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	5	1.638	0.204	0.202	-0.031
Asshlyn Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	3	1.517	0.215	0.190	-0.144
Pope Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	4	1.579	0.209	0.195	-0.085

Gregory Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	2	1.421	0.227	0.173	-0.315
Mermaid Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	5	1.633	0.237	0.210	-0.123
Jorrol	Kimberley	Sahul Shelf	Bonaparte	Kimberley	14	1.863	0.209	0.221	0.035
Hal's Pool	Kimberley	Sahul Shelf	Bonaparte	Kimberley	14	1.850	0.267	0.239	-0.086
Tallon Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	28	1.938	0.240	0.234	-0.013
Jackson Island	Kimberley	Sahul Shelf	Bonaparte	Kimberley	7	1.717	0.224	0.215	-0.047
Bowlun	Kimberley	Sahul Shelf	Bonaparte	Kimberley	3	1.503	0.224	0.187	-0.197
Shenton Bluff	Kimberley	Sahul Shelf	Bonaparte	Kimberley	41	1.962	0.208	0.226	0.068
Ngamakoon	Kimberley	NW OZ Shelf	EX to BRM	Canning	23	1.923	0.229	0.229	0.003
Emeriau Point	Kimberley	NW OZ Shelf	EX to BRM	Canning	30	1.946	0.241	0.236	-0.009
Cape Bossut	Kimberley	NW OZ Shelf	EX to BRM	Canning	30	1.945	0.267	0.241	-0.071
Cape Keraudren	Pilbara	NW OZ Shelf	EX to BRM	Canning	30	1.949	0.271	0.245	-0.073
Depuch Island	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	27	1.940	0.218	0.228	0.036
West Moore	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	25	1.937	0.218	0.230	0.044
Gidley Island	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	27	1.937	0.199	0.223	0.084
Rosemary Island	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	27	1.937	0.206	0.225	0.068
Cape Preston	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	30	1.950	0.255	0.239	-0.043
Passage Island	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	26	1.930	0.197	0.222	0.091
Montebello North	Pilbara	NW OZ Shelf	EX to BRM	Pilbara (Offshore)	26	1.935	0.198	0.221	0.082
Montebello South	Pilbara	NW OZ Shelf	EX to BRM	Pilbara (Offshore)	24	1.922	0.210	0.226	0.053
Thevenard Islands	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	25	1.930	0.199	0.222	0.086
Paroo Shoal	Pilbara	NW OZ Shelf	EX to BRM	Pilbara	26	1.931	0.213	0.226	0.049
Locker Point	Gascoyne	NW OZ Shelf	EX to BRM	Pilbara	24	1.926	0.256	0.239	-0.050
Bay of Rest	Gascoyne	NW OZ Shelf	EX to BRM	Pilbara	28	1.940	0.203	0.222	0.070
Roberts Island	Gascoyne	NW OZ Shelf	EX to BRM	Pilbara	27	1.938	0.201	0.224	0.090
Tantabiddi	Gascoyne	NW OZ Shelf	Ningaloo	Ningaloo	24	1.917	0.200	0.221	0.075

Milyering	Gascoyne	NW OZ Shelf	Ningaloo	Ningaloo	25	1.927	0.206	0.223	0.057
Bernier Island	Gascoyne	WC OZ Shelf	Shark Bay	Shark Bay	25	1.901	0.193	0.218	0.088
Dorre Island	Gascoyne	WC OZ Shelf	Shark Bay	Shark Bay	27	1.902	0.194	0.218	0.089

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Abbreviations: Northern Territory (NT), North West Australia (NW OZ), Buccaneer Archipelago (BA); Broome (BRM); Exmouth (EX); Sunday Islands (SI). Management Area refers to current State based fisheries management areas; Marine Ecoregions of the World (MEOW) derived from Spalding et al (2007) nested Ecoregions within Provinces; Integrated Marine and Coastal Regionalisation of Australia (IMCRA) meso-scale Bioregions derived from Commonwealth of Australia (2006).

## 2.2 DNA Extraction

DNA was extracted from tissue samples using 96-well plates according to the salt extraction method described by (Cawthorn et al. 2011), followed by purification with Zymo ZR-96 DNA Clean and Concentrator kits (Zymo Research, California, USA).

## 2.3 Reduced Representation SNP Genotyping

Downstream SNP genotyping was done using a modified DArTseq™ protocol (Grewe *et al.* 2015), which is a proprietary method for reduced representation genomic library preparation and NGS (Kilian *et al.* 2012; Cruz *et al.* 2013). In our case, genomic DNA was digested with two restriction enzymes (PstI-SphI and PstI-NspI) instead of one in order 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 sec, 58 °C for 30 sec, and 72 °C for 45 sec, 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 (Illumina) bridge PCR followed by sequencing on an Illumina HiSeq2500. The sequencing (single read) was run for 77 cycles.

## 2.4 SNP Calling

Read assembly, quality control, and SNP calling was done 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.

## 2.5 SNP Quality Control Filtering

Following SNP genotyping, additional quality control (QC) steps were performed to the 17,007 loci identified prior to genetic analyses: 1) rare alleles (frequency < 0.05) and highly variable loci (heterozygosity > 0.75) were removed, 2) loci with coverage less than 20X and greater than 200X were removed, and 3) individuals with more than 1% missing data were removed. Following these filtering steps, we were left with 5,094 loci. To comply with Hardy-Weinberg Equilibrium (HWE) and Linkage Disequilibrium (LD) expectations, we chose to exclude loci out of HWE in greater than 10 populations and loci that exhibited LD in greater than 5 populations. Testing for HWE made use of custom R scripts implemented within the R packages SNPAssoc (González *et al.* 2007) and pegas (González *et al.* 2007; Paradis 2010). Testing for LD made use of custom R scripts implemented within the R packages doParallel (Calaway *et al.* 2014) and Adegenet (Jombart 2008). After all the outlined filtering steps, we were left with 4,402 loci sampled at 51 sites. We additionally attempted filtering SNP loci using a number of different values for HWE, LD, and QC (+/- 15% of threshold), which did not impact the overall outcome (data not shown); we therefore only present data based on the outlined selection criteria. The resulting genind file was converted to other program specific input files using PGDSPIDER version 2.0.5.1 (Lischer & Excoffier 2012). Downstream genetic analyses were performed with all samples from all collection sites (full dataset) or with only those populations with  $N \geq 6$  or  $N \geq 20$  individuals collected (reduced dataset) to mitigate the effects of low sample size, where appropriate.

## 2.6 Population genetic statistics

$F_{ST}$ ,  $F_{IS}$ , 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. In order to compare the relative abundance of 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. It results in fewer false positive than other outlier tests, which appear to be influenced by the effects of demographic

history (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 removed from downstream analyses unless otherwise noted.

It should also be noted that individuals collected in the Pilbara bioregion in 2002 appeared genetically distinct from individuals collected in the same bioregion in 2015. We therefore compared SNP type (i.e. transition versus transversion) for a subsample of those individuals ( $N = 30$ ) collected in 2002 and 2015, respectively, to assess whether deamination (C/T transitions) or genetic damage could explain the genetic divergence between the older samples (2002) versus the newer samples (2015; see Appendix 1).

## 2.7 Model-Based Clustering analysis

To explore genetic structure across sampling sites, a clustering analysis was performed with STRUCTURE version 2.3.4 (Pritchard *et al.* 2000) using locations with  $N \geq 20$  individuals both with and without *a priori* information of 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 *et al.* 2003). The number of  $K$  (putative populations) ranged from one to eight and 20 replicate analyses were run for each value of  $K$ . Although we sampled more than eight sites, we found that  $K > 8$  was not necessary to identify the optimal number of clusters (data not shown). The number of clusters was inferred by comparing the  $\ln Pr(X|K)$  among different values of  $K$ . The value of  $K$  for which  $\ln Pr(X|K)$  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 *et al.* 2005) was also considered. After the initial set of runs, this process was repeated with only the identified outlier loci to assess the extent of natural selection on genetic differentiation (see above).

## 2.8 Discriminant Analysis of Principle Components (DAPC)

We employed Discriminant Analysis of Principle Components (DAPC) implemented in the R package Adegenet to identify and 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 (BIC) 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 analysis was repeated on the neutral and the outlier dataset.

## 2.9 Determinants of genetic differentiation

We used an information-theoretic approach (Anderson 2008) to determine the factors that influence genetic differentiation in this particular species of snapper. This method ranks alternative models according to empirical evidence versus excluding models (Correa & Hendry 2012). Sample sites with  $N < 6$  were excluded from the analysis given the uncertainty in  $F_{ST}$  estimates when based on low sample size (Willing *et al.* 2012). Environmental and geographical variables were included in the model selection process and each model was ranked based on their evidence ratio and posterior probability. Environmental factors were extracted from freely available ocean climate layers (MARSPEC, Sbrocco & Barber 2013; Bio-ORACLE, Tyberghein *et al.* 2012) and included 43 variables considered likely to influence fitness of larval fishes (e.g. sea surface salinity, sea surface temperature, nutrient load, bathymetry, tidal range). Because many of these variables were correlated, we reduced them into a single composite variable (*env*) by extracting the first component of a Principal Component Analysis (PCA), which accounted for 70% of the variability within the dataset based on the eight most influential factors extracted from Draftsman plots (see Appendix 2). Geographical factors included the Euclidean distance between sites (*Geo*) and the presence of three putative barriers to larval dispersal. Although

the northern and western coasts of Australia have been classified and re-classified according to a number of marine biogeographical boundaries (e.g. Fox & Beckley 2005; Spalding *et al.* 2007; Thackway & Cresswell 1998), we follow the marine ecoregions of the world (MEOW) of Spalding *et al.* (2007), which utilises the most recent quantitative data on marine fishes in this region. The ecoregional units we specifically test are the NT, Bonaparte Coast, Exmouth to Broome, and Ningaloo to Shark Bay. Note that although MEOW classification does not contain a NT ecoregion, we have included it in this analysis as there were limited samples through the north-eastern sector of the Bonaparte Coast, and the NT fisheries are managed separately to WA. 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 (Fig. 1A; Spalding *et al.* 2007; Travers *et al.* 2010; Thackway & Cresswell 1998). All barriers were considered independently and in combination (*barrier1\_2*, *barrier1\_3*, *barrier2\_3*, and *barrier1\_2\_3*). Barriers were modeled as a factor with 1 to 3 levels (number of barriers), where sites in the same level were on the same side of the barrier, and sites in different levels were on different sides of any of the three barriers. Overall, 67 models were fitted using both linear models (lm) and linear mixed effect models (lmer). Linear mixed effects models included site ID as a random effect in order to compensate for the fact that pairwise  $F_{ST}$  values are not independent among sites. For each model, the sample size-corrected Akaike information criterion (AIC) was computed as  $AICc = AIC + 2K(K + 1)/(n - K - 1)$ , where  $AIC = -2\log\text{-likelihood} + 2K$  ( $K$  = number of parameters in model,  $n$  = number of observations). Models were then ranked based on increasing  $AICc$  and further interpretation based on model probabilities ( $w$ ) and evidence ratios (Anderson 2008).

## 2.10 Spatial autocorrelation and IBD

GenAlEx version 6.502 (Peakall & Smouse 2006) was also used to quantify spatial autocorrelation for all sites with  $N \geq 6$  within the Kimberley cluster (0 to 256 km,  $N = 266$ ), within the Pilbara cluster (0 to 426 km,  $N = 391$ ), and within the transition zone between the two clusters (0 to 148 km,  $N = 193$ ). We conducted a multiple distance class spatial autocorrelation rather than conventional correlograms to accommodate uneven sample sizes and distances typical of reef topography (see Peakall *et al.* 2003). Geographic distances between sites were calculated based on the shortest across-water distance with a minimum water depth of 1m. These estimates were calculated with the Marmap R package (Pante & Simon-Bouhet 2013) and based on the GEBCO 2014 30-second bathymetry available from the British Oceanographic Data Centre.

We applied Mantel tests to evaluate the relationship between linearised  $F_{ST}$  ( $F_{ST}/(1-F_{ST})$ ) and distance. This analysis was based on 9999 permutations of the data calculated with the vegan R package (Oksanen *et al.* 2007). Mantel tests were applied to the entire dataset as well as the Kimberley and Pilbara sites separately.

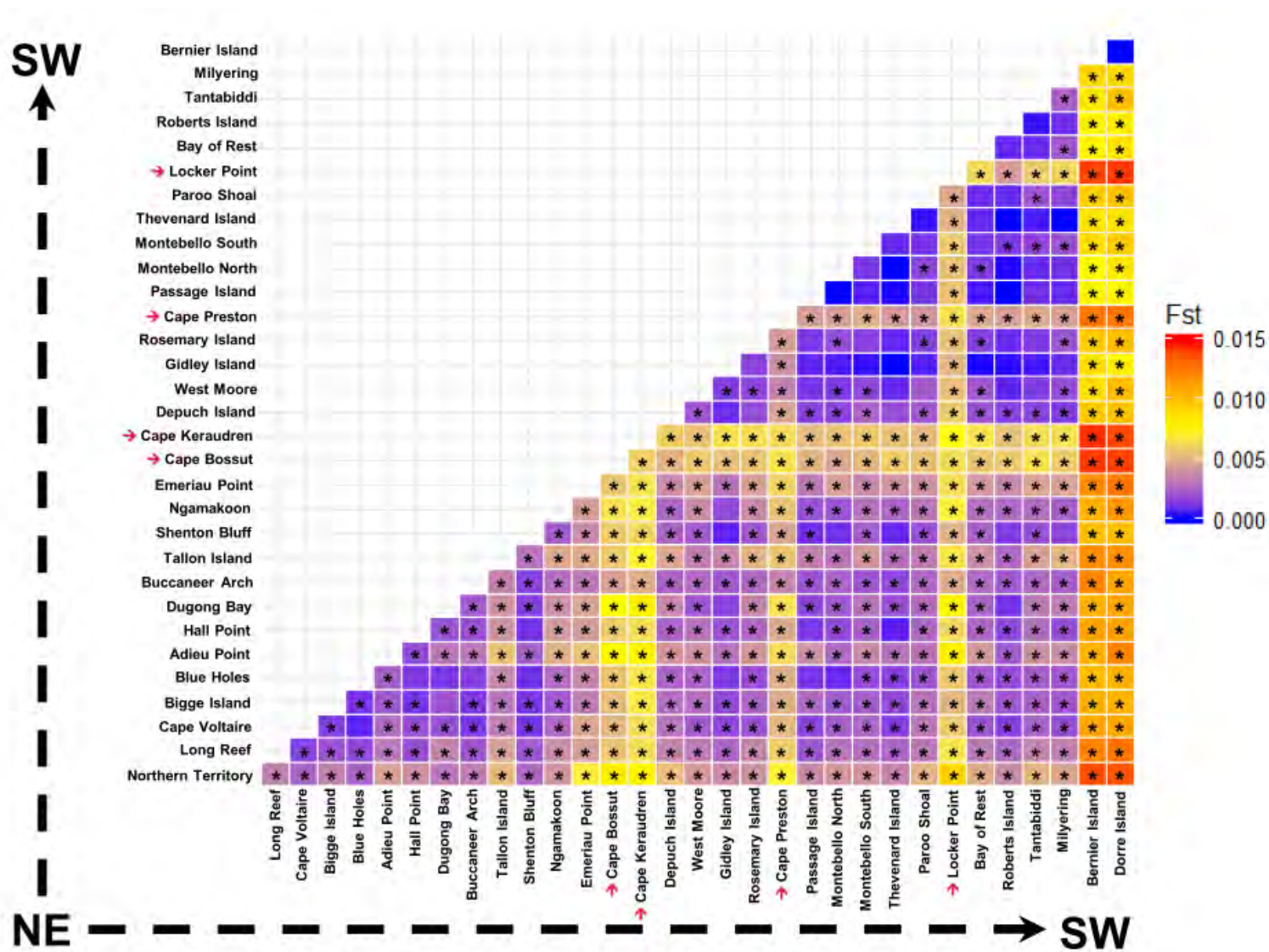
## 3 Results

### 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 are presented in Table 1. Based on the observed heterozygosity, genetic diversity was significantly higher in the southwestern bioregions (Canning, Pilbara, and Shark Bay) than the northeastern bioregions (NT and Kimberley; t-test:  $t = -4.19$  and  $P < 0.001$ ). Moreover, observed heterozygosity was only weakly correlated with the latitude of each site ( $R^2 = 0.159$ ), suggesting that it is a bioregional effect versus a direct distance effect.  $F_{IS}$  values were mostly positive in the SW regions, whereas in the northern region they were mostly negative, suggesting a greater amount of inbreeding in the Pilbara versus the Kimberley.  $F_{IS}$  values were similarly only weakly correlated with the latitude of each site ( $R^2 = 0.137$ ). This result based on  $F_{IS}$  values may also be an artefact of sampling, whereby Kimberley samples were collected by non-selective traps and Pilbara samples were collected in a more selective manner (i.e. speargun). Note that the only negative  $F_{IS}$  values in the Pilbara were the historic samples collected by traps. We also identified 66 outlier loci using Outflank, which represent a small proportion of the overall 4,402 SNP loci identified.

### 3.2 Genetic subdivision

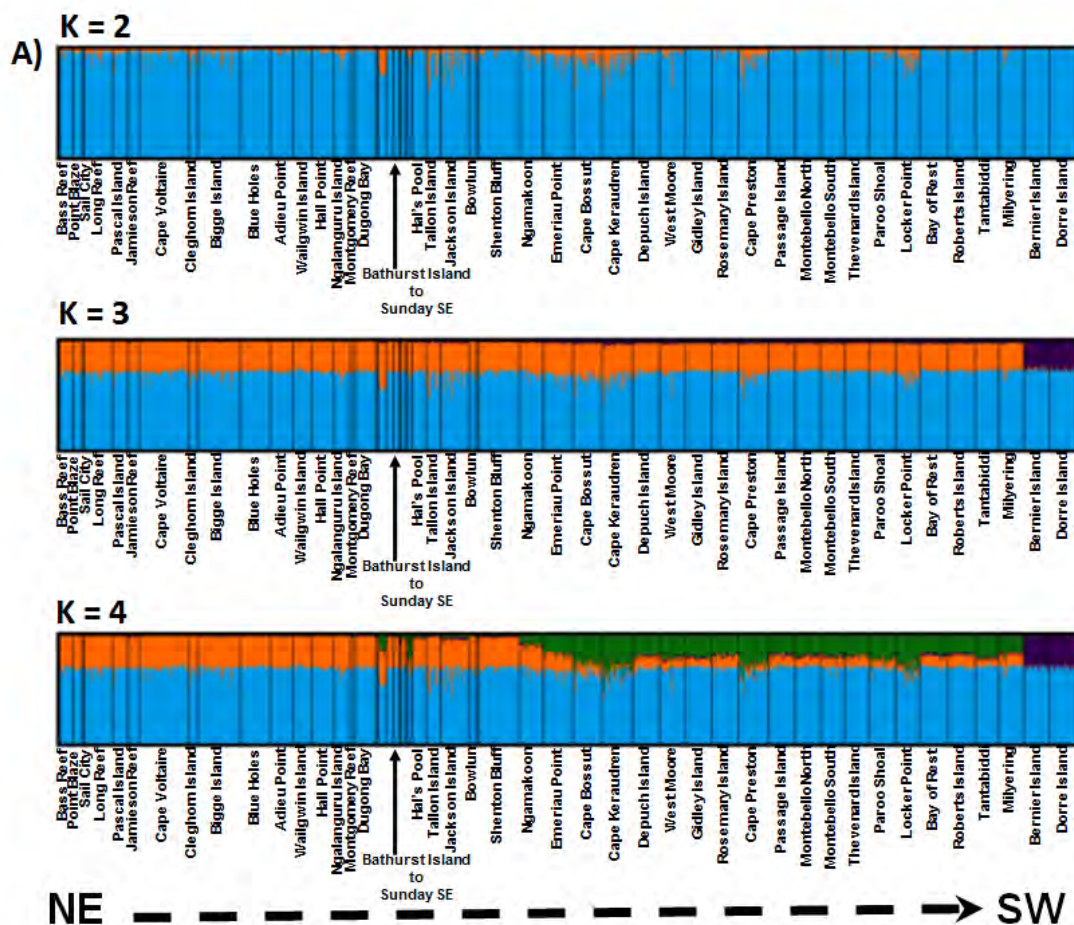
Patterns of pairwise genetic differentiation are summarized in Fig. 2, revealing small but significant genetic differences among most sampling locations (i.e. 424 out of 496 tests significant), which suggests restrictions in gene flow between geographically distant (e.g. NT and Shark Bay) but even in some cases, neighbouring sites *within* bioregions as little as a few kilometres apart. The historical samples collected from sites in the Pilbara in 2002 consistently exhibited higher levels of genetic differentiation from those collected in 2014 and 2015 (Fig. 2). Pairwise differentiation was greater in the Kimberley (92% pairwise comparisons significant) than the Pilbara (63% pairwise comparisons significant)(Fig. 2).

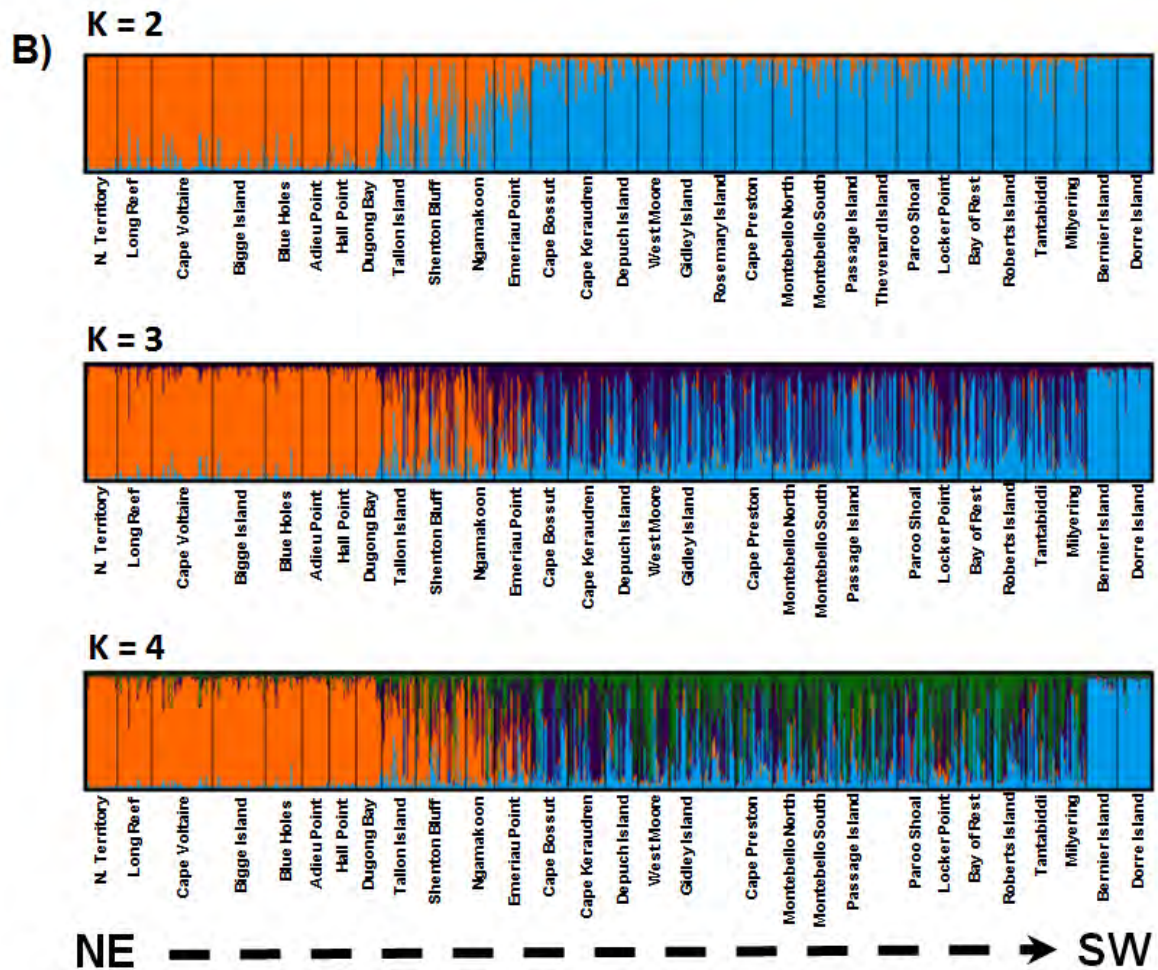


**Fig. 2** Heatmap of pairwise  $F_{ST}$  values for *L. carponotatus* populations with 20 or more individuals in NWA based on 4,402 SNP loci. \*indicates significant difference after Narum correction ( $P < 0.0074$ ). The four historical sample sites (i.e. 2002) are indicated by small, red arrows.

### 3.3 Model-Based Clustering analysis

Bayesian clustering analysis suggested  $K = 2$  populations as the most parsimonious partitioning of individuals based on the metric  $\Delta K$  (Evanno *et al.* 2005; also see Appendix 3,  $\Delta K = 910.944$ ). For clarity, we also present  $K = 3$  and  $K = 4$  (Fig. 3). The primary split corresponds to the boundary between Shark Bay and Ningaloo Bioregions with northern Ningaloo grouping with all locations of the North West Shelf towards NT. Also note a significant genetic ‘transition zone’ across a distance of < 80km in the region at the tip of the Dampier Peninsula, near the entrance to King Sound (i.e. Dugong Bay to Emeriau Point). The pattern remains the same whether we consider all 4,402 SNP loci (Fig. 3A) or only the 66 outlier loci (Fig. 3B), which may be subject to strong directional selection. Note that the NT sites and sites in the Buccaneer Archipelago with small sample sizes are pooled for inclusion in the outlier analysis.



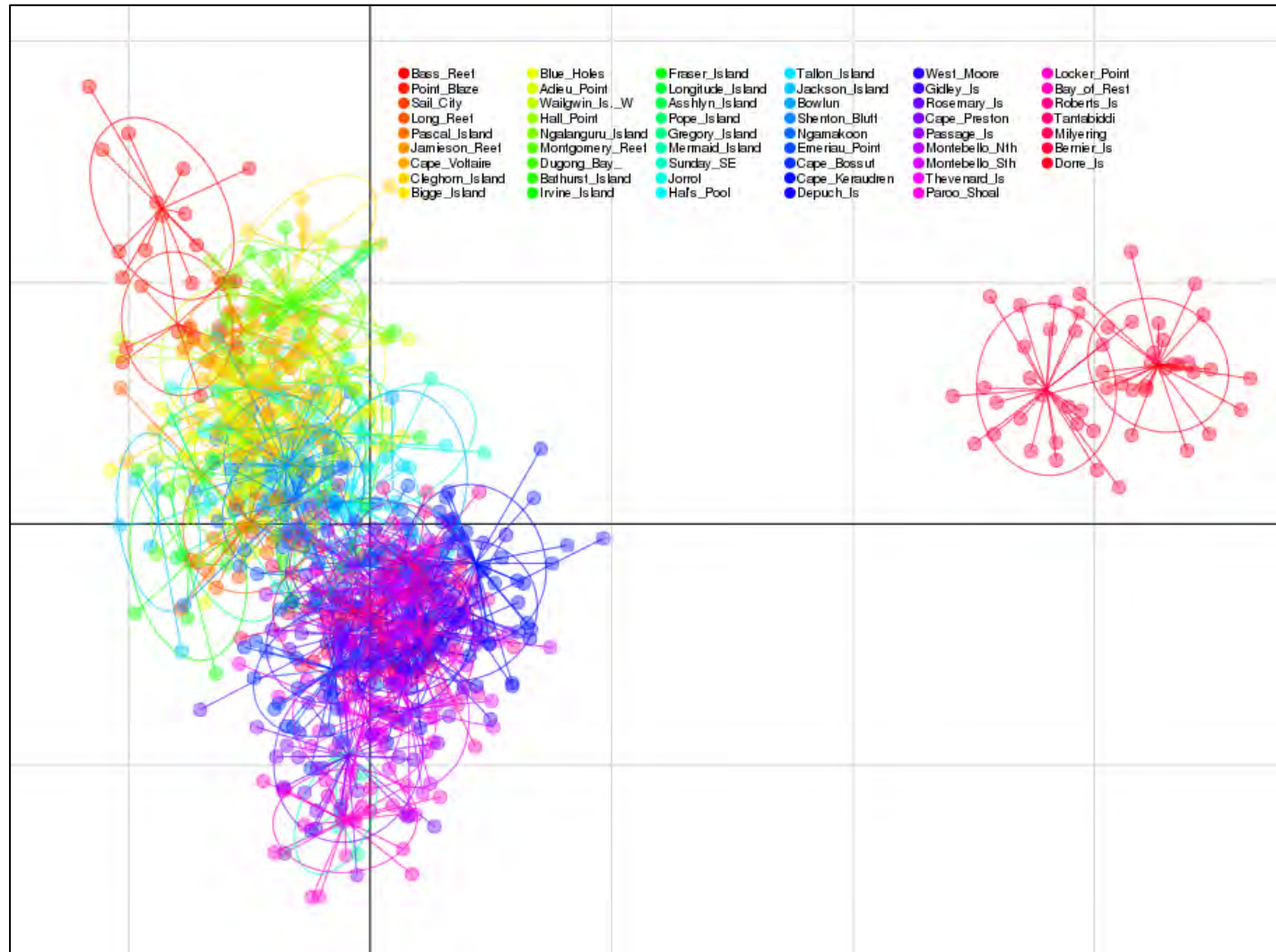


**Fig. 3** Results of Bayesian clustering for *L. carponotatus* populations in NWA based on (A) 4,402 SNP loci and (B) 66 outlier loci. Results from  $K = 2$ ,  $K = 3$ , and  $K = 4$  are presented;  $K = 2$  was the most likely number of clusters in both cases (see Appendix 3). No prior locations were input as priors in these runs. Individuals are represented by vertical bars, each divided according to their estimated probability of ancestry from each of the genetic clusters (represented by blue and orange). Sites are ordered northeast to southwest and from left to right. Note that the NT sites are pooled for inclusion in the outlier analysis only.

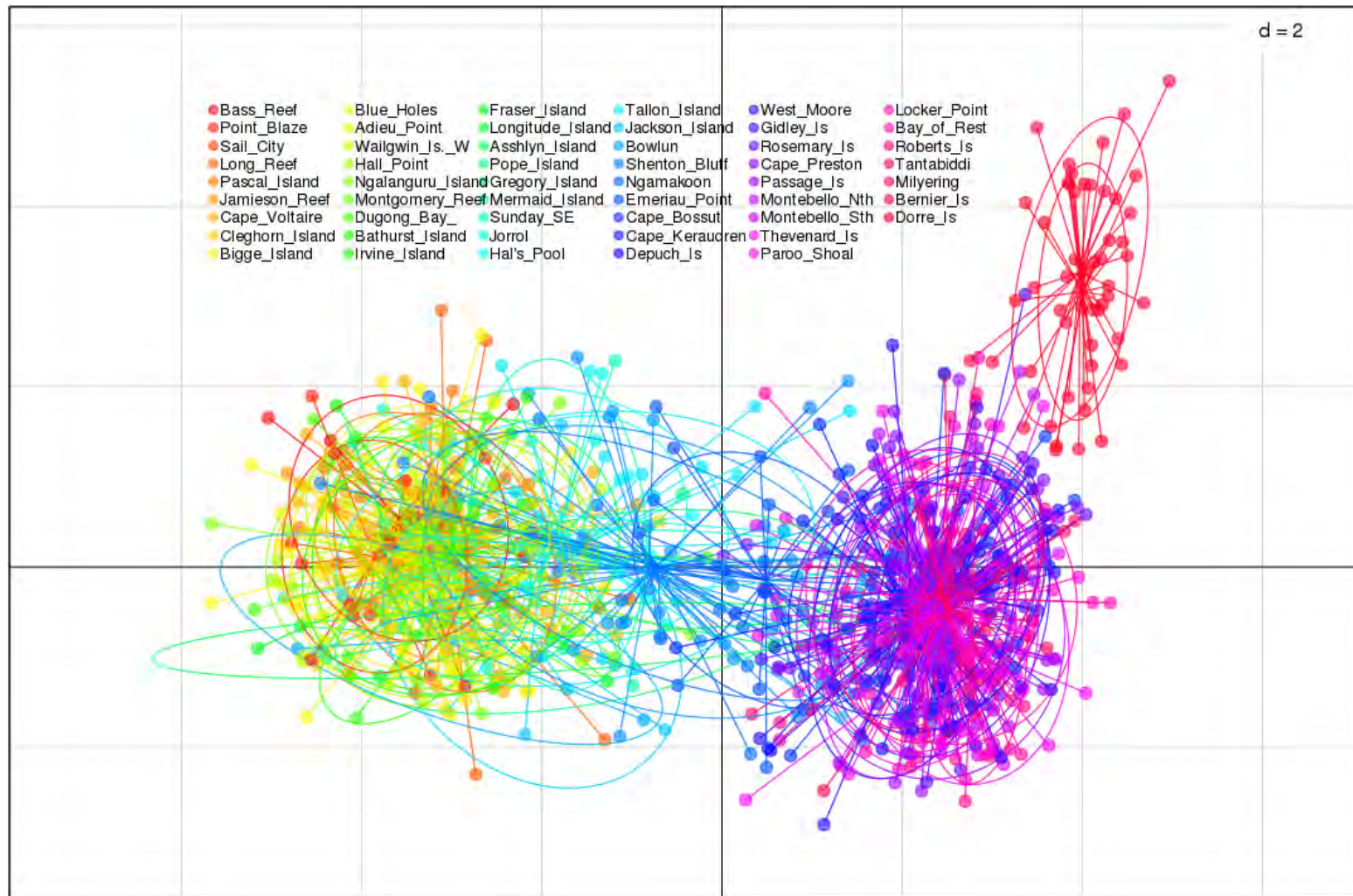
### 3.4 Discriminant Analysis of Principle Components (DAPC)

The k-means algorithm was optimised at  $K = 2$  in the neutral and outlier datasets. Linear discriminant analysis revealed that for the neutral dataset these groups corresponded to the Shark Bay bioregion versus all locations of the North West Shelf (Fig. 4). However, there appeared to be an approximate north to south isolation by distance pattern among the samples from the NT and Kimberley, but little discernible pattern among samples from the Pilbara bioregion (Fig. 4A). The DAPC analysis of the outlier dataset was less discriminating. The points representing samples from Shark Bay formed a distinct group on the right of the plot while those for the Pilbara and Canning exhibited minor overlap but no overlap with those representing Kimberley and NT samples. Pilbara and Kimberley samples were mostly distinct from each other; however sites between the Dampier Peninsula and Buccaneer Archipelago exhibited varying degrees of joint membership and intermediate positions between the majority of the Kimberley and Pilbara clusters (Fig. 4).

(A)



(B)



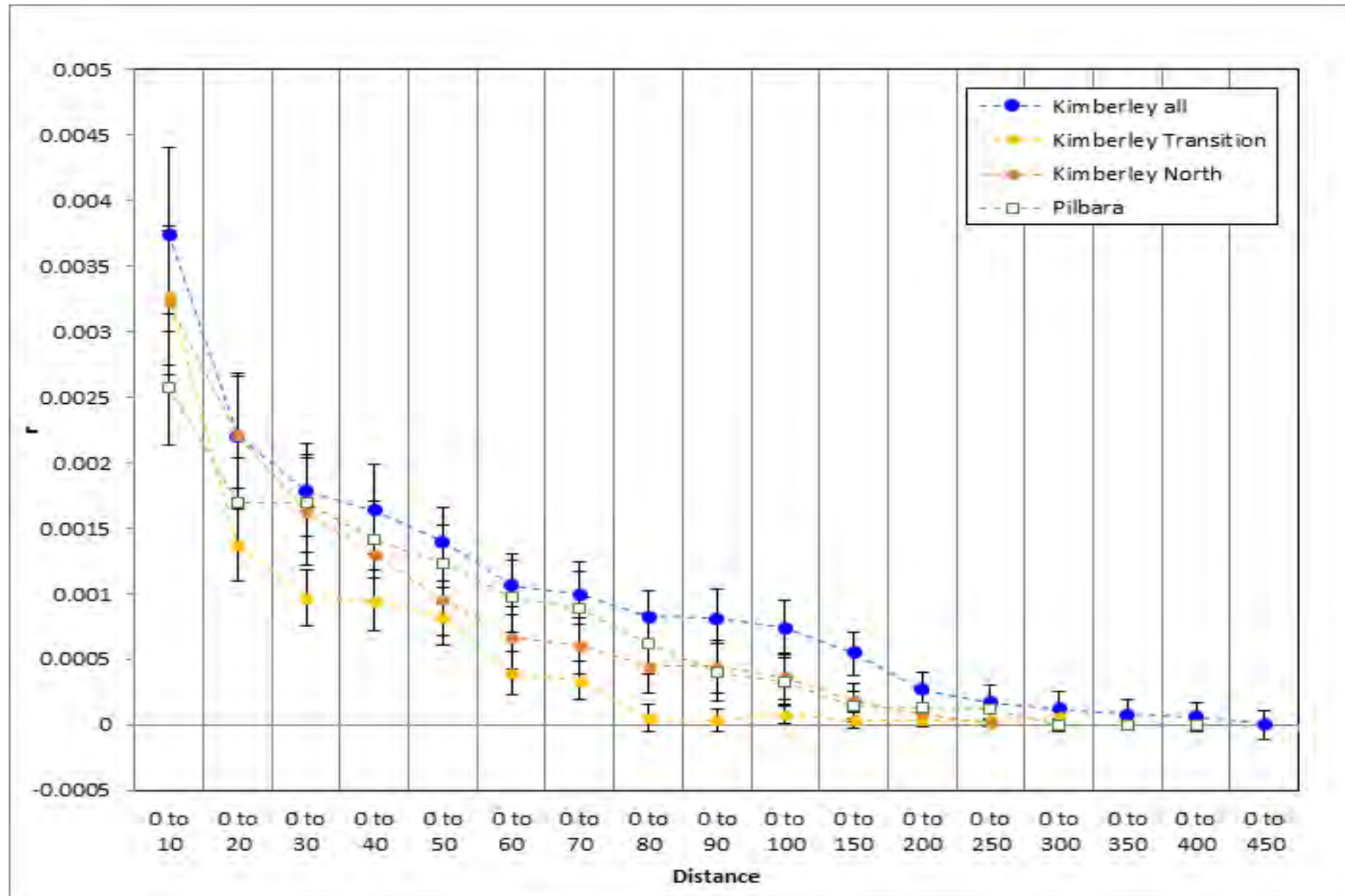
**Fig. 4** Scatterplot of DAPC performed on all *L. carponotatus* samples based on (A) 4,402 SNP loci and (B) 66 outlier loci. Populations are coloured in north to south order with 95% inertia ellipses. Dots represent individual genotypes and axes show the first two discriminant functions.

### 3.5 Determinants of genetic differentiation

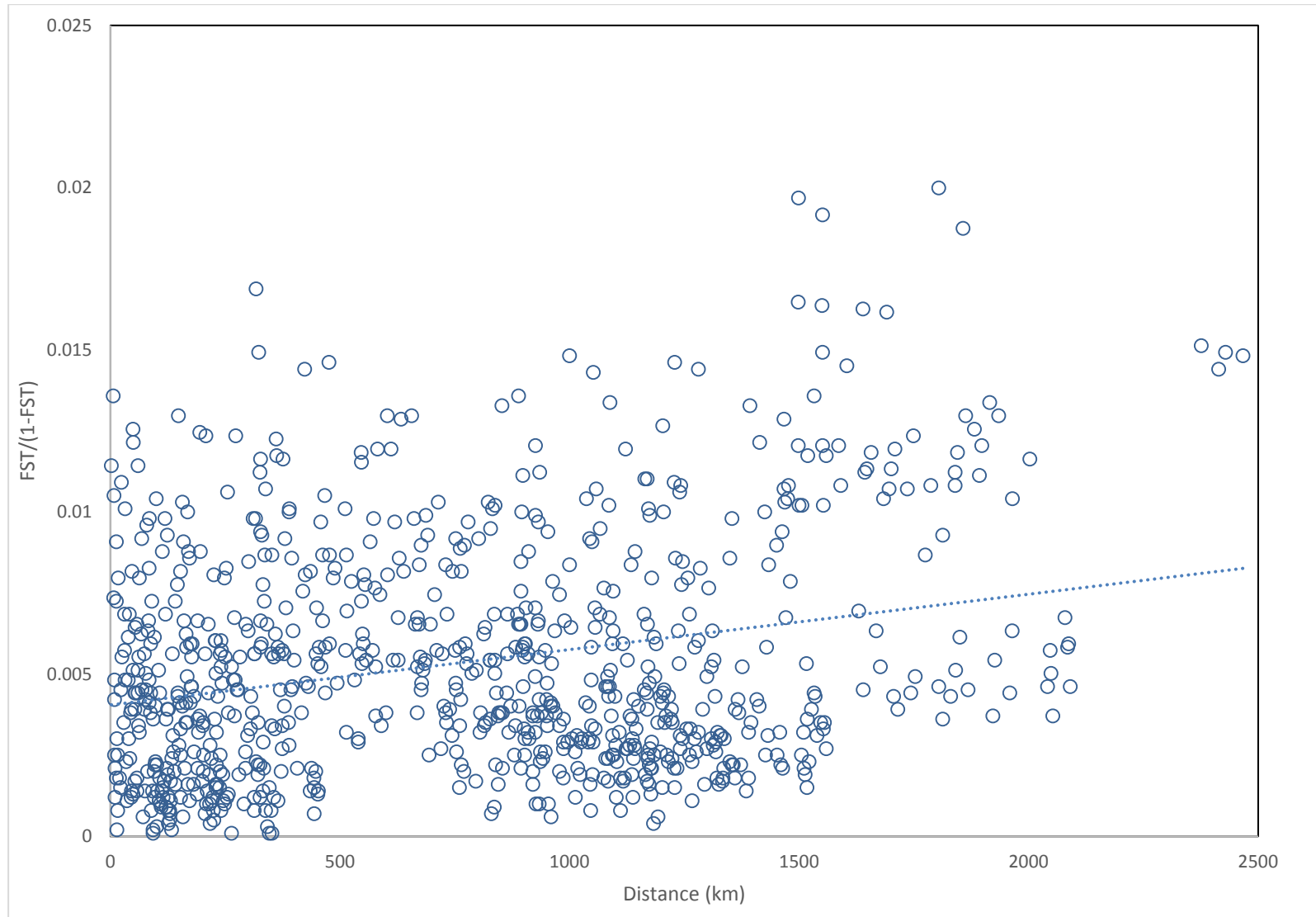
One model outperformed all the other models (model likelihood of 1.0 when compared to other models). This model included variables *geo*, *env*, the presence of all three barriers, as well as an interaction between these terms (Appendix 4). We repeated this analysis with outlier loci only and got a different result, only barrier 1 was represented in all four top models (i.e. barrier between the NT and the Kimberley). Thus, modelling the effects of barriers to dispersal, environmental attributes, 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 parsed from each other given the strong correlations among them (see Appendix 5).

### 3.6 Spatial autocorrelation and IBD

Results from the spatial autocorrelation analysis showed significant local scale genetic structure. The autocorrelation coefficient was modest ( $r \sim 0.0025$ ), but significantly positive as it dropped away from its initial plateau (Fig. 5). The distance where  $r$  first crossed the x-axis was roughly 300 km, except in the transition zone where it was only 80 km. Such reference points on the x-axis reveal the distance where the random effects of genetic drift, not gene flow, are the primary determinants of genetic composition in the different regions. A Mantel test revealed that when considering all data, distance was significantly correlated with genetic differentiation between sites ( $R = 0.25$ ,  $P < 0.001$ ; Fig. 6). Distance was not a significant correlate with genetic differentiation when considering sites in the Kimberley only ( $R = 0.08$ ,  $P = 0.23$ ), but was significantly correlated for the sites in the Pilbara ( $R = 0.50$ ,  $P = 0.01$ ).



**Fig. 5** Spatial autocorrelation as a function of cumulative geographic distance (in kilometres) for *L. carponotatus* populations with 20 or more individuals in NWA based on 4,402 SNP loci in all of the Kimberley, the Kimberley transition zone only, the Northern Kimberley only, or the Pilbara.



**Fig. 6** Isolation by distance for all *L. carponotatus* samples illustrating the relationship between geographic distance and linearised  $F_{ST}$ . Dashed line indicate best linear fit.

## 4 Discussion and Conclusions

This study, along with a companion study on the Miller's Damselfish (*Pomacentrus milleri*; sub-report 1.1.3.4a), is the first to investigate genetic connectivity within the coastal Kimberley Bioregion as well as other parts of WA and NT. The Stripey Snapper is probably representative of many widespread and abundant, pelagic spawning reef-associated fish species with relatively long pelagic larval durations in NWA. Many of these species are also recreationally and/or commercially targeted and therefore understanding the processes driving connectivity between populations can support more appropriate management decisions. Although larvae from these species are able to actively exercise some control over their dispersal and settlement, the powerful hydrodynamic forces in this region appear to play a significant role in distributing the larvae of *L. carponotatus*.

Primarily, the distribution of genetic subdivision in *L. carponotatus* across NWA follows an isolation-by-distance model of connectivity. This is probably facilitated by the prolonged duration larvae spend in the plankton where, on average, dispersal potential is in the order of up to 450km. However, it is also clear that within this, significant genetic breaks exist at well-recognised biogeographic boundaries. These results support previously hypothesised restrictions to connectivity between the Pilbara, northern Ningaloo and the Shark Bay bioregions based on allozyme electrophoresis for four other commercial fish species (Johnson *et al.* 1993) and allozyme and SNP data for the coral, *Pocillopora damicornis* (Whitaker 2006; Thomas *et al.* in review). Our study also provides evidence of restricted connectivity between geographically distant sites and, in some cases, neighbouring sites *within* bioregions separated by a few kilometres. The increased genetic resolution in the present study provided by thousands of SNP loci, with some under natural selection, also revealed a genetic transition zone in the macro-tidal region at the mouth of King Sound that has not been shown using other markers (Veilleux *et al.* 2011). This corresponds to a well-defined IMCRA biogeographic boundary between the Kimberley and Canning marine bioregions, based on shifts in faunal composition in a number of taxa, including fishes (Hutchins 2001; Travers *et al.* 2010) and molluscs (Wilson 2013), but now genetic differentiation is also confirmed at this location.

### 4.1 Genetic diversity is highest at range limits

Reduced levels of neutral genetic diversity are characteristic of populations at the edge of their range (Messmer *et al.* 2012), and can be attributed to isolation, small population size, and associated increases in genetic drift, as well as potentially strong selection (Kawecki 2008; Cahill & Levinton 2016). The range of *L. carponotatus* extends from Taiwan in the north to Shark Bay in the south and into eastern Australia. Although our sampling efforts did not include the full distributional range of this species, it was extensive (13° of latitude). Considering this, one might expect shifts in genetic connectivity and diversity to be present over this large spatial scale. Surprisingly, the reverse was observed, with levels of genetic diversity being similar throughout the sampling range. This homogeneity may be due to the relatively long PLD of this species and large genetic neighbourhoods that we observed, as evidenced in positive spatial autocorrelation up to 450 km. Despite such forces acting to homogenise genetic diversity metrics, many populations, particularly in the Kimberley bioregion, exhibited low but significant differentiation. The reasons for this pattern are unclear. However, its predominance among samples from the Kimberley and not the Pilbara indicates that patterns of dispersal are likely to differ between these bioregions, perhaps owing to their markedly different hydrodynamic conditions.

### 4.2 Broad-scale subdivision across NWA

Currently harvest of *L. carponotatus* from the Gascoyne and Ningaloo regions is considered separately from harvest throughout the remainder of NWA. Our results do not support this division, but instead show that *L. carponotatus* from Ningaloo has much higher levels of connectivity with samples from the Pilbara than with those from the Gascoyne. Two dominant patterns of genetic subdivision were evident from the SNP genotyping

of *L. carponotatus*. The first was a clear overall isolation by distance (IBD) effect, where on average sampling sites were genetically most similar to their closest neighbours and least similar to distant sites (Fig. 6). By implication, dispersal is limited on the scale of this investigation (~ 3000 km), and proceeds in a stepping-stone manner. Comparison with the demersal nesting and reef-obligate fish *P. milleri*, indicates that the IBD effect is much weaker in *L. carponotatus*, implying that, as expected considering its longer PLD and less reliance on patchy coral reefs to spawn, it has a higher level of connectivity throughout NWA. This pattern is likely also true for other lutjanid and lethrind species with similar life histories in the region.

In addition to the isolation by distance effect, several pronounced genetic discontinuities were evident among samples of *L. carponotatus* from across NWA. The two most obvious genetic breaks were firstly, a significant genetic subdivision between the Shark Bay Bioregion and all locations of the North West Shelf (Ningaloo, Pilbara, Canning and Kimberley) including the NT. This coincides with well-recognised biogeographic boundaries and oceanographic features south of the North West Cape (Commonwealth of Australia 2006; Woo *et al.* 2006; Spalding *et al.* 2007). Wilson (2013) suggested that the effect of the Leeuwin Current across this region results in a barrier that is probably ineffective in preventing exchange for species with planktotrophic larvae (such as *L. carponotatus*). However, these results (and those for *P. milleri*, subproject 1.1.3.4a), as well as for the coral *Cyphastrea microphthalmia* (Evans *et al.* in prep) and mangrove *Avicennia marina* (Binks *et al.* in prep) indicate the presence of some form of a barrier to genetic exchange even for planktotrophic species. Some studies have suggested that this barrier is probably gradual rather than abrupt (e.g. Johnson *et al.* 1993; Whitaker 2006; Thomas *et al.* 2014; Thomas *et al.* in review; R. Evans unpublished data), and potentially results from a mesoscale eddy at Point Cloates that advects larvae offshore (Woo *et al.* 2006). Our sampling was sparse in this region, however, and therefore we are unable to comment further on this hypothesis. Additional sampling south of Point Cloates would enable us to determine whether it represents an abrupt barrier, a similar isolation by distance pattern observed elsewhere in the range of *L. carponotatus*, or a more pronounced isolation by distance effect indicative of reduced connectivity compared to elsewhere on the NWA coastline.

A second apparent boundary was observed between the Kimberley and Canning marine bioregions (Fig. 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/NT, and the combined Pilbara and Canning bioregions. The result was also reflected in the DAPC analysis of both neutral and outlier SNPs, but again less clearly for the neutral dataset. These results, supported by a distinctive pattern of low spatial autocorrelation in this region (Fig. 5) indicate that it likely represents a region of restricted dispersal over a distance of ~ 80km near the tip of the Dampier Peninsula and the entrance to King Sound. Wilson (2013) has previously identified the tip of the Dampier Peninsula as an important biogeographic break in marine species that also reflects a change in the underlying geology and benthic habitat. It also represents an abrupt genetic break in *P. milleri* and the coral *Isopora breuggemanni* (see chapters 1.1.3.4a and 1.1.3.1). The uniquely powerful tidal regime in this region is a likely driver of this pattern. Hydrodynamic modelling conducted in WAMSI Kimberley project 2.2.7 (M. Feng, CSIRO, pers. comm.) show few opportunities for the movement of larvae westwards across Sunday Strait (see figure in sub-report 1.1.3 Synthesis).

Management of *L. carponotatus* in NWA is based in part on recognising three stocks corresponding to: 1) the Gascoyne (which includes both Shark Bay and Ningaloo in fisheries management arrangements); 2) combined Pilbara, Canning, and Kimberley; and 3) the NT. The distinctiveness of the Shark Bay samples from all other bioregions indicates that the Gascoyne management boundary is not supported. 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 (Fig. 2), and appeared weakly divergent in both STRUCTURE and DAPC analyses. However, a large sampling gap exists between the Kimberley and NT sites, and 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*. Unlike the region between Ningaloo and Shark Bay, *L. carponotatus* is abundant between the Kimberley and NT (Travers *et al.* 2010), and further sampling in this region is required to reveal the true nature of the relationship between these recognised stocks.

The integration of oceanographic and environmental variables to explain genetic signals of differentiation, often referred to as seascape genetics, is a growing field (Selkoe *et al.* 2016). Although we explored

environmental variables across the geographic range of *L. carponotatus*, linear distance provided a better explanation for the observed patterns of genetic structure. This reflects that the environmental data almost exactly tracked linear distance (i.e. collinearity) due 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 lends itself to environmental change relative to that particular gradient. The long distances, therefore, drive the collinearity of the environmental and the geographical distance. In addition, the environmental variables available had some limitations based on the nature of the data used in the PCA (i.e. remote sensing). That is, many of the sites are on shallow coral reefs or very close to islands or the mainland, and so this proximity reduces data confidence and results in the shifting of focal pixels to slightly deeper water. Pixel shifting creates a deviation from the modelled data to the actual environmental influence on the survival of individuals and their genetic expression. Therefore more confidence is placed in the outcomes of the geographical distance as a predictor in our models.

#### 4.3 Fine-scale connectivity across NWA

The broad-scale genetic discontinuities between bioregions were overlaid by subtle genetic differentiation within each bioregion. Patterns of genetic differentiation also differed between the bioregions, indicating that *L. carponotatus* dispersal behaviour also differs between the bioregions. On average, genetic differentiation between sites was higher in the Kimberley than the Pilbara (Fig. 2), implying that on average dispersal is more restricted in the Kimberley. A moderately pronounced isolation by distance effect was evident among Pilbara samples, yet not in the Kimberley. This also suggests greater restriction to gene flow in the Kimberley than the Pilbara, and its more idiosyncratic patterning likely reflects the more powerful tidal regime and complex coastal topography present in the Kimberley. Larval *L. carponotatus* on the Great Barrier Reef have an effective swimming ability and are capable of actively influencing their dispersal and settlement (Quere & Leis 2010). However, the maximum reported swimming speed recorded is  $\sim 33\text{cm/s}^{-1}$ , which is considerably less than the maximum tidal velocity in the vicinity of the transition zone ( $100\text{cm/s}^{-1}$ ; Wolanski & Spagnol, 2003; Lowe et al. 2015 ). Although spawning probably occurs during neap tides (Quere & Leis 2010), *L. carponotatus* have a relatively long PLD (33-38 days; Quere & Leis 2010), which would expose them to the full spectrum of tidal action in this region. This may limit opportunities for active dispersal to short windows of time around the change of tides and during neap tides. These results also closely reflect that observed for *P. milleri* and the seagrass *Thalassia hemprichii* (subchapter 1.1.3.2), indicating a consistent imprint of environment on the spatial ecology of a diverse range of marine taxa. Although the larger tidal flows in the Kimberley might be expected to promote greater dispersal and genetic homogenisation, the results for *L. carponotatus* and other taxa investigated in this project consistently exhibit the opposite.

Management of *L. carponotatus* north of Sunday Strait within the Kimberley Bioregion could treat it as being effectively a single stock over the ecological timeframes relevant to harvest management. Significant spatial autocorrelation indicates that dispersal is limited on average to distances of several hundred kilometres and less. However, local hydrodynamics probably also promote idiosyncratic spatial relationships among sites, so that a model of stepping stone connectivity doesn't apply like it does in the Pilbara. The transition zone identified around the tip of the Dampier Peninsula represents a region of limited connectivity and mixing between *L. carponotatus* from the Kimberley and the Pilbara/Canning populations. This region should be recognised by managers of coastal resources along these coasts.

## 5 References

- Anderson DR (2008) Information Theory and Entropy (pp. 51-82). Springer, New York.
- Andrews KR, Good JM, Miller MR, Luikart G, Hohenlohe PA (2016) Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics*, 17, 81-92.
- Balkenhol N, Waits LP, Dezzani RJ (2009) Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography*, 32, 818-830.
- Burgess SC, Nickols KJ, Griesemer CD, Barnett LA, Dedrick AG, Satterthwaite EV, Yamane L, Morgan SG, White JW, Botsford LW (2014) Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. *Ecological Applications*, 24, 257-270.
- Cahill AE, Levinton JS (2016) Genetic differentiation and reduced genetic diversity at the northern range edge of two species with different dispersal modes. *Molecular Ecology*, 25, 515-526.
- Calaway R, Weston S, Tenenbaum D (2014) doParallel: Foreach Parallel Adaptor for the 'parallel' Package. Available from
- Cawthorn D-M, Steinman HA, Witthuhn RC (2011) Comparative study of different methods for the extraction of DNA from fish species commercially available in South Africa. *Food Control* 22:231-244.
- Commonwealth of Australia (2006) A Guide to the Integrated Marine and Coastal Regionalisation of Australia Version 4.0., Department of the Environment and Heritage, Canberra, Australia.
- Commonwealth of Australia (2006) IMCRA.
- Condie S, Andrewartha J (2008) Circulation and connectivity on the Australian North West shelf. *Continental Shelf Research*, 28, 1724-1739.
- Correa C, Hendry AP (2012) Invasive salmonids and lake order interact in the decline of puye grande *Galaxias platei* in western Patagonia lakes. *Ecological Applications*, 22, 828-842.
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Marine Science*, 1.
- Cruz VM, Kilian A, Dierig DA (2013) Development of DArT marker platforms and genetic diversity assessment of the U.S. collection of the new oilseed crop *lesquerella* and related species. *PLoS One*, 8, e64062.
- D'Adamo ND, Fandry C, Buchan S, Domingues C (2009) Northern sources of the Leeuwin Current and the 'Holloway Current' on the North West Shelf. *Journal of the Royal Society of Western Australia*, 92, 53-66.
- Domingues CM, Maltrud ME, Wijffels SE, Church JA, Tomczak M (2007) Simulated Lagrangian pathways between the Leeuwin Current System and the upper-ocean circulation of the southeast Indian Ocean. *Deep-Sea Research Part II -Topical Studies in Oceanography*, 54, 797-817.
- Duke NC (2006) Australia's mangroves: the authoritative guide to Australia's mangrove plants. MER.
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, 14, 2611-2620.
- Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Marine Biology*, 161, 599-607.
- Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics*, 164, 1567-1587.
- Fox NJ, Beckley LE (2005) Priority areas for conservation of Western Australian coastal fishes: a comparison of hotspot, biogeographical and complementarity approaches. *Biological Conservation*, 125, 399-410.
- González JR, Armengol L, Solé X, Guinó E, Mercader JM, Estivill X, Moreno V (2007) SNPassoc: an R package to perform whole genome association studies. *Bioinformatics* 23:654-655.
- González JR, Armengol L, Solé X, Guinó E, Mercader JM, Estivill X, Moreno V (2007) SNPassoc: an R package to perform whole genome association studies. *Bioinformatics*, 23, 654-655.
- Grewe PM, Feutry P, Hill PL, Gunasekera RM, Schaefer KM, Itano DG, Fuller DW, Foster SD, Davies CR (2015) Evidence of discrete yellowfin tuna (*Thunnus albacares*) populations demands rethink of management for this globally important resource. *Scientific Reports*, 5.
- Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim KA, van Herwerden L, Planes S, Srinivasan M, Berumen ML (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology*, 22, 1023-1028.
- Horne JB, Momigliano P, van Herwerden L, Newman SJ (2013) Murky waters: Searching for structure in genetically depauperate blue threadfin populations of Western Australia. *Fisheries Research*, 146, 1-6.
- Horne JB, Momigliano P, Welch DJ, Newman SJ, van Herwerden L (2011) Limited ecological population connectivity suggests low demands on self-recruitment in a tropical inshore marine fish (*Eleutheronema tetradactylum*: Polynemidae). *Molecular Ecology*, 20, 2291-2306.
- Horne JB, Momigliano P, Welch DJ, Newman SJ, van Herwerden L (2012) Searching for common threads in threadfins: phylogeography of Australian polynemids in space and time. *Marine Ecology Progress Series*, 449, 263-276.

- Hutchins JB (2001) Biodiversity of shallow reef fish assemblages in Western Australia using a rapid censusing technique. *Records of the Western Australian Museum*, 20, 247-270.
- Johnson MS, Hebbert DR, Moran MJ (1993) Genetic analysis of populations of north-western Australian fish species. *Marine and Freshwater Research*, 44, 673-685.
- Johnson MS, Joll LM (1993) Genetic subdivision of the pearl oyster *Pinctata maxima* (Jameson, 1901)(Mollusca: Pteriidae) in northern Australia. *Marine and Freshwater Research*, 44, 519-526.
- Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24:1403-1405.
- Kawecki TJ (2008) Adaptation to marginal habitats. *Annual Review of Ecology, Evolution, and Systematics*, 39, 321-342.
- Kilian A, Wenzl P, Huttner E, Carling J, Xia L, Blois H, Caig V, Heller-Uszynska K, Jaccoud D, Hopper C, Aschenbrenner-Kilian M, Evers M, Peng K, Cayla C, Hok P, Uszynski G (2012) Diversity Arrays Technology: A Generic Genome Profiling Technology on Open Platforms. In: Pompanon F, Bonin A (eds) *Data Production and Analysis in Population Genomics: Methods and Protocols*. Humana Press, Totowa, NJ.
- Kritzer JP (2004) Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef. *Fisheries Bulletin*, 102, 94-107.
- Lischer HEL, Excoffier L (2012) PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, 28, 298-299.
- Lotterhos KE, Whitlock MC (2015) The relative power of genome scans to detect local adaptation depends on sampling design and statistical method. *Molecular Ecology* 24:1031-1046.
- Lowe RJ, Leon AS, Symonds G, Falter JL, Gruber R (2015) The intertidal hydraulics of tide-dominated reef platforms. *Journal of Geophysical Research: Oceans*, 120, doi:10.1002/2015JC010701.
- McLean DL, Langlois TJ, Newman SJ, Holmes TH, Birt MJ, Bornt KR, Bond T, Collins DL, Evans SN, Travers MJ, Wakefield CB, Babcock RC, Fisher R (2016) Distribution, abundance, diversity and habitat associations of fishes across a bioregion experiencing rapid coastal development. *Estuarine and Coastal Shelf Science*, 178, 36-47.
- Meirmans PG, Van Tienderen PH (2004) GENOTYPE and GENODIVE: two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes*, 4, 792-794.
- Messmer V, Jones GP, Munday PL, Planes S (2012) Concordance between genetic and species diversity in coral reef fishes across the Pacific ocean biodiversity gradient: parallel patterns in species and genetic diversity. *Evolution*, 66, 3902-3917.
- Moore GI, Morrison SM, Hutchins JB, Allen GR and Sampey A (2014) Kimberley marine biota. Historical data: fishes. *Records of the Western Australian Museum Supplement* 84: 161-206.
- Nosil P, Funk DJ, Ortiz-Barrientos, D (2009) Divergent selection and heterogeneous genomic divergence. *Molecular Ecology*, 18, 375-402.
- Oksanen J, Kindt R, Legendre P, et al. (2007) The vegan package. *Community ecology package*, 10.
- Pante E, Simon-Bouhet B (2013) marmap: A Package for Importing, Plotting and Analyzing Bathymetric and Topographic Data in R. *PLoS ONE* 8:e73051.
- Paradis E (2010) pegas: an R package for population genetics with an integrated-modular approach. *Bioinformatics*, 26, 419-420.
- Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution* 57:1182-1195.
- Peakall ROD, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, 6, 288-295.
- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, 155, 945-959.
- Pusack TJ, Christie MR, Johnson DW, Stallings CD, Hixon MA (2014) Spatial and temporal patterns of larval dispersal in a coral-reef fish metapopulation: evidence of variable reproductive success. *Molecular Ecology*, 23, 3396-3408.
- Quéré G, Leis JM (2010) Settlement behaviour of larvae of the Stripey Snapper, *Lutjanus carponotatus* (Teleostei: Lutjanidae). *Environmental Biology of Fishes*, 88, 227-238.
- Rellstab C, Gugerli F, Eckert AJ, Hancock AM, Holderegger R (2015) A practical guide to environmental association analysis in landscape genomics. *Molecular Ecology*, 24, 4348-4370.
- Richards ZT, Garcia RA, Wallace CC, Rosser NL, Muir PR (2015) A diverse assemblage of reef corals thriving in a dynamic intertidal reef setting (Bonaparte Archipelago, Kimberley, Australia). *PLoS One*, 10, e0117791.
- Riginos C, Liggins L (2013) Seascape genetics: populations, individuals, and genes marooned and adrift. *Geography Compass*, 7, 197-216.
- Sbrocco EJ, Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology. *Ecology*, 94, 979-979.
- Schiller A (2011) Ocean circulation on the North Australian Shelf. *Continental Shelf Research*, 31, 1087-1095.
- Selkoe K, D'Aloia C, Crandall E et al. (2016) A decade of seascape genetics: contributions to basic and applied marine connectivity. *Marine Ecology Progress Series*, 554, 1-19.
- Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana

- A, Lourie SA (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, 57, 573-583.
- Sprintall J, Wijffels S, Chereskin T, Bray N (2002) The JADE and WOCE I10/IR6 throughflow sections in the southeast Indian Ocean. Part 2: velocity and transports. *Deep-Sea Research Part II - Topical Studies in Oceanography*, 49, 1363-1389.
- Thackway R, Cresswell ID (1998) Interim Marine and Coastal Regionalisation for Australia: an ecosystem-based classification for marine and coastal environments. Version 3.3. In: *Environment Australia, Commonwealth Department of the Environment, Canberra*, p 102.
- Thomas L, Kendrick G, Stat M et al. (2014) Population genetic structure of the *Pocillopora damicornis* morphospecies along Ningaloo Reef, Western Australia. *Marine Ecology Progress Series*, 513, 111-119.
- Thomas L, Kennington WJ, Evans RD, Kendrick GA, Stat M (In review) Restricted gene flow and local adaptation highlight the vulnerability of high latitude reefs to rapid environmental change. *Global Change Biology*.
- Travers MJ, Potter IC, Clarke KR, Newman SJ, Hutchins JB (2010) The inshore fish faunas over soft substrates and reefs on the tropical west coast of Australia differ and change with latitude and bioregion. *J Biogeogr* 37:148-169.
- Trembl EA, Ford JR, Black KP, Swearer SE (2015) Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. *Movement Ecology*, 3, 1.
- Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, 21, 272-281.
- Veilleux HD, van Herwerden L, Evans RD, Travers MJ, Newman SJ (2011) Strong genetic subdivision generates high genetic variability among eastern and western Australian populations of *Lutjanus carponotatus* (Richardson). *Fisheries Research*, 108, 74-80.
- Waayers D, Fitzpatrick J (2013) Genetic affiliations and key habitats of marine turtles in the Kimberly region, western Australia. In *Proceedings of the First Western Australian Marine Turtle Symposium* (pp. 34-36).
- Walker DI (1990) Seagrass in Shark Bay. In: Berry PF, Bradshaw SD, Wilson BR (eds) *Research in Shark Bay: Report of the France-Australe Bicentenary Expedition Committee*. Western Australian Museum, Perth, p 101-106.
- Walker DI (1990) Seagrass in Shark Bay. In: Berry PF, Bradshaw SD, Wilson BR (eds) *Research in Shark Bay: Report of the France-Australe Bicentenary Expedition Committee*. Western Australian Museum, Perth.
- Wang LJ, Bradburd GS (2014) Isolation by environment. *Molecular Ecology*, 23, 5649-5662.
- Whitaker K (2006) Genetic evidence for mixed modes of reproduction in the coral *Pocillopora damicornis* and its effect on population structure. *Marine Ecology-Progress Series*, 306, 115-124.
- Whitlock MC, Lotterhos KE (2015) Reliable detection of loci responsible for local adaptation: inference of a null model through trimming the distribution of  $F_{ST}$ . *The American Naturalist*, 186, S24-36.
- Willing EM, Dreyer C, Van Oosterhout C (2012) Estimates of genetic differentiation measured by  $F_{ST}$  do not necessarily require large sample sizes when using many SNP markers. *PLoS One*, 7, e42649.
- Wilson B (2014) Kimberley marine biota. History and environment. *Records of the Western Australian Museum Supplement*, 84, 1-18.
- Wilson BR (2013) The biogeography of the Australian North West Shelf: environmental change and life's response, Vol. Elsevier Science Publishing Co., Inc., Philadelphia, PA.
- Wilson SK, Depczynski M, Fisher R et al. (2010) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. *PLoS ONE*, 5, e15185.
- Wolanski E, Spagnol S (2003) Dynamics of the turbidity maximum in King Sound, tropical Western Australia. *Estuarine Coastal and Shelf Science* 56, 877-890.
- Woo M, Pattiaratchi C, Schroeder W (2006) Dynamics of the Ningaloo Current off Point Cloates, Western Australia. *Marine and Freshwater Research*, 57, 291.
- Zhang Z, Lowe R, Falter J, Ivey G (2011) A numerical model of wave- and current-driven nutrient uptake by coral reef communities. *Ecological Modelling*, 222, 1456-1470.

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## 7 Data Availability

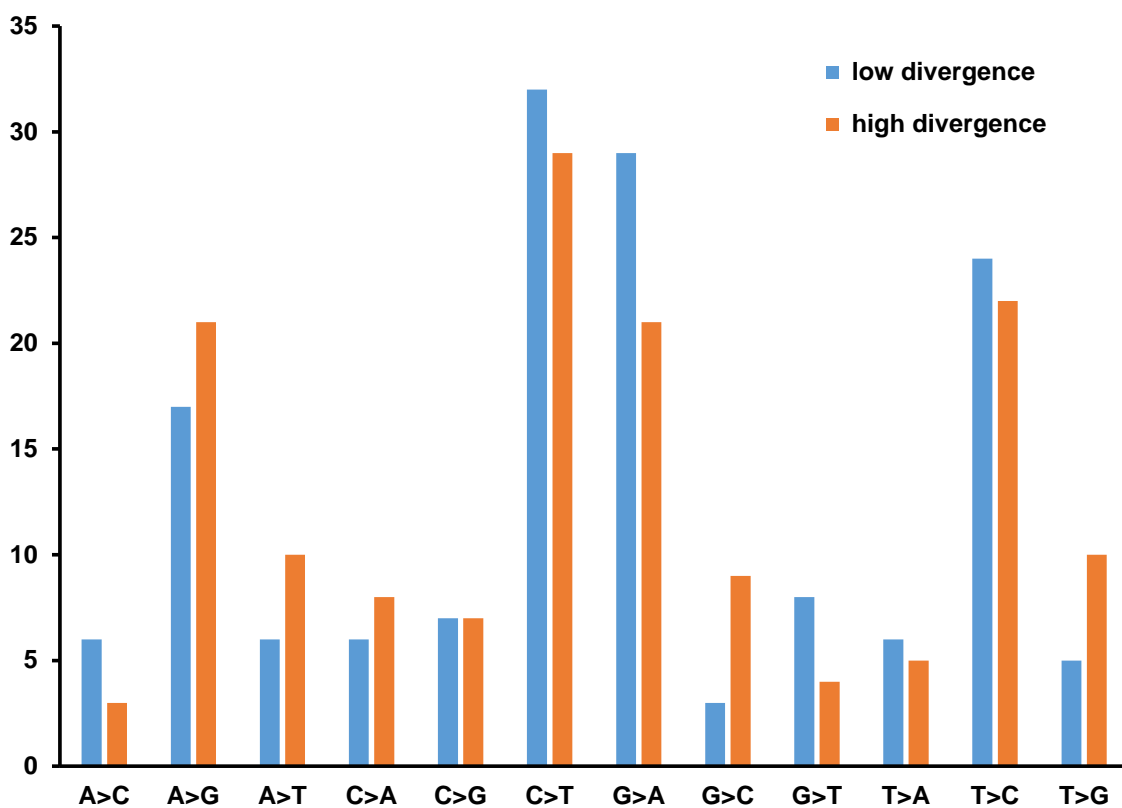
Data associated with this research is available on the CSIRO Data Access Portal at:

<https://data.csiro.au/dap/landingpage?pid=csiro:20195>.

## 8 Appendices

### Appendix 1. A comparison of SNP type

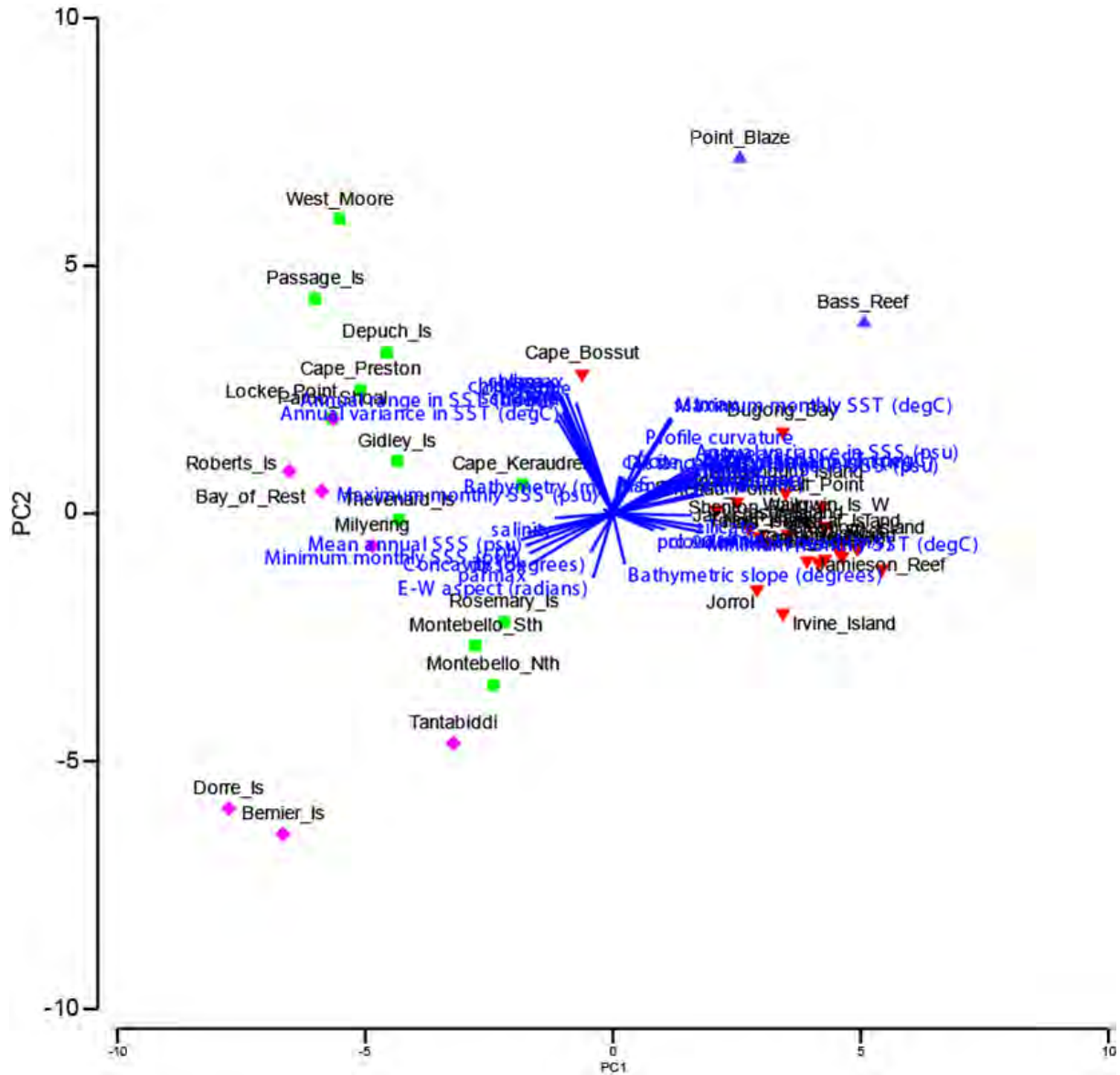
A comparison of SNP type (e.g. transition versus transversion) for 30 individual *L. carponotatus* sampled in 2002 and 2015, respectively, from the Pilbara bioregion. The comparison is based on the 150 SNPs that were the most different in frequency between the two groups based on  $F_{ST}$  (high divergence) and the 150 SNPs that were the least different (but still variable) in frequency between the two groups (low divergence). These two categories were not significantly different from each other based on a one-way ANOVA of the logarithmically transformed values ( $P = 0.846$ ). This result indicates deamination (C/T transitions) is not a likely cause of the genetic divergence between samples collected in 2002 versus 2015, although we cannot rule out other forms of DNA damage.



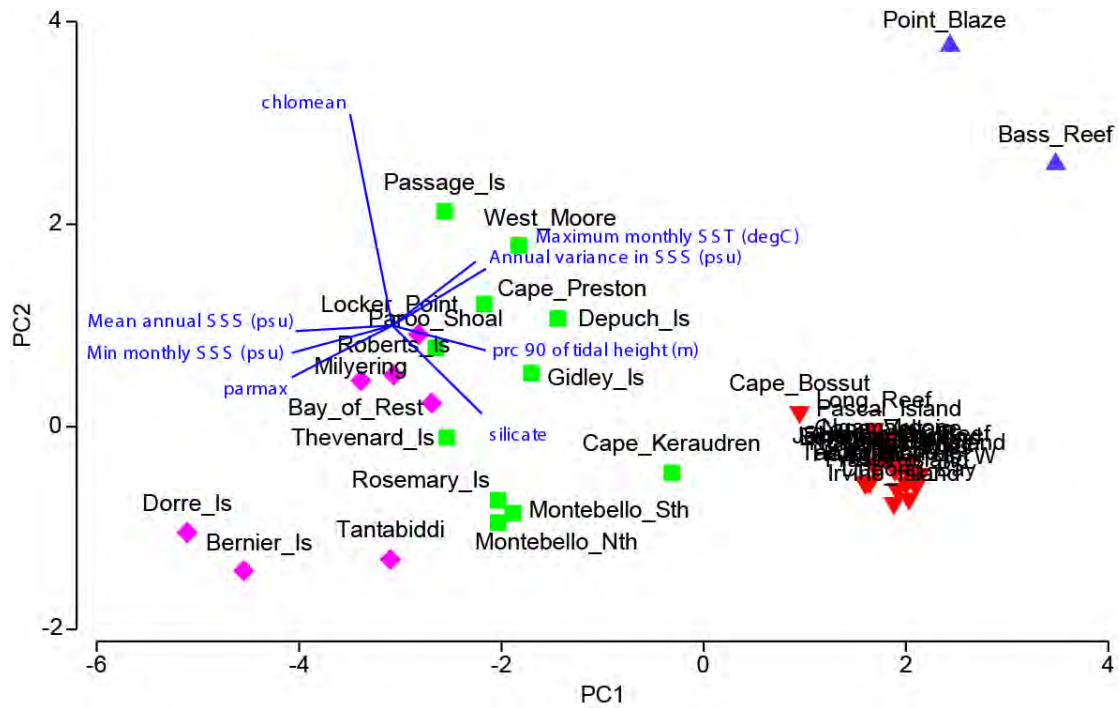
## Appendix 2. Principal Component Analysis

Principal Component Analysis (PCA) of 43 environmental variables extracted from freely available ocean climate layers MARSPEC (Sbrocco and Barber 2013) and Bio-ORACLE (Tyberghein et al. 2012). We here present PCA plots with: (A) all environmental variables included, and (B) the eight most influential variables (using Draughtsmans plots and inspecting the pairwise correlation matrix in all cases; data not shown).

(A)



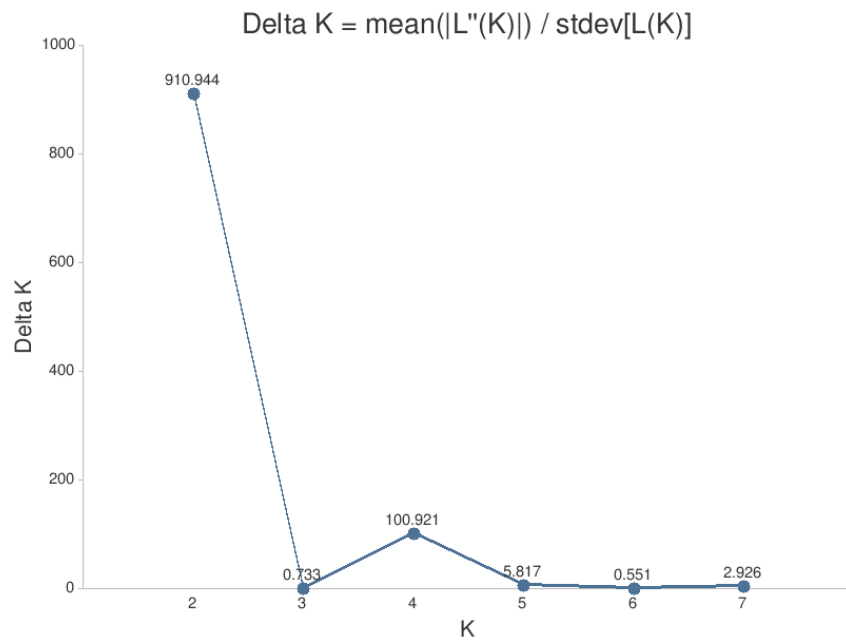
(B)



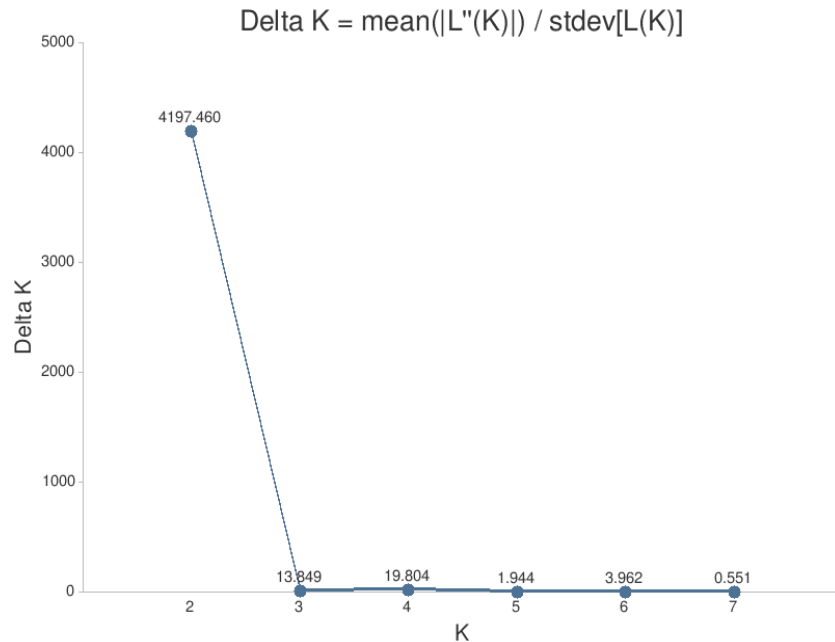
### Appendix 3. Structure Harvester analyses

Structure Harvester analyses used to determine that the most likely value of K was 2 for *L. carponotatus* populations with 20 or more individuals in NWA based on (A) 4,402 SNP loci and (B) 66 outlier loci.

(A)



(B)



#### Appendix 4. Linear model ranking

Linear model ranking for the effects of geographic distance, environmental distances, or a priori barriers to dispersal for *L. carponotatus* populations with 20 or more individuals in NWA based on (a) 4,402 SNP loci or (b) 66 outlier loci. Only models with a likelihood > 0 are presented here.

	Formula	K	AIC	AICc	RSS	R <sup>2</sup>	Adjusted R <sup>2</sup>	Delta AICc	Model likelihood	Model probability	Evidence ratio
(a) 4,402 SNP loci											
m65	b1_2_3 + env + geo + b1_2_3 * env + b1_2_3 *	13	2249.909	2250.339	667.2432	0.2241	0.2141	0	1	0.4918	1
m66	b1_2_3 * env + geo	10	2251.093	2251.352	672.8341	0.2176	0.2103	1.0134	0.6025	0.2963	1.6598
m64	b1_2_3 * env	9	2251.921	2252.133	675.0476	0.2151	0.2086	1.794	0.4078	0.2006	2.4522
m38	b3 + env + geo + b3 * env + b3 * geo	7	2257.751	2257.882	682.7983	0.206	0.2014	7.5431	0.023	0.0113	43.4477
(b) 66 outlier SNP loci											
m22	b1 * geo + env	6	1091.7667	1091.8651	176.6732	0.7946	0.7936	0	1	0.4107	1
m21	b1 * env + geo	6	1091.7694	1091.8678	176.6738	0.7946	0.7936	0.0027	0.9986	0.4102	1.0014
m20	b1 + env + geo + b1 * env + b1 * geo	7	1093.6166	1093.7479	176.6424	0.7946	0.7934	1.8828	0.3901	0.1602	2.5636
m14	b1 + env + geo	5	1097.9555	1098.0257	178.3616	0.7926	0.7919	6.1607	0.0459	0.0189	21.7656

#### Appendix 5. Correlation between pairwise genetic distance, geographic, and environmental distances

Correlation between pairwise genetic distance, geographic, and environmental distances for *L. carponotatus* in NWA based on 4,402 SNP loci. In each case, genetic distance ( $F_{ST}$ ) was compared to geographic distance, environmental distance, and the combined geographic-environmental distance, with red dots corresponding to the pairwise comparison of sites with no modelled barriers between them, green dots corresponding to the pairwise comparison of sites with one barrier between them, blue dots corresponding to the pairwise comparison of sites with two barrier between them, and purple dots corresponding to the pairwise comparison of sites with all three barriers between them.

