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Oceanic and coastal populations of a harvested macroinvertebrate *Rochia nilotica* in north-western Australia are isolated and may be locally adapted

Oliver Berry [A,D,H,I], *Zoe Richards* [B,C,D], *Glenn Moore* [C,D], *Udhi Hernawan* [D,E], *Mike Travers* [F] *and Bernd Gruber* [G]

[A]CSIRO Oceans and Atmosphere, Indian Ocean Marine Research Centre, The University of Western Australia, Crawley, WA 6009, Australia.
[B]Trace and Environmental DNA Laboratory, School of Molecular and Life Sciences, Curtin University, Bentley, WA 6102, Australia.
[C]Department of Aquatic Zoology, Western Australian Museum, Locked Bag 49 Welshpool DC, WA 6986, Australia.
[D]Western Australian Marine Science Institution. Indian Ocean Marine Research Centre, The University of Western Australia, Crawley, WA 6009, Australia.
[E]Centre for Marine Ecosystems Research, Edith Cowan University, 270 Joondalup Drive, Joondalup, WA 6027, Australia.
[F]Fisheries Division, Department of Primary Industries and Regional Development, 39 Northside Drive, Hillarys, WA 6025, Australia.
[G]Institute for Applied Ecology, Faculty of Applied Science, University of Canberra, ACT 2601, Australia.
[H]Present address: CSIRO Environomics Future Science Platform, The University of Western Australia, Crawley, WA 6009, Australia.
[I]Corresponding author. Email: oliver.berry@csiro.au

Abstract. Marine macroinvertebrates support important fisheries throughout the Indo-Pacific, but stocks of species such as trochus (*Rochia nilotica*) are easily overharvested. In north-western Australia, trochus are taken from inshore reefs by Indigenous Australians and oceanic reefs by artisanal Indonesian fishers. The management of these environmentally distinct regions relies on understanding their spatial interdependencies, yet connectivity between them has not been evaluated empirically. Here, we used genotype-by-sequencing analysis of 514 trochus samples collected from 17 locations (15 in the inshore Kimberley, 2 offshore oceanic sites). Analysis of 5428 polymorphic single nucleotide polymorphism loci revealed significant genetic subdivision between the oceanic and coastal sites, and a subset of loci exhibited significantly higher subdivision, suggesting they are subject to directional selection. Population differentiation was also evident between the two oceanic sites, but not between coastal sites. Trochus populations from the coastal Kimberley and oceanic reefs represent two genetically and demographically independent units, with preliminary evidence for local adaptation to these distinctive environments. Management strategies for *R. nilotica* reflect these divisions, but the limited connectivity among oceanic populations indicates that they are vulnerable to overexploitation. Furthermore, their potential adaptive distinctiveness indicates that coastal stocks may be unsuitable for replenishing oceanic stocks.

Additional keywords: fisheries management, genomic, population connectivity, *Tectus*, trochus.

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Introduction

Marine macroinvertebrates, including trochus, giant clams, sea cucumbers and abalone, are vital cultural, economic and subsistence resources for many of the Indo-Pacific region's poorest communities (Conand and Bryne 1993; Foale 2008). Numerous species are overharvested, threatening to further impoverish those communities (Adams *et al.* 1996; Allison and Ellis 2001; Friedman and Teitelbaum 2008). This typically occurs as a consequence of multiple factors, including inadequate resourcing, the logistical challenges of managing remote areas, cultural or traditional entitlements and a lack of understanding of key biological traits (Anderson *et al.* 2011; Purcell *et al.* 2013).

Trochus *Rochia nilotica* (Linnaeus, 1767) (Class Gastropoda, Family Tegulidae), also known as topshell, is a

large herbivorous gastropod (basal diameter up to 12 cm) that occurs on intertidal and subtidal tropical reefs throughout the Indo-Pacific. It is a vital subsistence and economic resource for many communities, but is often overexploited in artisanal fisheries (Gillett 2010). Although estimating harvest rates of trochus is difficult (ICECON 1997), the annual global demand can exceed 7000 t, largely for the production of buttons, but also as a raw material in paint, cosmetics, furniture and jewellery (Amos 1997).

The tendency for *R. nilotica* to be overexploited is consistent with its short, non-feeding larval phase (~4 days; Heslinga 1981; Heslinga and Hillmann 1981); for marine species this trait typically results in limited dispersive capabilities, with local rather than regional environmental and hydrodynamic processes being the most important drivers of the spatial dynamics of recruitment (Sammarco and Andrews 1989). For this reason there has been concern that recruitment in *R. nilotica* may be primarily local, making the species vulnerable to overharvest (Heslinga 1981; Bartlett *et al.* 2009). Furthermore, it has been argued that establishing permanent adjacent no-take regions would be an effective way to sustain populations of *R. nilotica* (Heslinga *et al.* 1984).

The merits of marine no-take reserves for artisanal fisheries such as trochus in the Indo-Pacific, and indeed more generally, has been a subject of debate (Hilborn *et al.* 2004). The design and effectiveness of reserves depends on several factors, including the dispersal capacity of target organisms (Hilborn *et al.* 2004). Yet, aside from its short larval duration, little is understood about realised dispersal in *R. nilotica*, potentially limiting effective management (Foale 1998; Stutterd and Williams 2003; Kendrick *et al.* 2016). A lack of information on spatial process is common in marine systems because tracking dispersive larvae is difficult (Cowen and Sponaugle 2009). A useful and widely used indirect approach to understanding spatial interdependencies in marine systems is the analysis of the distribution of genetic diversity (Selkoe *et al.* 2016).

An investigation of genetic subdivision in *R. nilotica* on the Australian Great Barrier Reef based on three polymorphic allozyme loci indicated that gene flow, and, by inference, larval dispersal, was extensive over almost 1000 km (Borsa and Benzie 1996). These conclusions were weakly supported because the markers exhibited little variation. Nevertheless, they point to a paradox between the observation of short larval duration and susceptibility to local overexploitation, and widespread realised dispersal. Similar observations have been made for other top shells in the family Tegulidae with short larval durations (Díaz-Ferguson *et al.* 2010). One explanation for this may be that the capacity for oceanographic processes to distribute *R. nilotica* larvae is not properly appreciated. Indeed, the species has a widespread native distribution across Indo-Pacific island archipelagos, indicating capacity for broad dispersal over long time frames (Donald *et al.* 2005).

Trochus are taken alongside other macroinvertebrates in north-western Australia along the Kimberley coastal bioregion and adjacent oceanic waters to the continental shelf (Purcell and Cheng 2010). This region is a marine biodiversity hot spot but, compared with other parts of the world, is little studied (Wilson 2013; Richards *et al.* 2015). The Kimberley coast and adjacent oceanic waters support both commercial and artisanal mixed-species fisheries, including Indonesian artisanal fishers (oceanic reefs) permitted to fish under a memorandum of understanding (MOU) between Australia and Indonesia (in the MOU 74 Box) and Australian Indigenous fishers (coastal reefs). Local depletions of trochus stocks have been documented on both oceanic reefs (Skewes *et al.* 1999; Ceccarelli *et al.* 2011) and, historically, in some coastal Kimberley regions (Purcell and Cheng 2010), but stocks in the latter region have recovered and are currently unfished (Hart *et al.* 2013).

These regions of Western Australia are characterised by distinctive 'coastal' and 'oceanic' faunal assemblages (Wilson 2013; Jones *et al.* 2017). The existence of these characteristic assemblages has been attributed to the distinctive hydrodynamic, geological and water column properties of the Kimberley and oceanic regions (Wilson 2013). The hydrodynamics of the oceanic reefs are dominated by a south-west flowing extension of the Indonesian Throughflow (ITF). This current carries warm, clear oligotrophic waters from the west Pacific Ocean southwards through passages in the eastern Indonesian archipelago and along the Australian western continental margin (Fig. 1*a*). The biogeographic affinities of oceanic biota to Indonesian marine communities and the prevalence of species with planktotrophic larvae with widespread distributions in the Indo-West Pacific indicates that the ITF provides significant biogeographic linkage among oceanic reefs (Wilson 2013).

However, the ITF does not typically reach coastal Kimberley waters (Cresswell *et al.* 1993; Condie and Andrewartha 2008). In contrast with oceanic reefs, the hydrodynamics of the coastal reefs are dominated by extremely large semidiurnal tides (up to 11 m), which, although typically acting cross-shelf, interact with the shallow and complex bathymetry and island archipelagos to produce powerful multidirectional and highly idiosyncratic currents (Holloway 1983). Despite this turbulent environment, higher levels of nutrients and freshwater and sediment inputs from large rivers, which result in highly turbid environments, the Kimberley coast hosts a huge variety of sedentary benthic marine organisms (Richards *et al.* 2015; Jones *et al.* 2017).

Whether the distinctive oceanic and coastal faunas can be attributed to these pronounced environmental differences or to hydrodynamic isolation has been a point of discussion among biogeographers (Wilson 2013). Levels of genetic connectivity between corals and fishes inhabiting oceanic reefs have confirmed that rare gene flow occurs between widely separated reefs (~500 km apart; Underwood *et al.* 2009, 2012). This is consistent with hydrodynamic modelling of the ITF and its derivative currents, which predicts organisms could be transported between oceanic reefs if larval durations exceed a month (Condie and Andrewartha 2008; Kool and Nichol 2015). Hydrodynamic models also indicate that connectivity between the oceanic reefs and coastal Kimberley environments is significantly weaker than among oceanic reefs (Condie and Andrewartha 2008; Kool and Nichol 2015). However, this model-based hypothesis is untested. Filling this knowledge gap is important to understanding the origins and affinities of the coastal Kimberley faunas (Wilson 2013). However, more urgently, there is a need to understand the likely demographic dependencies among these reefs because of the well-documented reduced abundances of trochus and other macroinvertebrates at multiple offshore oceanic reefs in north-western Australia (Rees *et al.* 2003; Ceccarelli *et al.* 2011).

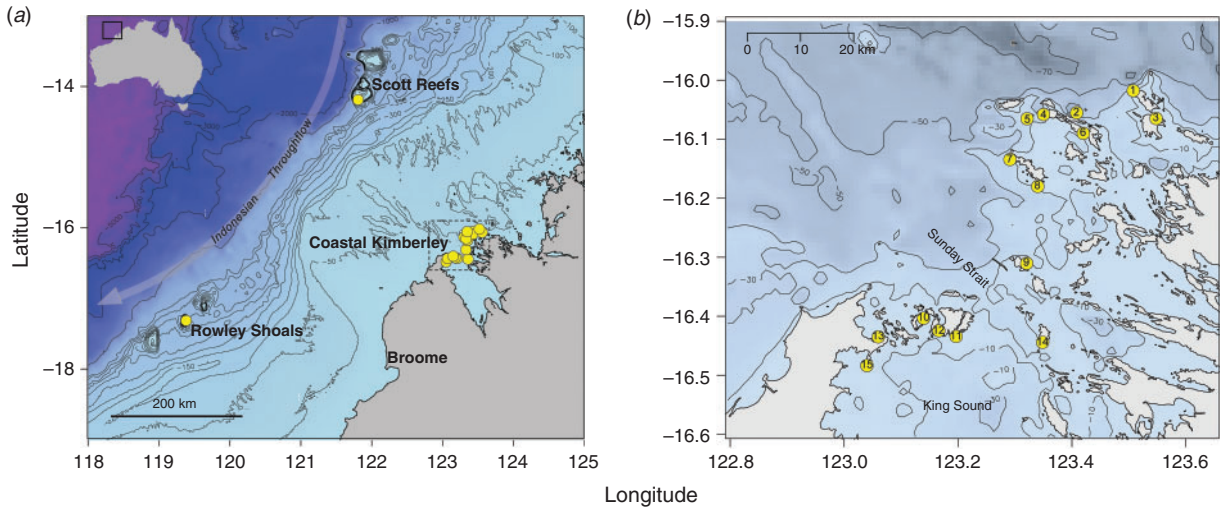

Fig. 1. (*a*) Map showing the entire study region, bathymetry and sampling sites for *Rochia nilotica* (yellow circles). The area enclosed by the dashed lines indicates coastal locations (see *b*). (*b*) Map showing the sampling sites for *R. nilotica* within the coastal Kimberley region (yellow circles). Numbers correspond to sites listed in Table S1.

In this study, we used a genotype-by-sequencing approach to reveal the extent of genetic structure within coastal and oceanic *R. nilotica* populations in north-western Australia, testing the hypothesis that connectivity is greater within each of these regions than between them. We also used particle tracking simulations to evaluate the role of coastal currents and tides in dictating the observed genetic structure in this prominent species from the coastal Kimberley environment. Finally, we used genome scans to test for evidence of adaptive differentiation between oceanic and coastal populations because assisted translocation and restocking of broodstock are widely practiced for trochus in the Indo-Pacific region (Crowe *et al.* 1997). This study represents the first genome-wide characterisation of population connectivity in this highly targeted macroinvertebrate. We consider the underlying processes that likely led to the present-day patterns, and the implications for the management of this valuable resource.

Materials and methods

Sampling

Coastal samples were collected from the Dampier Peninsula and Buccaneer Archipelago (King Sound) in the Kimberley bioregion in August and October 2014 respectively (Fig. 1*b*). This region includes the only gazetted commercial trochus fishery in Western Australia (Anon. 2010) and is the centre of trochus harvest by Indigenous fishers (Ostle 1997). Oceanic Rowley Shoals and Scott Reefs samples were collected in October 2014 and April 2015 respectively. Trochus from both oceanic sites were historically targeted by Indonesian fishers, but only Scott Reefs has been accessible to these fishers since *c.* 1974 under the MOU between Australia and Indonesia (Fox 2009). Sites were selected based on past records of occurrence and suitability of rocky reef habitat. *R. nilotica* individuals were collected by hand from reef platforms at low tide, or at Scott Reefs by SCUBA at water depth <10 m. Global positioning system (GPS) coordinates were obtained for each individual. Samples were collected from a total of 15 coastal sites in the Dampier Peninsula and Buccaneer Archipelago, six locations at Rowley Shoals (pooled as a single oceanic site) and three locations at Scott Reefs (pooled as a single oceanic site). Individuals were returned to a central processing area where a small biopsy (~3 × 8 mm) was taken from the edge of the extended foot. After processing, the *R. nilotica* individuals were returned alive to their point of capture. In all, 524 individuals were sampled (see Table S1, available as Supplementary material to this paper). All activities took place under exemption permits SF009910 and 2485 from the Western Australian Department of Parks and Wildlife and Department of Fisheries respectively.

DNA extraction

DNA was extracted from tissue samples according to the salt extraction method described by Cawthorn *et al.* (2011), followed by purification with the Zymo ZR-96 DNA Clean and Concentrator kit (Zymo Research, Irvine, CA, USA).

Reduced representation single nucleotide polymorphism genotyping

Single nucleotide polymorphism (SNP) genotypes were obtained with DArTSeq, a combination of the Diversity Arrays Technology (DArT) complexity reduction methods and next-generation sequencing (Sansaloni *et al.* 2011; Kilian *et al.* 2012; Cruz *et al.* 2013). The method is conceptually similar to RadSeq (restriction enzyme associated markers) methods but offers several advantages, including: (1) the use of lower DNA input; (2) greater tolerance to lower-quality DNA; and (3) a higher call rate or frequency of markers shared among the samples in the experiment (Sansaloni *et al.* 2011). Four enzyme systems for complexity reduction were tested in *R. nilotica* (data not shown) and the *Pst*I–*Hpa*II method was selected. DNA samples were processed in digestion and ligation reactions principally (as per Kilian *et al.* 2012) but replacing a single *Pst*I-compatible adaptor with *Pst*I and *Hpa*II adaptors. The *Pst*I-compatible

adaptor was designed to include an Illumina flow cell attachment sequence, sequencing primer and a 'staggered' barcode region of varying lengths (see Elshire *et al.* 2011). The reverse adaptor contained a flow cell attachment region and an *Hpa*II-compatible overhang sequence. Only 'mixed fragments' (*Pst*I–*Hpa*II) were effectively amplified. Polymerase chain reaction (PCR) conditions consisted of an initial denaturation 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 the PCR, equimolar amplification products from each sample were pooled and applied to a cBot (Illumina, San Diego, CA, USA) bridge PCR followed by sequencing on an Illumina Hiseq2500. The sequencing (single read) was run for 77 cycles.

SNP calling

Sequences were processed using proprietary DArTseq analytical pipelines. In the primary pipeline, poor-quality sequences were initially filtered from FASTQ files, applying higher stringency to the barcode region than to the rest of the sequence (barcode minimum Phred score 30, minimum pass percentage 75; whole-read minimum Phred score 10, minimum pass percentage 50). Approximately 2 000 000 sequences per barcode or sample were identified and used for marker calling. Identical sequences were collapsed into 'fastqcoll' files, which were groomed using the proprietary algorithm in DArT that corrects low-quality bases from singleton reads using collapsed reads with multiple members as a template. The groomed fastqcoll files were used in the secondary pipeline for DArT's proprietary SNP calling algorithms (DArTsoft14). All reads from all libraries were clustered using DArT's C++ algorithm at the threshold distance of 3 (number of different bases occupying a specific position in the sequence), followed by parsing of the clusters into separate SNP loci using a range of technical parameters, especially the balance of read counts for the allelic pairs. Additional selection criteria were added to the algorithm based on analysis of ~1000 controlled cross-populations. These crosses permitted testing for Mendelian distribution of alleles in these populations and facilitated selection of technical parameters discriminating true allelic variants from paralogous sequences. In addition, approximately one-third of samples were genotyped twice as technical replicates, and scoring consistency was used as the main selection criterion for high-quality and low-error rate markers. In all, 29 552 SNPs were identified. Raw data are available from the CSIRO Data Access Portal at https://doi.org/10.4225/08/5a7bee08b1e5d.

SNP quality control filtering

SNPs identified by the DArTsoft14 pipeline were subjected to a further series of quality control filters based on descriptive statistics from the DArTSeq pipeline using the R package dartR (ver. 0.79, see https://cran.r-project.org/web/packages/dartR/index.html; Gruber *et al.* 2018). These settings were as follows: minimum allele frequency ≥0.05, heterozygosity ≤0.75, number of reads ≥20 and ≤200, repeatability of technical replicates ≥0.98, call rate per locus ≥0.95, missing data per individual ≤0.01 and missing data per SNP <5%. After filtering, 5960 loci and 516 (of 524) individuals remained, which corresponded to a dataset-wide missing data rate of 0.64% (Fig. S1, available as Supplementary material to this paper).

Locus selection

Filtered SNPs were subject to further checks for departure from Hardy–Weinberg equilibrium (HWE) and gametic-phase linkage disequilibrium (LD) expectations with the R package dartR (Gruber *et al.* 2018). Both HWE and gametic-phase LD testing was conducted separately for each sampling site, and only applied to 13 sites where the sample size was greater than 20. For HWE testing we removed loci that showed departures from expectations at $P < 0.05$ in 5 or more of the 13 sample sites. For gametic-phase LD, we removed loci with $R^2 > 0.8$ in 5 or more of the 13 sampling sites. After these filters, 5548 loci remained. Further analyses completed with different thresholds (three to seven populations) for numbers of populations in LD and HWE testing returned near-identical results for all analyses (data not shown).

Testing for outlier loci

We used two approaches, outFlank (ver. 0.2, see https://github.com/whitlock/OutFLANK, accessed March 2019; Whitlock and Lotterhos 2015) and BayeScan (ver. 2.1, see www.cmpg.unibe.ch/software/BayeScan, accessed 24 October 2019; Foll and Gaggiotti 2008), to identify outlier loci putatively experiencing directional selection. All analyses were conducted on either the full dataset composed only of sites with greater than 20 samples or on a dataset consisting only of sites from the coastal Kimberley with greater than 20 samples. The Outflank method was implemented in the R package dartR (Gruber *et al.* 2018). The approach is based on an improved method for deriving the null distribution of population differentiation for neutral loci. It results in fewer false positives than other outlier tests, which are more affected by demographic history (Lotterhos and Whitlock 2015). We ran OutFlank with 5% left and right trim for the null distribution of fixation index (F_{ST}), minimum heterozygosity for loci of 0.1 and a 5% false discovery rate (q-value). In all, 109 outlier SNPs under putative directional selection, and with sufficiently high heterozygosity, were identified.

A second set of tests for outlier loci was completed with the program BayeScan 2.1, as implemented in the R package radiator (ver. 0.0.18, T. Gosselin, see https://github.com/thierrygosselin/radiator, accessed March 2019). BayeScan was run with 5000 iterations, a thinning interval of 10, 20 pilot runs and prior odds for the neutral model set at 1000. Five outlier SNPs under putative directional selection were identified. Four of the five loci identified by BayeScan were also identified using OutFlank (Fig. S2, available as Supplementary material to this paper). All outlier loci (110 in total) were removed from further analyses unless noted otherwise.

Outlier loci identified by BayeScan and OutFlank were tested for homology to known genes with the BLASTn algorithm applied to the Ensemble database. Search criteria were a maximum E-value of 1.00×10^{-5} and identity ≥85%. All tests were also implemented on datasets before removal of loci based on HWE and gametic-phase LD tests. However, results were negligibly different, so are not shown.

Descriptive statistics

Levels of genetic diversity (observed and expected heterozygosity, allelic richness) and the inbreeding coefficient (F_{IS}) were

calculated for each sampling site with the R package hierfstat (ver. 0.04-22, see https://cran.r-project.org/web/packages/hierfstat/index.html, accessed March 2019; Goudet 2005).

Genetic subdivision

The F_{ST} of genetic subdivision was estimated overall and pairwise between each sampling site according to the method of Weir and Cockerham (1984) using the R package STAMPP (ver. 1.4, see https://cran.r-project.org/web/packages/StAMPP/index.html, accessed December 2016; Pembleton *et al.* 2013). The significance of the observed subdivision between all pairs of sampling sites was tested with 9999 bootstraps over loci. Tests of overall genetic differentiation among sampling sites and between coastal Kimberley sampling sites were conducted with GenePop (Rousset 2008), based on genotypic differentiation and exact G tests. Markov chain Monte Carlo (MCMC) settings were as follows: dememorisation 1000, batches 100, iterations per batch 1000.

Principal components analysis and discriminant analysis of principal components

Initially we used the k-means algorithm to evaluate support for between 1 and 15 potential clusters (K) in the data. This was implemented in the R package adegenet (ver. 2.0, see https://cran.r-project.org/web/packages/adegenet/index.html, accessed March 2019). Support for alternative values of K was evaluated with the Bayesian information content (BIC) based on retaining all principal components. A discriminant analysis of principal components (DAPC) was then conducted on the data without specifying K and based on 100 retained principal components (optimised based on α score). In addition, a principal-components analysis (PCA) was conducted on the data with the glPCA function in adegenet (ver. 2.0). All analyses were repeated on the coastal sites only (i.e. excluding Rowley Shoals and Scott Reefs).

Model-based clustering analysis

We used a model-based clustering approach to evaluate whether genetic variation was partitioned geographically, and at what scale. This was implemented in the software Structure (ver. 2.3.4, see https://web.stanford.edu/group/pritchardlab/structure_software/release_versions/v2.3.4/html/structure.html; Pritchard *et al.* 2000). Structure seeks to group individuals in such a way that the groups maximise conformity to HWE and gametic-phase equilibrium. We ran Structure across multiple predefined values for K (number of clusters) and evaluated the fit of the data to different values of K. We conducted an overall analysis incorporating all 17 sampling sites and varied K between 2 and 17, and conducted the same analysis on the coastal sites only. The fits of alternative models were evaluated with the ΔK method (Evanno *et al.* 2005) implemented in Clumpak (ver. beta, see www.clumpak.tau.ac.il/index.html, accessed 24 October 2019; Kopelman *et al.* 2015) and based on 20 independent runs for each value of K. For all runs we incorporated a 200 000 iteration burn-in followed by 500 000 clustering iterations. We ensured the adequacy of the run length by checking the runtime likelihood and α for stability. For all runs we assumed that allele frequencies were correlated between sampling sites and allowed for admixture. We repeated runs with and without location information incorporated as a Bayesian prior.

Hydrodynamic connectivity

Hydrodynamic connectivity between sampling sites in the coastal Kimberley was calculated through particle tracking simulations run within the Regional Ocean Modelling System (ROMS) with a resolution of 2 km to construct a site-pairwise matrix of oceanographic connectivity. The ROMS model was nested within the Ocean Forecasting for Australia Model 3 (OFAM3) simulation (Feng *et al.* 2016) and forced by 3-h meteorological measures derived from Kobayashi *et al.* (2015). The model simulation was based on observations from 2011. Hourly sea surface current velocities (at depths of 0–5 m) were extracted from the model output and used for particle tracking modelling. In all, 100 particles were seeded at each sampling site for the entire year at 3-day intervals. *R. nilotica* in our study area is reproductively active all year (Gimin and Lee 1997). A fourth-order Runga-Kutta subtime-stepping scheme was used to update the particle locations every hour (Feng *et al.* 2016). Using the random walk effect of 1 m s^{-1}, particles were tracked for 8 days. The locations of particles were recorded over a period of 4–8 days because *R. nilotica* larvae become competent to settle after 3–4 days (Heslinga and Hillmann 1981) and can remain in the water column for up to 10 days in the absence of settlement cues (Heslinga 1981). The grid size for tracking the particles from each sampling site was set to 500 m^{-2}. Connectivity among sampling sites was estimated as 1 minus the proportion of particles released from Site i that were tracked to be in Site j during the competency period. To make this matrix symmetric, we summed connectivity between i and j and between j and i. Oceanographic connectivity was calculated as the proportion of released particles from i and j that settled at i and j. This value was converted to oceanographic resistance as 1 minus oceanographic connectivity. Values were arcsine transformed before further analysis.

Isolation by distance

We used partial Mantel tests to evaluate correlations between linearised F_{ST} ($F_{ST} \div (1 - F_{ST})$) and log distance as well as log oceanographic distance. Mantel tests were conducted on the whole dataset and on the coastal Kimberley dataset. Geographic distances between sites were calculated based on the shortest across-water distance with a minimum water depth of 1 m because this was the minimum depth specifiable. These estimates were calculated with the marmap package (ver. 0.94, see https://cran.r-project.org/web/packages/marmap/index.html, accessed December 2016; Pante and Simon-Bouhet 2013) in R (R Foundation for Statistical Computing, Vienna, Austria) and based on the GEBCO 2014 30-s bathymetry available from the British Oceanographic Data Centre (see https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_30_second_grid, accessed December 2016). We used partial Mantel tests to test for a correlation between linearised F_{ST} and oceanographic resistance while controlling for log geographic distance. This analysis was conducted using the vegan package (ver. 2.3.2, see https://cran.r-project.org/web/packages/vegan/index.html, accessed December 2016; Dixon 2003) in R.

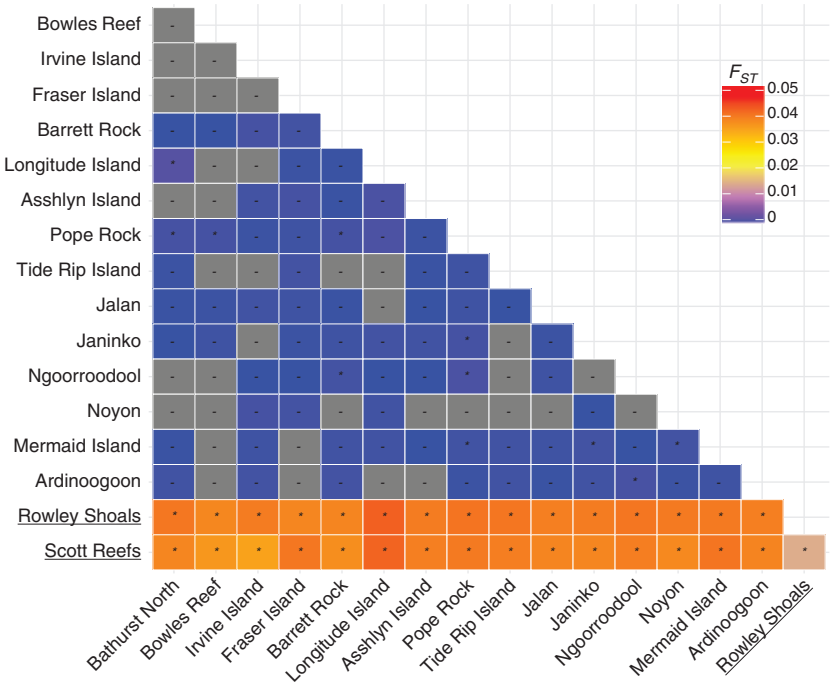

Fig. 2. Fixation index (F_{ST}) values for pairwise comparisons of populations of *Rochia nilotica*. Coastal sites are ordered north to south; oceanic sites are underlined. F_{ST} values were calculated using the STAMPP package (ver. 1.4, see https://cran.r-project.org/web/packages/StAMPP/index.html, accessed December 2016; Pembleton *et al.* 2013) in R (R Foundation for Statistical Computing, Vienna, Austria) based on the method of Weir and Cockerham (1984). Asterisks indicate $P \leq 0.5$ (calculated based on 1000 bootstraps over loci). Grey cells indicate a F_{ST} of zero.

Results

Descriptive statistics

After quality control, HWE and gametic-phase LD filtering and outlier analyses, 5548 SNP loci remained. Table S1 presents estimates of genetic diversity at each sampling site and overall. The two oceanic sites exhibited lower observed and expected heterozygosity than all coastal sites.

Detection of outlier loci

In an analysis of the full dataset, 110 loci were identified as having significantly higher levels of genetic subdivision than expected for neutral loci under a model of mutation–drift equilibrium (positive outliers) when both the OutFlank and BayeScan results were combined. In the coastal Kimberley dataset (excluding Rowley Shoals and Scott Reefs) no outlier loci were identified. Only a single outlier locus showed significant BLAST homology to DNA sequences in the Ensembl genome database, and this was a 96.3% identity to an insect mitochondrial cytochrome oxidase gene (*Prodoxidae* sp.; GenBank Accession KM549916).

Genetic subdivision

The overall mean (±s.e.m.) level of genetic subdivision based on the putatively neutral markers (positive outliers removed) as estimated by F_{ST} was 0.0053 ± 0.0001, which corresponded to a significant genotypic differentiation among sampling sites ($P < 0.001$). Mean (±s.e.m.) F_{ST} based on outlier loci was 0.0998 ± 0.0051, and the mean (±s.e.m.) F_{ST} among the coastal sites was $5.44 \times 10^{-5} \pm 8.89 \times 10^{-5}$, which corresponded to a non-significant difference in genotypic differentiation ($P = 0.19$). Pairwise F_{ST} between coastal sites was typically low, and only 11 of 105 pairs were significantly different from zero at $P < 0.05$ (Fig. 2; F_{ST} range 0–0.002). The mean (±s.e.m.) F_{ST} between Rowley Shoals and Scott Reefs was 0.0163 ± 0.0001, which was significantly different from zero ($P < 0.001$). The mean (±s.e.m.) F_{ST} between combined coastal sites and combined oceanic sites was 0.0348 ± 0.0008), which was significantly different from zero ($P < 0.0001$), in contrast with F_{ST} based on outlier loci, which was 0.3518 ± 0.0022).

Model-based clustering

The data best supported two genetically discrete groups of *R. nilotica* individuals; maximum ΔK was obtained for $K = 2$, whether location prior was included or not ($\Delta K = 321.4$ (Fig. S3) and 34.8 respectively). These two groups corresponded to a clear division between coastal and oceanic sites (Fig. 3).

PCA and DAPC

Based on BIC, the k-means algorithm was optimised at $K = 2$ (Fig. S3). Both PCA and DAPC revealed that these groups corresponded exactly to oceanic and coastal sites (Fig. 4), and that all individuals were assigned to their correct group at ≥0.99 probability of membership in the DAPC analysis. No grouping with a geographical basis was observed in the analysis of the coastal sites only.

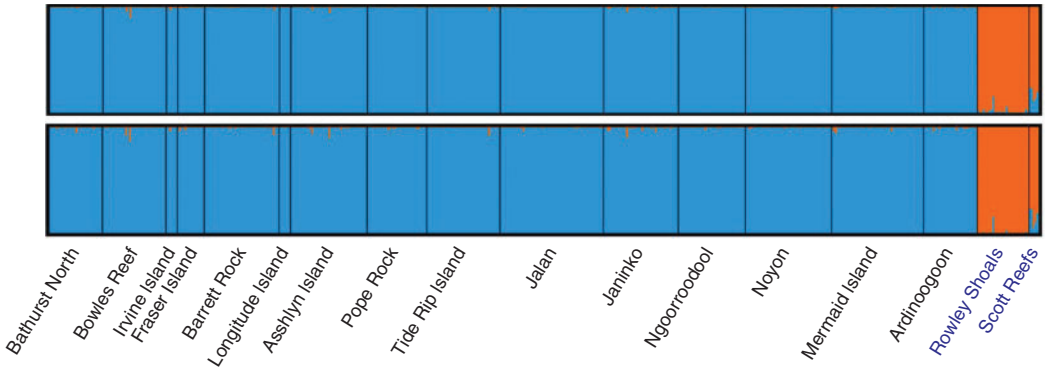

Fig. 3. Bar plots indicating the probability of ancestry (q; y-axis) for 514 *Rochia nilotica* individuals (x-axis) from the coastal Kimberley and from Rowley Shoals and Scott Reefs. Plots are based on $K = 2$ (two genetic clusters assumed). Individuals are represented by vertical bars, each divided according to their estimated probability of ancestry from each of two genetic clusters (represented by blue and orange). Coastal sites are ordered north to south from left to right. Oceanic sites labelled in blue. The upper panel indicates analysis completed with locations set as Bayesian priors in the analysis, whereas the lower panel shows results without prior location assumptions.

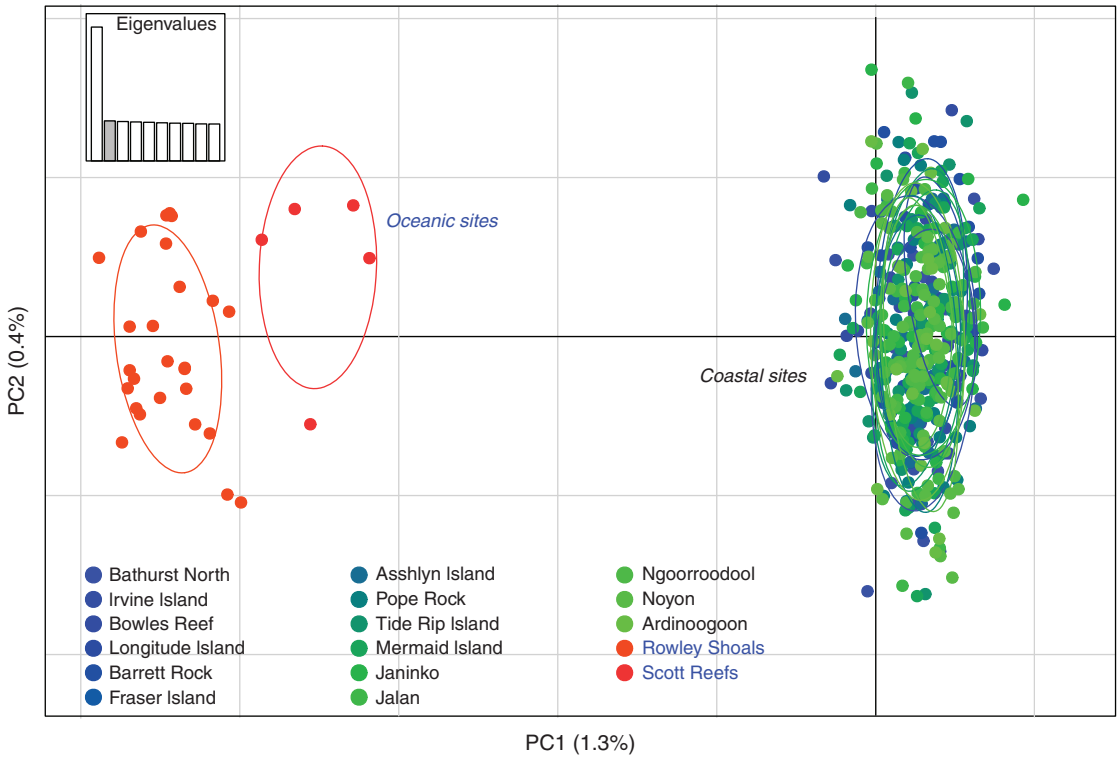

Fig. 4. Principal-components analysis (PCA) for 514 *Rochia nilotica* individuals. Inertia ellipses are centred on the mean coordinates of points from each sampling site and width and height correspond to variances on each axis. Here they are scaled to incorporate ~77% of the points from each sampling site (1.5× variance). In the legend, samples are ordered from north to south, but with the two oceanic sites listed last and in blue.

Isolation by distance and oceanographic resistance

Within the coastal Kimberley there was no significant relationship between linearised F_{ST} and shortest cross-water (log) distance between sampling sites ($R = 0.042$, $P = 0.36$). Neither was there a significant relationship between linearised F_{ST} and oceanographic resistance ($R = -0.04$, $P = 0.62$). Geographic distance and oceanographic resistance were strongly correlated based on the 8-day particle tracking run ($R = 0.76$, $P < 0.01$). A partial Mantel test that controlled for geographic distance did not reveal a significant relationship between linearised F_{ST} and oceanographic resistance based on an 8-day run ($R = -0.118$, $P = 0.809$).

Discussion

We have shown that trochus populations from the west Kimberley and adjacent oceanic reefs represent two genetically and, by implication, largely demographically independent units, with the oceanic trochus populations further subdivided into two genetically distinct units corresponding to the Rowley Shoals and Scott Reefs systems. The high level of genetic subdivision between oceanic and coastal populations exhibited in a subset of SNP loci is evidence that divergent selection may be driving evolutionary adaptation to these distinctive environments, and should be investigated further because it has implications for the selection of stocks for translocations.

These conclusions are based on a large dataset of both individuals and, importantly, SNP markers, meaning that, unlike previous genetic studies of *R. nilotica* (Borsa and Benzie 1996), the power to detect population structure was high (Willing *et al.* 2012). Accordingly, the lack of genetic structure observed across the region encompassing the gazetted commercial fishery between the Dampier Peninsula and Buccaneer Archipelago strongly indicates that this species comprises a single genetic unit, which contrasts with recent investigations of corals, seagrasses and fish in this region (DiBattista *et al.* 2017; McMahon *et al.* 2017; Underwood *et al.* 2017).

The small sample size for Scott Reefs reflects the lower abundance of *R. nilotica* at this location due to overexploitation (Skewes *et al.* 1999). Although it would be ideal to base analyses on larger samples from this location, the PCA and model-based clustering analysis based on individual genotypes rather than population allele frequencies indicate that samples from Scott Reefs are readily distinguished from coastal populations, and from the Rowley Shoals.

Connectivity between coastal and oceanic reefs

This is the first time that realised connectivity between coastal Kimberley and Rowley Shoals and Scott Reefs has been examined with high-resolution SNP data. It confirms modelling results that the two regions have very limited hydrodynamic connectivity (Condie and Andrewartha 2008; Kool and Nichol 2015), which explains, in part, the widely divergent reef biotas (Wilson 2013; Richards *et al.* 2018). It is also consistent with recent observations using microsatellite markers in two species of coral that exhibit strong genetic subdivision between oceanic and coastal regions in north-western Australia (Underwood *et al.* 2017). However, the magnitude of the subdivision in the corals (F_{ST} >0.3 and >0.4) was greater than in *R. nilotica* (F_{ST} = ~0.04), likely indicative of a much smaller effective population size or lower dispersal ability in the corals.

Connectivity between oceanic reefs

Hydrodynamic modelling predicts that larvae are unlikely to be transported between the isolated oceanic atoll systems such as Rowley Shoals and Scott Reefs unless their pelagic larval duration exceeds 30 days (Kool and Nichol 2015). This has been tested with genetic markers in several species, including fishes and corals, which confirmed that transport is uncommon enough that the systems are demographically independent (Underwood *et al.* 2009, 2012). *R. nilotica* (F_{ST} = ~0.02) adds a further example, but the level of differentiation between Rowley Shoals and Scott Reefs for this mollusc is an order of magnitude larger than that observed in the demersal nesting fish *Chromis margaritifer* (F_{ST} = 0.002; Underwood *et al.* 2012), similar to that observed in the broadcast-spawning coral *Acropora tenuis* (F_{ST} = 0.03; Underwood *et al.* 2009) and an order of magnitude lower than that observed in the brooding coral *Seriatopora hystrix* (F_{ST} = 0.3; Underwood *et al.* 2009). This variability among species likely reflects different capacities for dispersal or effective population sizes in these organisms.

Recovery of *R. nilotica* after disturbances on these oceanic atoll systems is unlikely to be driven by recruitment from external sites. This is relevant to the exploitation of *R. nilotica* by artisanal Indonesian fishers, where the stocks are significantly depleted (Skewes *et al.* 1999; Rees *et al.* 2003; Bryce 2006). The Scott Reefs stock is unlikely to recover unless local recruitment is increased because recruitment from other sources is demographically insignificant. Trochus are heavily depleted on other atolls in north-western Australia, such as Ashmore Reef, which is the closest external recruitment source, some 230 km to the north-west (Ceccarelli *et al.* 2011). It is likely these stocks are similarly demographically isolated and highly reliant on local recruitment, although this requires investigation.

Potential for local adaptation

The geographic and hydrodynamic barriers that result in the isolation of coastal and oceanic reefs in north-western Australia may explain, in part, their distinctive ecological communities (Wilson 2013). Their unique biogeographic histories and the effect of the ITF on oceanic reefs likely also promote their distinctiveness (Wilson 2013). A further potential driver of diversification, as indicated by the detection of a subset of loci much more divergent than most (outlier loci), is diversifying selection promoting local adaptation in trochus. These molecular results require experimental validation, for example by reciprocal transplants or common garden experiments (Sanford and Kelly 2011). However, local adaptation would be unsurprising considering the vastly different environmental conditions these regions experienced and their limited genetic exchange (Wilson 2013; Richards *et al.* 2015). Regrettably, the limited availability of annotated genome data for Tegulidae precludes functional interpretation of the outlier loci.

Translocations of *R. nilotica* have been used throughout its range to supplement stocks with mixed success (Stutterd and Williams 2003). If coastal and oceanic populations have accumulated adaptive differences, supplementation of oceanic populations like those at Scott Reefs may best be sourced from similar oceanic reefs. The same may apply elsewhere in the Indo-Pacific for translocations, *de novo* establishment or aquaculture in this species. It is unclear whether the low success rates observed in some translocation programs for *R. nilotica* (Stutterd and Williams 2003) can be attributed, in part, to maladaptation. However, this effect has been observed widely in aquaculture and translocation (Allendorf 1987; Hereford 2009; Fraser *et al.* 2011), and could be a focus of future research into the improvement of trochus fisheries.

Connectivity among coastal reefs in the Kimberley

The absence of genetic structure within the coastal Kimberley indicates that this region should continue to be considered to function as a single demographic unit for the purpose of managing *R. nilotica*. This result differs from that seen in a pelagic spawning fish *Lutjanus carponotatus*, which, despite a lengthy pelagic larval duration, exhibits genetic differentiation over the same coastal sampling range (DiBattista *et al.* 2017). The seagrasses *Halophila ovalis* and *Thalassia hemprichii* also exhibit moderately strong genetic subdivision across the same region and possess longer fruiting and seed dispersive phases than *R. nilotica* (McMahon *et al.* 2017). However, our results are consistent with those reported for *R. nilotica* on the Great Barrier Reef (Borsa and Benzie 1996), and for top shells elsewhere (Díaz-Ferguson *et al.* 2010; Nikula *et al.* 2011), yet are paradoxical considering the apparently brief non-feeding larval period and assumption that larval dispersal and gene flow are limited in the species (Foale and Day 1997). As has been discussed elsewhere (Cowen and Sponaugle 2009), aspects other than pelagic larval duration, such as motility and behaviour, settlement cues and post-settlement selection, likely make important contributions to observed patterns of marine connectivity.

The specific reasons for this paradox in *R. nilotica* are unclear, but two unique properties of the Dampier Peninsula and Buccaneer Archipelago may be relevant. First, the region experiences extreme tidal velocities up to 2 m s^{-1} (Cresswell and Badcock 2000), which, in principle, are capable of transporting propagules a great distance in a single 6-h tidal cycle. The second is that in King Sound, unlike most of its range, *R. nilotica* reproduces continuously throughout the year (Gimin and Lee 1997). Therefore, larvae are exposed to the complete spectrum of hydrodynamic conditions experienced in the region. It has been argued that establishing marine reserves for *R. nilotica* close to fished areas is a way to compensate for localised recruitment patterns in the species (Heslinga *et al.* 1984). However, in the case of King Sound, the hydrodynamic mixing appears to be strong enough that even distant reefs within the region would be well connected.

R. nilotica has a broad Indo-Pacific distribution, and the present investigation focused entirely on the south-westernmost part of its range, which is separated from other high-density populations in Australia, Indonesia and on oceanic atolls (Stutterd and Williams 2003). The broad distribution of *R. nilotica* in the tropical Indo-Pacific, incorporating a variety of reef types and hydrodynamic conditions, means that it is unlikely that the spatial scale of genetic structure detected here will be reflected throughout its range. Similarly, environmental differences throughout the species' range may exert a range of selective pressures. Considering the economic and cultural significance of the species to many people (Amos 1997; Gillett and Tauati 2018), a broader investigation of the population structure in *R. nilotica* and its biophysical drivers deserves consideration.

Conclusions

Both hydrodynamic isolation and environmental differences have been hypothesised to explain the starkly different coral reef faunas on oceanic and coastal regions of north-western Australia (Wilson 2013). Our results indicate that both these hypotheses may be true. Not only is there little genetic exchange between coastal and oceanic populations of *R. nilotica*, but there is also a significant number of genomic regions exhibiting strong differentiation that is consistent with evolutionary adaptation to divergent local conditions, although this requires experimental validation.

The existing separate management of these regions is supported by the new evidence for their isolation presented here. Two additional implications for the management of *R. nilotica* are: (1) the isolation of the oceanic reefs from other sources of recruits indicates that they are reliant on local recruitment to offset harvest; and (2) *R. nilotica* on the Dampier Peninsula and Buccaneer Archipelago represent a single stock within this region, and should be replenished with recruits from neighbouring reefs within years, so long as management ensures that such sites exist and allows for the slow growth of the species.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

Adams, T., Dalzell, P., and Farman, R. (1996). Status of Pacific Island coral reef fisheries. In 'Proceedings of the 8th International Coral Reef Symposium', 24–29 June 1996, Panama City, Panama. (Eds H. A. Lessios and I. G. Macintyre.) pp. 1977–1980. (University of Panama and the Smithsonian Tropical Research Institute.)

Allendorf, F. W. (1987) 'Conservation and Genetics of Salmonid Fishes.' (Washington University Press: Seattle, WA, USA.)

Allison, E. H., and Ellis, F. (2001). The livelihoods approach and management of small-scale fisheries. *Marine Policy* **25**(5), 377–388. doi:10.1016/S0308-597X(01)00023-9

Amos, M. (1997). Management policy for trochus fishery in the Pacific. In 'Trochus: Status, Hatchery Practice and Nutrition', 6–7 June 1996, Darwin, NT, Australia. (Eds C. L. Lee and P. W. Lynch.) pp. 164–169. (Australian Centre for International Agricultural Research: Canberra, ACT, Australia.)

Anderson, S. C., Mills Flemming, J., Watson, R., and Lotze, H. K. (2011). Rapid global expansion of invertebrate fisheries: trends, drivers, and ecosystem effects. *PLoS One* **6**(3), e14735. doi:10.1371/JOURNAL.PONE.0014735

Anon. (2010). Western Australian trochus fishery: ecological risk assessment 2010. Department of Fisheries Western Australia, Perth, WA, Australia. Available at https://www.environment.gov.au/system/files/pages/1ce79a6e-f9d6-4295-9866-a4e6705535fd/files/wa-trochus-ecological-risk-assessment-2010.pdf [Verified 19 September 2019].

Bartlett, C., Manua, C., Cinner, J., Sutton, S., Jimmy, R., South, R., Nilsson, J., and Raina, J. (2009). Comparison of outcomes of permanently closed and periodically harvested coral reef reserves. *Conservation Biology* **23**(6), 1475–1484. doi:10.1111/J.1523-1739.2009.01293.X

Borsa, P., and Benzie, J. (1996). Population genetics of *Trochus niloticus* and *Tectus coerulescens*, topshells with short-lived larvae. *Marine Biology* **125**(3), 531–541.

Bryce, C. (2006). Invertebrate marine resources of Scott and Seringapatam Reefs (and Browse Island). Report produced for URS and Woodside Energy, Western Australian Museum, Perth, WA, Australia.

Cawthorn, D.-M., Steinman, H. A., and Witthuhn, R. C. (2011). Comparative study of different methods for the extraction of DNA from fish species commercially available in South Africa. *Food Control* **22**(2), 231–244. doi:10.1016/J.FOODCONT.2010.07.003

Ceccarelli, D. M., Beger, M., Kospartov, M. C., Richards, Z. T., and Birrell, C. L. (2011). Population trends of remote invertebrate resources in a marine reserve: trochus and holothurians at Ashmore Reef. *Pacific Conservation Biology* **17**(2), 132–140. doi:10.1071/PC110132

Conand, C., and Bryne, M. (1993). A review of recent developments in the world sea cucumber fisheries. *Marine Fisheries Review* **55**(4), 1–13.

Condie, S., and Andrewartha, J. (2008). Circulation and connectivity on the Australian North West shelf. *Continental Shelf Research* **28**(14), 1724–1739. doi:10.1016/J.CSR.2008.04.003

Cowen, R. K., and Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science* **1**, 443–466. doi:10.1146/ANNUREV.MARINE.010908.163757

Cresswell, G. R., and Badcock, K. A. (2000). Tidal mixing near the Kimberley coast of NW Australia. *Marine and Freshwater Research* **51**(7), 641–646. doi:10.1071/MF99154

Cresswell, G., Frische, A., Peterson, J., and Quadfasel, D. (1993). Circulation in the Timor Sea. *Journal of Geophysical Research. Oceans* **98**, 14379–14389. doi:10.1029/93JC00317

Crowe, T. P., Amos, M., and Lee, C. L. (1997). The potential of reseeding with juveniles as a tool for the management of trochus fisheries. In 'Trochus: Status, Hatchery Practice and Nutrition', 6–7 June 1996, Darwin, Australia. (Eds. CL Lee and PW Lynch), pp. 170–177. (Australian Centre for International Agricultural Research: Canberra, ACT, Australia.)

Cruz, V. M., Kilian, A., and Dierig, D. A. (2013). Development of DArT marker platforms and genetic diversity assessment of the US collection of the new oilseed crop *Lesquerella* and related species. *PLoS One* **8**(5), e64062. doi:10.1371/JOURNAL.PONE.0064062

Díaz-Ferguson, E., Haney, R., Wares, J., and Silliman, B. (2010). Population genetics of a trochid gastropod broadens picture of Caribbean Sea connectivity. *PLoS One* **5**(9), e12675. doi:10.1371/JOURNAL.PONE.0012675

DiBattista, J. D., Travers, M. J., Moore, G. I., Evans, R. D., Newman, S. J., Feng, M., Moyle, S. D., Gorton, R. J., Saunders, T., and Berry, O. (2017). Seascape genomics reveals fine-scale patterns of dispersal for a reef fish along the ecologically divergent coast of northwestern Australia. *Molecular Ecology* **26**, 6206–6223. doi:10.1111/MEC.14352

Dixon, P. (2003). Vegan, a package of R functions for community ecology. *Journal of Vegetation Science* **14**(6), 927–930. doi:10.1111/J.1654-1103.2003.TB02228.X

Donald, K. M., Kennedy, M., and Spencer, H. G. (2005). Cladogenesis as the result of long-distance rafting events in South Pacific topshells (Gastropoda, Trochidae). *Evolution* **59**(8), 1701–1711. doi:10.1111/J.0014-3820.2005.TB01819.X

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., and Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS One* **6**(5), e19379. doi:10.1371/JOURNAL.PONE.0019379

Evanno, G., Regnaut, S., and Goudet, J. (2005). Detecting the number of clusters of individuals using the software structure: a simulation study. *Molecular Ecology* **14**(8), 2611–2620. doi:10.1111/J.1365-294X.2005.02553.X

Feng, M., Zhang, X., Oke, P., Monselesan, D., Chamberlain, M., Matear, R., and Schiller, A. (2016). Invigorating ocean boundary current systems around Australia during 1979–2014: as simulated in a near-global eddy-resolving ocean model. *Journal of Geophysical Research. Oceans* **121**, 3395–3408. doi:10.1002/2016JC011842

Foale, S. (1998). Assessment and management of the trochus fishery at West Nggela, Solomon Islands: an interdisciplinary approach. *Ocean and Coastal Management* **40**(2–3), 187–205. doi:10.1016/S0964-5691(98)00044-1

Foale, S. (2008). Appraising the resilience of trochus and other nearshore artisanal fisheries in the Western Pacific. *Pacific Community (SPC) Trochus Information Bulletin* **14**, 12–15.

Foale, S., and Day, R. (1997). Stock assessment of trochus (*Trochus niloticus*) (Gastropoda: Trochidae) fisheries at West Nggela, Solomon Islands. *Fisheries Research* **33**(1–3), 1–16. doi:10.1016/S0165-7836(97)00062-3

Foll, M., and Gaggiotti, O. E. (2008). A genome scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics* **180**, 977–993. doi:10.1534/GENETICS.108.092221

Fox, J. J. (2009). Legal and illegal Indonesian fishing in Australian waters. In 'Indonesia Beyond the Water's Edge: Managing an Archipelagic State'. (Eds R. B. Cribb and M. Ford.) pp. 195–220. (Institute of Southeast Asian Studies: Singapore.)

Fraser, D. J., Weir, L. K., Bernatchez, L., Hansen, M. M., and Taylor, E. B. (2011). Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity* **106**, 404–420. doi:10.1038/HDY.2010.167

Friedman, K., and Teitelbaum, A. (2008). Re-introduction of giant clams in the Indo-Pacific. In 'Global Reintroduction Perspectives: Re-Introduction Case-Studies from around the Globe'. (Ed. P. Soorae.) pp. 4–10. (IUCN/SSC Re-Introduction Specialist Group: Abu Dhabi, UAE.)

Gillett, R. (2010). 'Marine Fishery Resources of the Pacific Islands.' (Food and Agriculture Organization of the United Nations: Rome, Italy.)

Gillett, R., and Tauati, M. I. (2018). Fisheries of the Pacific Islands: regional and national information. FAO number 2070-7010, Food and Agriculture Organization of the United Nations, Apia, Samoa.

Gimin, R., and Lee, C. (1997). The reproductive cycle of *Trochus niloticus* in King Sound, Western Australia. In 'Trochus: Status, Hatchery Practice and Nutrition', 6–7 June 1996, Darwin, NT, Australia. (Eds C. L. Lee and P. W. Lynch.) pp. 52–59. (Australian Centre for International Agricultural Research: Canberra, ACT, Australia.)

Goudet, J. (2005). Hierfstat, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes* **5**(1), 184–186. doi:10.1111/J.1471-8286.2004.00828.X

Gruber, B., Unmack, P. J., Berry, O. F., and Georges, A. (2018). DARTR: an R package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Molecular Ecology Resources* **18**(3), 691–699. doi:10.1111/1755-0998.12745

Hart, A. M., Hesp, S. A., Fabris, F. F., Ryan, K., Caputi, N., Fletcher, R. J., Gaughan, D. J., and Travaille, K. (2013). North coast trochus fishery

resource assessment report. Prepared for the Marine Stewardship Council MSC Principle 1, Department of Fisheries, Perth, WA, Australia.

Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist* **173**(5), 579–588. doi:10.1086/597611

Heslinga, G. A. (1981). Larval development, settlement and metamorphosis of the tropical gastropod *Trochus niloticus. Malacologia* **20**, 349–357.

Heslinga, G. A., and Hillmann, A. (1981). Hatchery culture of the commercial top snail *Trochus niloticus* in Palau, Caroline Islands. *Aquaculture* **22**, 35–43. doi:10.1016/0044-8486(81)90131-9

Heslinga, G. A., Orak, O., and Ngiramengior, M. (1984). Coral reef sanctuaries for trochus shells. *Marine Fisheries Review* **46**(4), 73–80.

Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K. L., Garcia, S., Hall, S. J., Kirkwood, G. P., Sainsbury, K., Stefansson, G., and Walters, C. (2004). When can marine reserves improve fisheries management? *Ocean and Coastal Management* **47**(3–4), 197–205. doi:10.1016/J.OCECOAMAN.2004.04.001

Holloway, P. (1983). Tides on the Australian north-west shelf. *Australian Journal of Marine and Freshwater Research* **34**(1), 213–230. doi:10.1071/MF9830213

ICECON (1997). Aspects of the industry, trade, and marketing of pacific island trochus. *Pacific Community (SPC) Trochus Information Bulletin* **5**, 2–17.

Jones, D., Bryce, C., Fromont, J., and Moore, G. (2017). Marine biodiversity of the Kimberley 1880s–2009. *Records of the Western Australian Museum* **84**, 69–100.

Kendrick, A., Wilson, S., Friedman, K., Waples, K., Whiting, S., Holmes, T., Rule, M., Halford, A., Quartermaine, T., and Bobojcov, A. (2016). Strategic marine ecological research priorities for CALM Act marine parks and reserves 2016–2021. *Conservation Science Western Australia* **10**(7), 1–15.

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., and Uszynski, G. (2012). Diversity arrays technology: a generic genome profiling technology on open platforms. In 'Data Production and Analysis in Population Genomics: Methods and Protocols'. (Eds F. Pompanon and A. Bonin.) pp. 67–89. (Humana Press: Totowa, NJ, USA.)

Kobayashi, S., Ota, Y., Harada, Y., Ebita, A., Moriya, M., Onoda, H., Onogi, K., Kamahori, H., Kobayashi, C., Endo, H., Miyaoka, K., and Takahashi, K. (2015). The JRA-55 reanalysis: general specifications and basic characteristics. *Journal of the Meteorological Society of Japan* **93**, 5–48. doi:10.2151/JMSJ.2015-001

Kool, J. T., and Nichol, S. L. (2015). Four-dimensional connectivity modelling with application to Australia's north and northwest marine environments. *Environmental Modelling & Software* **65**, 67–78. doi:10.1016/J.ENVSOFT.2014.11.022

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., and Mayrose, I. (2015). Clumpak: a program for identifying clustering modes and packaging population structure inferences across *K*. *Molecular Ecology Resources* **15**, 1179–1191. doi:10.1111/1755-0998.12387

Lotterhos, K. E., and Whitlock, M. C. (2015). The relative power of genome scans to detect local adaptation depends on sampling design and statistical method. *Molecular Ecology* **24**(5), 1031–1046. doi:10.1111/MEC.13100

McMahon, K., Hernawan, U., Dawkins, K., van Dijk, K., and Waycott, M. (2017). Population genetic diversity, structure and connectivity of two seagrass species, *Thalassia hemprichii* and *Halophila ovalis* in the Kimberley. Report of project 1.1.3–Project1.1.3.2 prepared for the Kimberley Marine Research Program. (Western Australian Marine Science Institution: Perth, WA, Australia.) Available at https://www.wamsi.org.au/sites/wamsi.org.au/files/files/Connectivity_Seagrass%20Report%20WAMSI%20KMRP%20Project%201_1_3_2_McMahon%20et%20al%202017_Final.pdf [Verified 19 September 2019].

Nikula, R., Spencer, H. G., and Waters, J. M. (2011). Comparison of population-genetic structuring in congeneric kelp- versus rock-associated snails: a test of a dispersal-by-rafting hypothesis. *Ecology and Evolution* **1**(2), 169–180. doi:10.1002/ECE3.16

Ostle, C. (1997). A review of the trochus fishery in King Sound, Western Australia. In 'Trochus: Status, Hatchery Practice and Nutrition', 6–7 June 1996, Darwin, NT, Australia. (Eds C. L. Lee and P. W. Lynch.) pp. 22–24. (Australian Centre for International Agricultural Research: Canberra, ACT, Australia.)

Pante, E., and Simon-Bouhet, B. (2013). Marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. *PLoS One* **8**(9), e73051. doi:10.1371/JOURNAL.PONE.0073051

Pembleton, L. W., Cogan, N. O., and Forster, J. W. (2013). StAMPP: an R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. *Molecular Ecology Resources* **13**(5), 946–952. doi:10.1111/1755-0998.12129

Pritchard, J. K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.

Purcell, S. W., and Cheng, Y. W. (2010). Experimental restocking and seasonal visibility of a coral reef gastropod assessed by temporal modelling. *Aquatic Biology* **9**(3), 227–238. doi:10.3354/AB00253

Purcell, S. W., Mercier, A., Conand, C., Hamel, J.-F., Toral-Granda, M. V., Lovatelli, A., and Uthicke, S. (2013). Sea cucumber fisheries: global analysis of stocks, management measures and drivers of overfishing. *Fish and Fisheries* **14**(1), 34–59. doi:10.1111/J.1467-2979.2011.00443.X

Rees, M., Colquhoun, J., Smith, L., and Heyward, A. (2003). Surveys of trochus, holothuria, giant clams and the coral communities at Ashmore Reef, Cartier Reef and Mermaid Reef. Australian Institute of Marine Science, Townsville, Qld, Australia.

Richards, Z. T., Garcia, R. A., Wallace, C. C., Rosser, N. L., and Muir, P. R. (2015). A diverse assemblage of reef corals thriving in a dynamic intertidal reef setting (Bonaparte Archipelago, Kimberley, Australia). *PLoS One* **10**(2), e0117791. doi:10.1371/JOURNAL.PONE.0117791

Richards, Z., Bryce, M., and Bryce, C. (2018). The composition and structure of shallow benthic reef communities in the Kimberley, NW Australia. *Records of the Western Australian Museum* **85**, 75–103. doi:10.18195/ISSN.0313-122X.85.2018.075-103

Rousset, F. (2008). Genepop'007: a complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources* **8**(1), 103–106. doi:10.1111/J.1471-8286.2007.01931.X

Sammarco, P. W., and Andrews, J. C. (1989). The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. *Limnology and Oceanography* **34**(5), 896–912. doi:10.4319/LO.1989.34.5.0896

Sanford, E., and Kelly, M. W. (2011). Local adaptation in marine invertebrates. *Annual Review of Marine Science* **3**(1), 509–535. doi:10.1146/ANNUREV-MARINE-120709-142756

Sansaloni, C., Petroli, C., Jaccoud, D., Carling, J., Detering, F., Grattapaglia, D., and Kilian, A. (2011). Diversity Arrays Technology (DArT) and next-generation sequencing combined: genome-wide, high throughput, highly informative genotyping for molecular breeding of *Eucalyptus*. *BMC Proceedings* **5**(S7), P54. doi:10.1186/1753-6561-5-S7-P54

Selkoe, K., D'Aloia, C., Crandall, E., Iacchei, M., Liggins, L., Puritz, J., von der Heyden, S., and Toonen, R. (2016). A decade of seascape genetics: contributions to basic and applied marine connectivity. *Marine Ecology Progress Series* **554**, 1–19. doi:10.3354/MEPS11792

Skewes, T., Dennis, D., Jacobs, D., Gordon, S., Taranto, T., Haywood, M., Pitcher, C., Smith, G., Milton, D., and Poiner, I. (1999). Survey and stock size estimates of the shallow reef (0–15 m deep) and shoal area (15–50 m deep) marine resources and habitat mapping within the Timor Sea MOU74 Box. CSIRO Marine Research, Hobart, Tas., Australia.

Stutterd, E., and Williams, G. (2003). The future of Bêche-De-Mer and trochus fisheries and aquaculture in Australia. Final report to the Fisheries Resources Research Fund, Bureau of Rural Sciences, Canberra, ACT, Australia.

Underwood, J. N., Smith, L. D., van Oppen, M. J. H., and Gilmour, J. P. (2009). Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecological Applications* **19**(1), 18–29. doi:10.1890/07-1461.1

Underwood, J. N., Travers, M. J., and Gilmour, J. P. (2012). Subtle genetic structure reveals restricted connectivity among populations of a coral reef fish inhabiting remote atolls. *Ecology and Evolution* **2**(3), 666–679. doi:10.1002/ECE3.80

Underwood, J., Richards, Z., Berry, O., and Gilmour, J. (2017). Population connectivity and genetic diversity in brooding and broadcast spawning corals in the Kimberley. Western Australian Marine Science Institution, Perth, WA, Australia.

Weir, B. S., and Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* **38**, 1358–1370.

Whitlock, M. C., and Lotterhos, K. E. (2015). Reliable detection of loci responsible for local adaptation: inference of a null model through trimming the distribution of F_{ST}. *American Naturalist* **186**, S24–S36. doi:10.1086/682949

Willing, E.-M., Dreyer, C., and 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**(8), e42649. doi:10.1371/JOURNAL.PONE.0042649

Wilson, B. (2013) 'The Biogeography of the Australian North West Shelf: Environmental Change and Life's Response.' (Elsevier: Amsterdam, Netherlands)

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