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Cryptic marine barriers to gene flow in a vulnerable coastal species, the dugong (*Dugong dugon*)

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Abstract

Despite the lack of obvious physical barriers and their ability to travel significant distances, many marine mammals exhibit substantial population structuring over relatively short geographical distances. The dugong (*Dugong dugon*), the only extant representative of family Dugongidae, is listed as Vulnerable to Extinction globally. We investigated the genetic population structure of dugongs in the shallow coastal waters along >2,000 km of the eastern Queensland coast, including the Great Barrier Reef region. Microsatellite genotypes for 22 loci in 293 dugongs, SNP genotypes based on 10,690 loci in 43 dugongs, and 410 bp mitochondrial control-region sequences from 639 dugongs were analyzed. Clustering analysis techniques consistently identified an abrupt genetic break in the Whitsunday Islands region (20.3°S), which interrupts an overall pattern of isolation-by-distance. Geographic distance was relatively more important than sea-surface temperature and seagrass distribution in explaining pairwise microsatellite genetic distances. The cause of reduced dispersal across this region is unknown but might relate to an unusual tidal and current mix, termed the "sticky-water" effect, and/or a break in the geographical

distribution of off-shore seagrass meadows. The genetic structure suggests distinct breeding units north and south of the Whitsunday Islands region for consideration in further developing management plans for Queensland dugongs.

KEYWORDS
conservation, *Dugong dugon*, gene flow, Great Barrier Reef, isolation-by-distance, population structure, Queensland, RADseq SNP, seagrass, sticky water

1 | INTRODUCTION

Identification of genetic structure among populations of vulnerable species is important for effective conservation management. Population size, genetic diversity, and connectivity all have a direct bearing on population viability, particularly fitness, persistence, and resilience. Populations that are large and have high levels of genetic variation are possibly more resilient to environmental change through their capacity for novel adaptations than those that are small and genetically homogeneous (Sgrò et al., 2011; Spielman et al., 2004). An additional advantage is conferred on vagile species that can move freely between suitable habitat patches and reproduce widely, particularly for long-term survival under the rapidly changing conditions caused by climate change (Gilbert-Norton et al., 2010; IPCC, 2022; Switzer, 1993). The vagility of wildlife in relation to their habitat use may be a function of their intrinsic nature (e.g., body size and metabolism, locomotory mode, and capacity for travel), their environment (e.g., distribution of resources), and dependence on culture (e.g., socially learned behavior and migration patterns; Brakes et al., 2019). Understanding the distribution, extent, and connectivity of populations in relation to their environment is critical to identification and management of threats.

Environmental constraints to movements of marine wildlife that might affect population structuring may be difficult to identify not only because of the limited opportunities to observe their dispersal and behavior, but because there may be nonapparent barriers that impede gene flow compared to terrestrial systems (Selkoe et al., 2016). For marine wildlife, ecological barriers to movement may include geographic features, e.g., land masses, promontories, archipelagos, ice shelves, or bathymetric features (Viricel & Rosel, 2014), or less obvious physical impediments, including oceanographic features, e.g., currents and eddies (Briscoe et al., 2017), water velocity (Barceló et al., 2022), water depth, or sea surface temperature (Pratt et al., 2022; Sellas et al., 2005; Viricel & Rosel, 2014). In some cases, fine population structuring in highly mobile marine species with continuous distributions has been linked to social/cultural (e.g., Hoelzel et al., 2007; Whitehead, 2017) and/or ecological barriers, including distance between resource patches (e.g., Amaral et al., 2012; Ansmann et al., 2015).

The dugong (*Dugong dugon*, Müller, order Sirenia) is an apparently mobile marine mammal and an obligate herbivore that favors relatively shallow coastal regions with meadows of seagrass (Marsh et al., 2011). It is a long-lived species, with a generation length of 22–25 years (Marsh & Sobtzick et al., 2019). The species' vast range includes the entire tropical and subtropical inshore waters and islands of the Indo-West Pacific region. The IUCN lists the dugong as a threatened and declining species, i.e., *Vulnerable to Extinction* (Marsh & Sobtzick, 2019) at a global scale. Mitochondrial DNA (mtDNA) analysis indicates significant genetic structuring across its distribution with high diversity in the Indo-Australian region (Plön et al., 2019; Poommouang et al., 2021). Australia supports one of the largest remaining populations in the world, both in terms of distribution and total numbers (Marsh et al., 2011; Marsh & Sobtzick, 2019). Although the dugong does not qualify for listing as a *Threatened Species* at a national scale in Australia, the most recent Australian State of the Environment Report (Clark et al., 2021) states that the condition of the dugong along the urbanized coast of Queensland south of Cooktown (15.5°S) is "poor" and its trend is "deteriorating." The size of the global population is not known but the most recent estimates of the Australian population sum to ~165,000 (Clark et al., 2021).

In Australia, dugongs occur along the northern coastline from Shark Bay in Western Australia (25.4°S, 113.5°E), to Moreton Bay, Queensland (27.3°S, 153.3°E). Dugongs are seagrass community specialists (Marsh et al., 2018) and are generally sighted in the vicinity of seagrass meadows. Unlike the related Florida manatee (*Trichechus manatus latirostris*, order Sirenia) that displays predictable movement patterns in response to seasonal changes in sea temperature (Deutsch et al., 2003), lack of consistency in the direction and length of movements made by dugongs indicates that their movements are individualistic rather than migratory (Deutsch et al., 2022). Most dugongs that have been tracked by satellite telemetry along the eastern Queensland coast have remained relatively sedentary, although some have traveled distances in excess of 100 km and two individuals were tracked more than 500 km from their capture locations (Sheppard et al., 2006). Thus, although dugongs appear to be physically capable of long-range movements, these may be uncommon and may not result in genetically effective migration (i.e., dispersal with mating).

A previous population genetics study of dugongs along a 700 km stretch of the southern Queensland coast, using both mitochondrial and microsatellite markers, found fine-scale genetic structuring across four major foraging grounds associated with seagrass beds (Seddon et al., 2014). An isolation-by-distance pattern was suggested among the four foraging grounds on this coastal strip (Seddon et al., 2014). However, low but significant population structuring detected between Great Sandy Straits (GSS) and Hervey Bay (HB), separated by only 30 km, was surprising for large, apparently mobile, mammals (Seddon et al., 2014). Pedigree analysis based on these genetic data suggested a low migration rate along the southern Queensland coast, indicating that there was limited gene flow between these largely separate breeding groups (Cope et al., 2015; Seddon et al., 2014).

While we might expect an isolation-by-distance pattern in a species with a linear coastal distribution, the presence of genetic structuring in dugongs in southern Queensland waters suggests that there are likely to be other, more discreet, barriers to the dispersal of this marine species within its broader Queensland distribution, and these may be of importance to dugong conservation management. The aim of the present study was to extend the analysis of genetic population structure and connectivity of dugong populations to the entire eastern Queensland coast from Torres Strait in the north to Moreton Bay in the south, a straight-line distance approximating 2,000 km, and including the Great Barrier Reef region. We outline the discovery of more than 10,000 single nucleotide polymorphisms (SNPs) markers and use this large marker panel to assess dugong population structure alongside microsatellite genotypes and mitochondrial sequences. Understanding the patterns of structure and connectivity are important for appropriate management of such a vulnerable species.

2 | METHODS

2.1 | Study sites

Tissue samples were collected from dugongs (live and recovered carcasses) from major dugong foraging sites along the Queensland coast from Torres Strait, north Queensland (10°S), south to Moreton Bay in southeast Queensland (27.4°S), a distance of >2,000 km (Figure 1, Table S1). Some of these sites have been designated as Dugong Protection Areas (DPAs; Great Barrier Reef Marine Park Authority, 2019) and samples were collected from live dugongs in all DPAs (see Table S1), except Hinchinbrook (where carcass samples were available) and Taylor's Beach (no sample). Tissue samples were obtained opportunistically from non-DPA regions to increase sampling coverage of the eastern Queensland coast.

2.2 | Sample collection

Tissue samples (skin, muscle, and/or liver, $n = 249$) were collected from live and dead dugongs using several methods over the period August 1997 to April 2016 inclusive. Skin samples were collected from the back of either

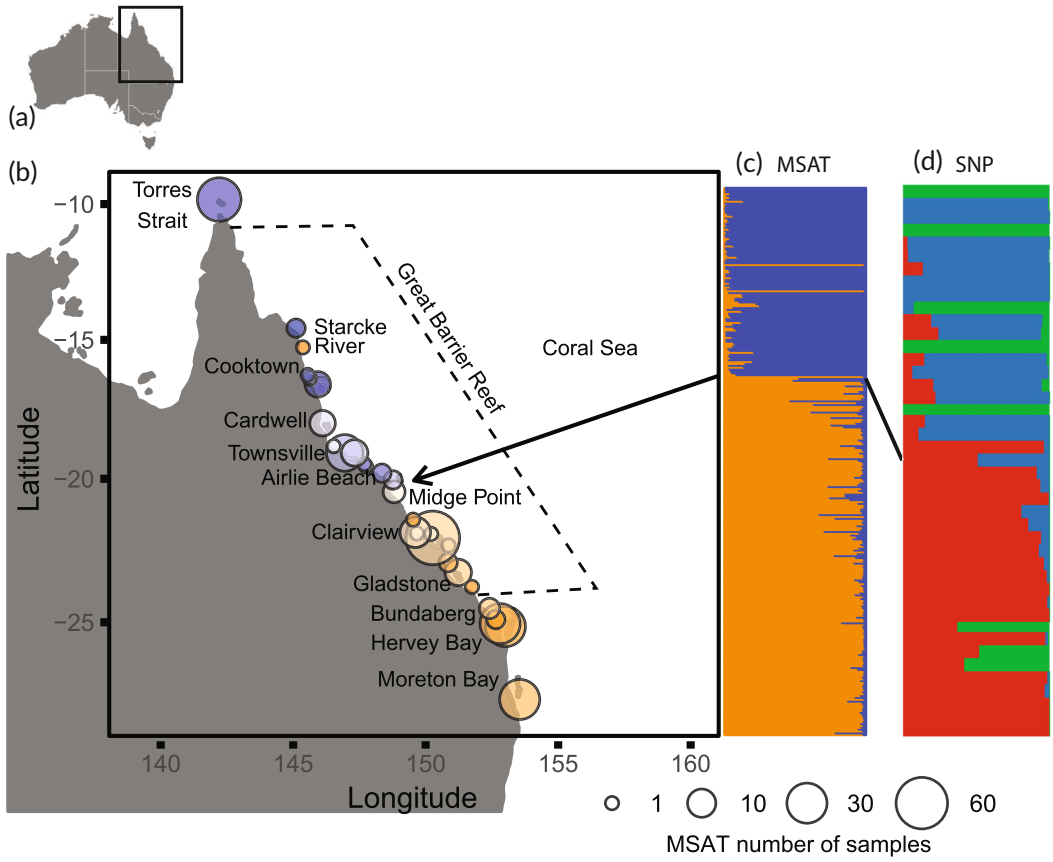

FIGURE 1 The sampling localities of dugongs in Queensland, Australia, together with the genetic clusters from genotype analyses. (a) Location of Queensland. (b) Sample locations with circles indicating the cumulative assignment probabilities of individual dugongs sampled at each coastal location to one of the two clusters identified by the best-fitting STRUCTURE model using microsatellite genotypes. Colors of circles are shown on a gradient ranging from blue (Cluster N) to white to orange (Cluster S). The number of samples collected at each location is represented by the size of the circles. (c) The microsatellite genotype STRUCTURE plot for $K = 2$ (from the maximum LnP(D) run) shows assignment probability to the two clusters shown for each individual arranged north to south. The arrow indicates the Whitsunday Islands region (between Airlie Beach and Midge Point), the geographical location of the cluster separation. (d) The SNP-based assignment probabilities of individual dugongs arranged north to south. The plot indicates the assignment for each dugong to one of the three clusters (1 – blue, 2 – red, 3 – green) identified by the *snmf* admixture analysis of 10,690 SNPs. The oblique black line indicates the geographical region of disjunction between clusters in both the SNPs and microsatellite analyses.

free-swimming dugongs as they surfaced to breathe, using a hand-held scraping device deployed from a boat (Lanyon et al., 2010) or during live capture (Lanyon et al., 2006; Sheppard et al., 2006). Tissue samples (skin, liver, and/or muscle) were also collected opportunistically from dugong carcasses recovered along the Queensland coast. Samples were from dugongs of both sexes and all age classes. Three cow/calf pairs were skin-scraped and in each case the sample from the mother was removed from the analysis. Fresh skin samples and most carcass samples were stored in salt-saturated dimethyl sulfoxide (DMSO, 20%) solution, placed on ice in the field, and then stored frozen at −20°C. The remaining carcass samples were dry frozen at −20°C.

2.3 | DNA extraction

DNA from ~10 mg of dugong tissue was extracted using the MagJET Genomic DNA Kit and KingFisher Flex (Thermo Scientific). The final concentrations ranging between 13 and 3,810 ng/μl (assessed by NanoDrop ND-1000).

2.4 | Microsatellite genotyping and analysis

Dugong samples ($n = 293$) were genotyped at 24 species-specific microsatellite loci (Broderick et al., 2007). Eight multiplex PCR reactions were performed as previously described (Seddon et al., 2014; Supplementary Material). Null alleles were investigated using MICRO-CHECKER version 2.2.1 (Van Oosterhout et al., 2004). Deviation from Hardy–Weinberg equilibrium (HWE) was assessed in GENEPOP web version 4.2 using exact tests (Raymond & Rousset, 1995) and loci DduF07 and DduD08 were discarded from the final analysis due to excess homozygosity. Ninety of the microsatellite genotypes (Moreton Bay, $n = 30$; Hervey Bay, $n = 30$; and Great Sandy Straits, $n = 30$) were included from Seddon et al., (2014). Internal controls were included on genotyping runs to ensure consistency of allele binning. The data set for analysis comprised microsatellite genotypes at 22 loci for 293 different dugongs.

Population structure was determined in two ways. A principal coordinates analysis (PCoA), a multivariate technique to plot similarity among individuals based on genetic distance without spatial data, was conducted in the program GenAlEx (version 6.5) (Peakall & Smouse, 2012). Secondly, Bayesian clustering methods implemented in STRUCTURE 2.3.4 (Pritchard et al., 2000) were employed to deduce the underlying population structure based on variation in allele frequencies without prior population definition. For all analyses, the "admixture" model was used as each population was not considered to be discrete. Ten independent runs were performed for each of $K = 1$–10 clusters with 300,000 iterations and a discarded burn-in length of 150,000 for each run (using default settings for other parameters). Convergence was assessed by visual inspection of the summary statistics. The number of clusters (K) best-fitting the data set was inferred using the ΔK index (Evanno et al., 2005). The STRUCTURE results for the 10 independent runs for each K were visualized using the CLUMPAK (Kopelman et al., 2015) program indicating the proportion of an individual's genome assigned to each cluster. A hierarchical STRUCTURE analysis approach was undertaken, with analyses repeated separately for the northern and southern clusters to identify possible evidence of substructuring.

Genetic diversity metrics (mean observed number of alleles per locus, n_a; mean observed heterozygosity, H_O; and mean expected heterozygosity, H_E) were calculated for each STRUCTURE cluster. Allelic richness was estimated for each combination of cluster and locus using rarefaction, with sample sizes based on the smallest number of alleles observed across all cluster × locus combinations. Pairwise F_{ST} values between clusters were calculated following Nei (1987). Individual dugongs were initially assigned to one of two clusters with a 0.5 assignment cut-off, but 95% confidence intervals were determined for genetic diversity, allelic richness, and F_{ST} by 1,000 iterations with random draws to allow for the uncertainty in cluster assignment. All microsatellite differentiation metrics were calculated in the R programming language (R Core Team, 2016) using functions in the hierfstat package (Goudet & Jombart, 2015). Isolation-by-distance was explored by plotting pairwise genetic distance against pairwise geographic distance using the function *gd.kosman* in the R package PopGenReport (Adamack & Gruber, 2014). Geographic distances were calculated between sampling GPS coordinates as straight-line distances in kilometers. Individual pairwise genetic distances were calculated following the multilocus genetic dissimilarity measure proposed by Kosman and Leonard (2005). A bidirectional estimate of migration between dugongs sampled north and south of the Whitsundays was undertaken in BayesAss (version 3.0.4.2; Wilson & Rannala, 2003). This analysis estimated the proportion of each population that derived from that region and the proportion that might have migrated from the other population. Mixing parameters were tested and were acceptable at default values (acceptance rate ΔM [migration rate] = 0.25, ΔA [allele frequencies] = 0.45, and ΔF [inbreeding coefficients] = 0.45). Analysis was run for 10^7

iterations with 10^6 burn-in and a sampling frequency of 1,000. Ten repeated runs with different starting seeds showed consistency of runs and the lowest log likelihood run was reported.

Associations of genetic differences between Queensland dugongs with geographical distance, sea surface temperature, and seagrass distribution were tested using the microsatellite data set. Mean summer and mean winter night-time sea surface temperatures (°C), averaged over 10 years (January 2006–April 2016), were estimated as described in the Supplementary Material. These values showed a clear decrease in temperature from north to south (Table S1). Summer SST varied from 28.82°C in Cardwell to 23.88°C in Moreton Bay and the winter SST varied from 25.95°C in Torres Strait to 19.13°C in Great Sandy Straits/Hervey Bay, with a general trend of decreasing temperatures with increasing latitude. Seagrass distribution mapping along the Queensland coast is incomplete and so we based our analysis on the modeled habitat suitability of coastal seagrass distribution for the Great Barrier Reef (GBR) region during the dry season (Grech & Coles, 2010) as detailed in the Supplementary Material. The association between genetic distance and these standardized ecological variables were explored using multiple regression on distance matrices (fitted using functions in the R package ecodist; Goslee & Urban, 2007) to assess their relative importance.

2.5 | SNP discovery and genotyping

A subset of 47 samples was selected to cover the full length of the Queensland coast for SNP analysis. Samples were selected at random from among those that had complete microsatellite genotyping data (locations in Table S1). DNA was quantified using QuantiFluor (Promega, Madison, WI) and then visualized on a Genomic DNA ScreenTape (Agilent). SNPs were identified using a ddRADseq approach (Peterson et al., 2012). Three samples (one each from Torres Strait, Townsville, and Moreton Bay) were used to determine the final restriction enzymes (EcoRI and HpyCH4IV) and size-selection window (280–375 bp). The final analysis followed the library preparation protocol of Peterson et al., (2012), size selection with the Blue Pippin (Sage Science), library amplification with indexed primers and paired-end 150 bp sequencing on an Illumina NextSeq500. All ddRADseq protocols were undertaken by the Australian Genome Research Facility (Melbourne, Australia). SNP genotyping was performed using Stacks pipeline (version 147; Catchen et al., 2013) using the functions *process_radtags* (demultiplexing, filtering, and removal of low-quality reads), *ustacks* (builds loci), *cstacks* (creates catalog of loci), *sstacks* (matches samples against the catalog of tags) and *genotypes* (determines sample genotypes from common variants). Sequences in FASTQ.GZ format were checked for read depth demultiplexed for each read according to the inline barcodes. FASTQ files created for each sample were trimmed to the shortest read size minus two bases to compensate for differences in read length. The de novo alignment process then created stacks of similar reads, also known as tags, for each sample. The tags that were common across samples were then gathered into catalog tags and genotypes calculated from the common polymorphic sites. Filtering of genotypes was conducted in R using functions in the package dartR (version 1.1.11). Loci with a call rate of <95% as well as monomorphic loci were removed prior to analysis.

Genetic population structure was investigated using SNP genotypes in the *snmf* function in the R package LEA (version 2.6.0), which estimates admixture coefficients for individuals from the genotype matrix and provides least-squares estimates of ancestry proportions (Frichot et al., 2014). The optimal number of clusters was based on the cross-entropy criterion, selecting the smallest value run. Individuals were assigned to a cluster in the absence of prior population association, with the total number of ancestral population clusters (K) assessed for $K = 1$–10 using 100 repetitions. In addition, a PCoA was conducted to visualize the similarities and dissimilarities between individual samples and amongst geographical locations using the dartR package in R (Gruber et al., 2018). The dartR package was also used to generate a genomic relatedness matrix network using the *gl.grm* function. Genetic diversity metrics (mean observed heterozygosity, H_O and mean expected heterozygosity, H_E) for each cluster and pairwise F_{ST} values between clusters were calculated using methods described above. F_{IS} values were calculated following Nei (1987) using the STRUCTURE.popgen package in R. Tests for adaptation or selection were not performed and were beyond the scope of this study.

2.6 | Mitochondrial DNA sequencing and analysis

A total of 240 samples were sequenced for a 726 base-pair (bp) fragment of the mitochondrial control region to further understand maternal lineage distribution and female philopatry across this region. Primers were as described previously (Seddon et al., 2014). PCR and sequencing conditions are provided in the Supplementary Material. In addition, mitochondrial control region sequences ($n = 182$) from southern Queensland utilized in the Seddon et al. (2014) study and a data set of sequences (410 bp, $n = 217$) used by Blair et al. (2014) were incorporated into this study. The latter data set included samples from locations between Torres Strait and Moreton Bay. Sequences were aligned by eye and the alignment trimmed to the shared 410 bp fragment prior to analysis, which resulted in the exclusion of five variable sites. Hence the final mtDNA data set contained a 410 bp segment of mtDNA control region sequence for 639 dugongs.

Descriptive statistics (nucleotide diversity, haplotype diversity, number of haplotypes, number of variable sites) for the mitochondrial sequences were generated in the program DNASP v5.10.1 (Librado & Rozas, 2009). A median-joining network was constructed using NETWORK v5.0 2015 (Fluxus Technology Ltd.; Bandelt et al., 1999) allowing visualization of the haplotypes and the phylogeography.

To assess the concordance of the mtDNA data with the population structure based on the microsatellite data, four location-based groups were defined as the two STRUCTURE subclusters from each of the two major geographical clusters (see Results for details). Population-pairwise values of F_{ST} were estimated based on haplotype frequencies alone (conventional F_{ST}) and by taking into account pairwise differences between haplotypes (using the Kimura-2-parameter model with gamma shape parameter $\alpha = 0.05$; equivalent to Φ_{ST}; Excoffier et al., 1992) calculated in the program Arlequin v3.5 (Excoffier & Lischer, 2010). The most appropriate model of sequence evolution was calculated in MEGA X (Kumar et al., 2018). Overall values for F_{ST} (Φ_{ST}) (and for F_{SC}—assessing departure from panmixia among subclusters within clusters and F_{CT}—assessing departure from panmixia among clusters) were also calculated in an analysis of molecular variance (AMOVA) framework in Arlequin v3.5 (Excoffier & Lischer, 2010), specifying a priori the same groupings of clusters and subclusters.

2.7 | Oceanographic modeling

Oceanographic modeling was conducted to determine if there was any influence of currents and tides on dugong population structure along the eastern Queensland coast. We used the second-generation Louvain-la-Neuve Ice-Ocean Model (SLIM). This is a discontinuous Galerkin finite element model (Critchell et al., 2015; Delandmeter et al., 2017; Lambrechts et al., 2008) that has been successfully verified and used to simulate the hydrodynamics of the GBR, which is characterized by a complex topography and strong velocity gradients. Bathymetry data were sourced from https://www.deepreef.org/2010/07/06/3dgbr-bathy/. Figure S1 shows the model domain and its mesh (the model grid, i.e., the spatial resolution) used by SLIM for this study. The domain comprised the entire GBR lagoon. The eastern boundary was the shelf break at 200 m depth where the oceanographic forcing by the Coral Sea was applied. The resolution was very high in the Whitsunday Islands area of central Queensland. We also modeled the fate of potential waterborne particles in this region using the SLIM Lagrangian advection–diffusion model; the value of the horizontal eddy diffusion coefficient, which parameterizes submesh size turbulent mixing (i.e., mixing within a cell of the model), was set equal to 0.5 m^2/s following Wolanski and Kingsford (2014).

3 | RESULTS

3.1 | Microsatellite data

Of the 249 dugongs genotyped across 22 loci, 37 samples were removed because of excess missing data (genotypes present at fewer than 13 loci). Duplicates of nine pairs of samples were identified using exact genotyping matching

in GenAlEx (version 6.5; Peakall & Smouse, 2012), supported by biological data, where available, and one of each duplicate pair was removed prior to analysis. In addition, 90 microsatellite genotypes were included from our database representing individual dugongs (selected at random) from southern Queensland sampled in Moreton Bay ($n = 30$), Hervey Bay ($n = 30$), and Great Sandy Straits ($n = 30$) from Seddon et al. (2014). Hence, the data set for analysis comprised microsatellite genotypes at 22 loci for 293 dugongs.

3.2 | SNP data

A total of 142,887,564 demultiplexed raw reads across four lanes were generated from the sequencing, yielding 21.58 GB of raw sequence data. Individual sample reads ranged from 437,972 to 7,598,616 with a mean of 2,961,519 reads per individual sample. Prior to filtering, 1,048,574 catalog tags were identified with 10,690 retained after filtering. Four samples (one each from Cairns, Cardwell, Townsville, and Midge Point) were removed from the final analysis due to low call rates. Hence the SNP data set contained genotypes at 10,690 SNP loci for 43 dugong samples.

3.3 | Population differentiation: microsatellite data

The Bayesian clustering analyses executed in STRUCTURE identified $K = 2$ clusters using ΔK, with consistent results among replicate runs. The geographical boundary between the two clusters was the Whitsunday Islands region (20.32°S; Figure 1b,c). Cluster N (northern cluster) included dugongs sampled from Torres Strait (10.03°S) south to Airlie Beach (20.23°S), with two individuals from this region showing a high probability of being assigned to Cluster S (southern cluster; Figure 1c). Cluster S included all dugongs sampled from Midge Point (20.65°S) south to Moreton Bay (27.44°S; Figure 1c). The pairwise F_{ST} value between the two STRUCTURE clusters was 0.011, 95% CI [0.009, 0.013]. STRUCTURE plots for $K = 2$, 3, 4, and 5 all showed a consistent division at the Whitsunday Islands region (Figure S2). The PCoA plot showed two incompletely distinct genetic groups separated along the first axis, with these two groups largely consistent with geographical separation to the north and south of the Whitsunday Islands (Figure 2).

Cluster S had higher genetic diversity values than Cluster N (Table 1). All 22 microsatellite loci were polymorphic for both Clusters N and S. Allelic richness values for both clusters at each locus ranged from 2.00 to 14.08 alleles/locus (Figure S3), with average values for each cluster presented in Table 1. No loci were identified as being out of HWE in both clusters (Table S2).

Both N and S clusters showed two subclusters on hierarchical STRUCTURE analyses. Within Cluster N (samples between Torres Strait and Airlie Beach), the two subclusters (termed Na and Nb) were incompletely associated with geography but tended to separate those samples from the region south of Starcke River where Nb predominated, from samples in the Torres Strait where Na predominated (Figure S4). However, this pattern might be accentuated by a region of approximately 500 km region between Torres Strait and Starcke River from which we had no samples. Analysis of samples from Cluster S (between Midge Point and Moreton Bay) found a high value at $K = 2$ for the ΔK index with the two subclusters largely aligning with geography. Subcluster Sa was predominately comprised of samples to the north of Gladstone with subcluster Sb samples predominately to the south of Bundaberg (Figure S5).

A significant isolation-by-distance pattern was observed for the entire data set ($R^2 = 0.29$, $p < .001$; Figure 3a) and a weaker but significant IBD for each cluster (Cluster N $R^2 = 0.07$, $p < .001$, Figure 3b; Cluster S $R^2 = 0.03$, $p < .001$, Figure 3c). IBD was stronger for dugongs sampled along a 500 km strip of coastline centered on the Whitsunday Islands ($R^2 = 0.18$, $p < .01$) than for dugongs along 500 km to the north or south of the Whitsunday Islands (north $R^2 = 0.03$, $p < .01$; south, $R^2 = 0.07$, $p < .01$). Summary statistics for the isolation-by-distance analyses are presented in Table S3.

The BayesAss bidirectional migration analysis identified only 1.45% (*SE* 0.08%) of dugongs to the north of the Whitsundays and 0.43% (*SE* 0.33%) of dugongs to the south of the Whitsundays were migrants from the other region.

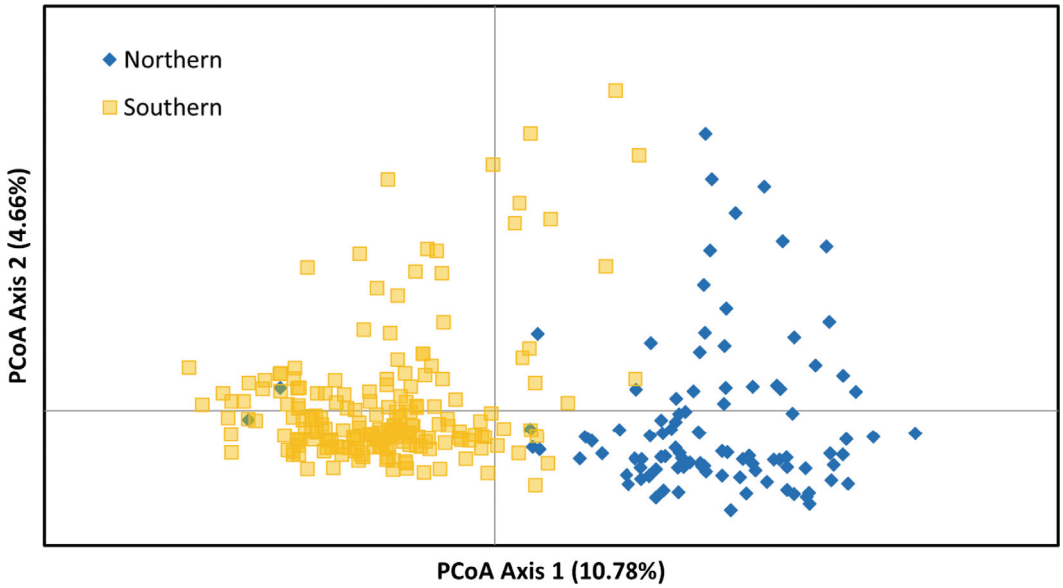

FIGURE 2 Principal coordinate analysis (PCoA) plot based on pairwise genetic distances of microsatellite data with individual dugongs colored to indicate those sampled north or south of the Whitsunday Islands region.

TABLE 1 Microsatellite diversity metrics (estimated across 1,000 iterations) for the two primary clusters identified in STRUCTURE. Sample size for each cluster (n = number of individual dugongs whose assignment probabilities were most strongly associated with each cluster (>60% assignment)), mean observed number of alleles per locus (n_a), average allelic richness per cluster (AR), observed heterozygosity (H_O), expected heterozygosity (H_E). Brackets show 95% confidence intervals. Note that diversity metrics and their associated confidence intervals reflect uncertainty in admixture assignments.

Cluster	n	n_a	AR	H_O	H_E
N (north)	100	6.99 [6.95, 7.03]	6.45 [6.41, 6.49]	0.546 [0.543, 0.549]	0.585 [0.582, 0.587]
S (south)	193	7.67 [7.62, 7.72]	7.04 [7.00, 7.08]	0.568 [0.565, 0.570]	0.612 [0.609, 0.615]

Evaluation of the associations between microsatellite genetic variation among individual dugongs and ecological variables showed that geographic distance had a much higher relative importance than seagrass distribution or the mean summer and winter sea-surface temperatures in explaining the pairwise genetic (microsatellite) distance (Table 2).

3.4 | SNP population differentiation

Admixture analysis using the 10,690 SNP loci identified three ancestral populations (K) for dugong samples collected along the Queensland coast (Figure 1d). Two of these clusters were separated latitudinally, with a clear divide at Airlie Beach in the Whitsunday Island region, largely consistent with the microsatellite data structuring. Samples collected from Torres Strait south to and including Airlie Beach formed Cluster 1 (northern cluster, blue color in Figure 1d) while samples from and including Airlie Beach south to Moreton Bay formed Cluster 2 (southern cluster, red color in Figure 1d). The sample from Midge Point (Whitsunday Islands region) had an approximately 50% split in

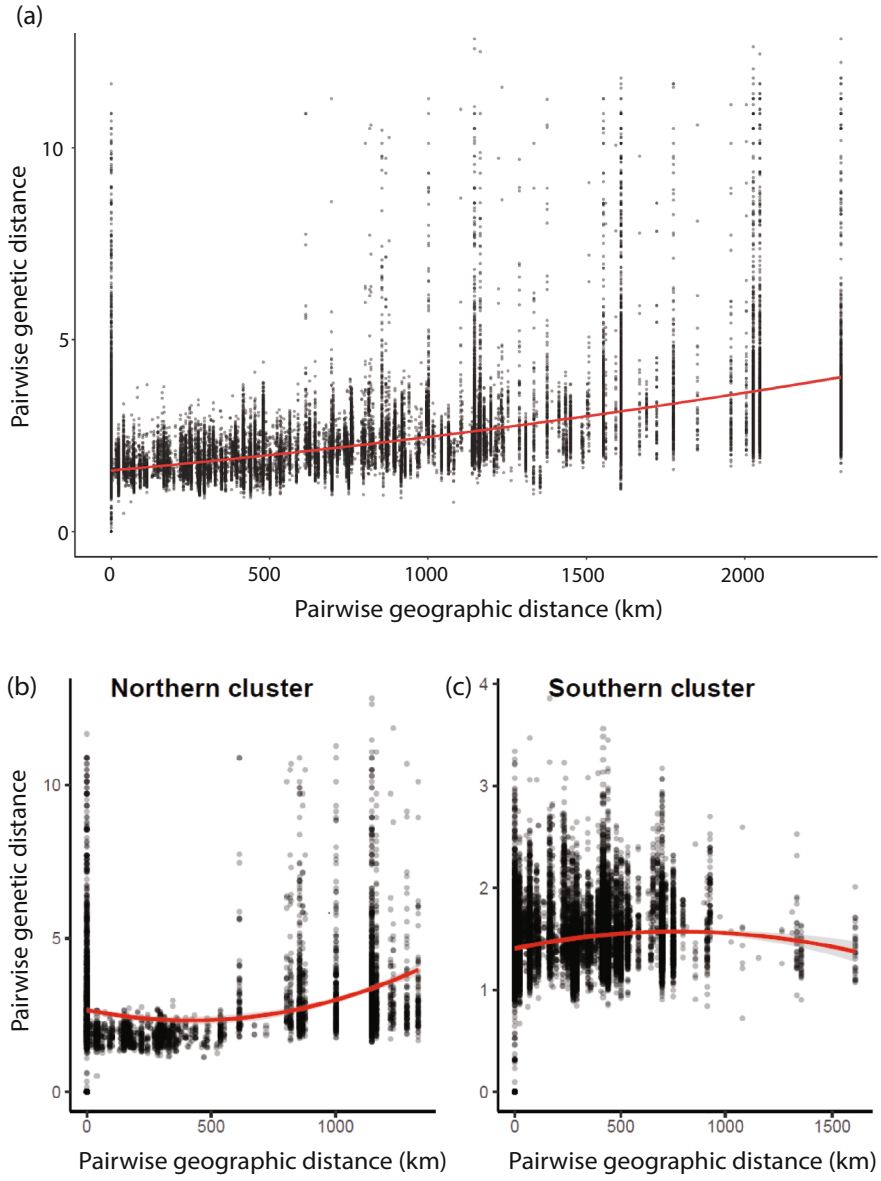

FIGURE 3 Isolation-by-distance plot of pairwise genetic distance, calculated using genotypes from 293 individual dugongs across 22 microsatellite loci, against pairwise geographic distance (kilometers) between the sampling locations. The red line indicates the best fit of a regression for the effect of geographic distance on pairwise genetic distance. (a) Whole data set; $R^2 = 0.29$, $p < .001$. (b) Northern cluster, $R^2 = 0.07$, $p < .001$. (c) southern cluster, $R^2 = 0.03$, $p < .001$.

assignment to Clusters 1 and 2. The third cluster (Cluster 3; green in Figure 1d) contained a small number of individual dugongs from disparate northern Queensland locations, including Torres Strait, Cairns, Townsville, Bowling Green Bay, and Airlie Beach, and three of four Great Sandy Straits samples had a mixed assignment to this Cluster 3. A genomic relatedness matrix network found support for two clusters, consistent with the northern and southern clusters identified in the microsatellite analysis (Figure S6). The multidimensional analysis (PCoA) indicated groupings of dugongs on Axis 1 separated by the Whitsundays region, with additional Axis 2 separation of dugongs from Great

TABLE 2 Results from the multiple regression on distance matrices to examine relationships between individual pairwise genetic (microsatellite) distance and environmental seascape distances. Statistics show mean values taken across 1,000 iterations; brackets show 95% quantiles. The R^2 value for the combined model was 0.3189, 95% CI [0.3178, 0.3216]. SST, sea surface temperature.

Distance	Regression statistic	Relative importance
Geographic distance	0.279 [0.277, 0.281]	0.790 [0.757, 0.824]
Mean summer SST	−0.106 [−0.109, −0.103]	0.113 [0.102, 0.126]
Mean winter SST	−0.019 [−0.020, −0.017]	0.004 [0.003, 0.004]
Seagrass distribution	−0.096 [−0.119, 0.065]	0.093 [0.046, 0.138]

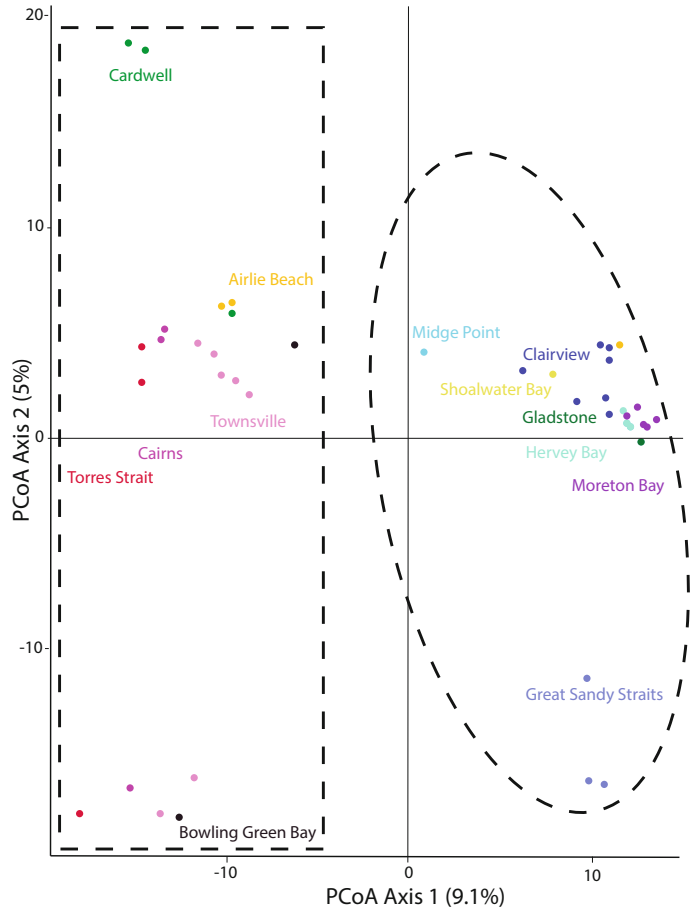

FIGURE 4 Principal coordinate analysis (PCoA) plot based on pairwise genetic distances of SNP genotypes for individual dugongs. Colors indicate different geographic locations. Locations within the dashed rectangle are north of the Whitsunday Islands and those in the dashed oval are to the south of these Islands.

Sandy Straits, Cardwell, and Bowling Green Bay (Figure 4). Genetic diversity was higher in the northern cluster 1 (H_O = 0.290, H_E = 0.311) than the southern cluster 2 (H_O = 0.199, H_E = 0.226) or cluster 3 (H_O = 0.215, H_E = 0.238). Point estimates of pairwise F_{ST} values were similar among clusters: Clusters 1 and 2 (0.023, 95% CI [0.019, 0.031]), Clusters 2 and 3 (0.025, 95% CI [0.021, 0.032]), and Clusters 1 and 3 (0.019, 95% CI [0.016, 0.023]).

3.5 | mtDNA diversity and population differentiation

Forty-seven mtDNA haplotypes were identified with 45 variable sites. Numbers of haplotypes and of variable sites, haplotype diversity and nucleotide diversity, as well as the average number of differences between sequences, all tended to increase from south to north.

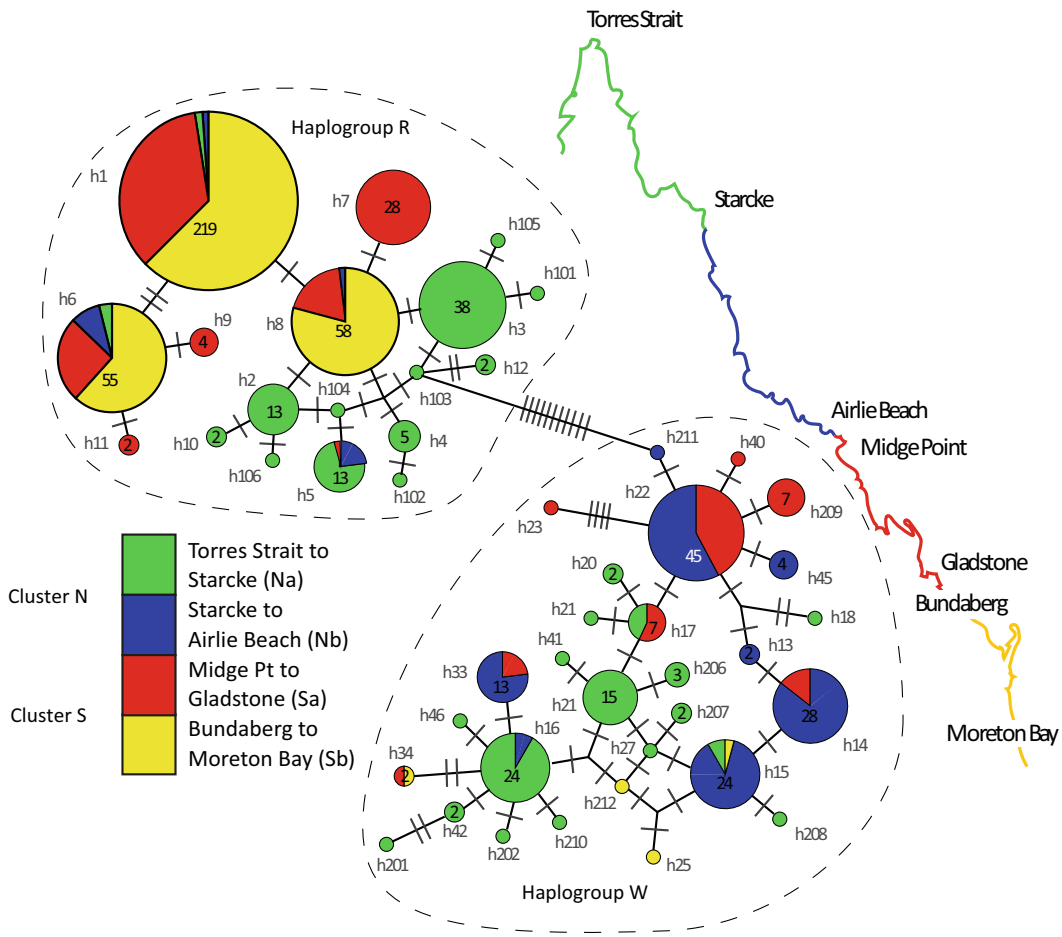

FIGURE 5 Median-joining network showing relationships among mitochondrial control-region haplotypes from 639 individual dugongs, the proportions of each haplotype and their geographical origins. Colors indicate geographical origins and subclustering locations identified using the microsatellite data. An outline of the Queensland eastern coast with relevant geographical locations is shown on the right. Dashed lines surround Haplogroup R and Haplogroup W. Circle size is proportional to haplotype frequency. Numbers within circles indicate number of individuals represented when >1. Haplotype identification (h) numbers extend those of Blair et al., (2014). Slash lines across a line connecting haplotypes or median vectors indicate the number of inferred mutational changes between haplotypes.

Phylogenetic analysis of the mtDNA sequences found 445 dugong samples falling into Haplogroup R (i.e., the "restricted lineage" of Blair et al. (2014) rarely found west of Torres Strait) and 194 into Haplogroup W (i.e., the "widespread lineage" found across the entire northern Australian range of the dugong; Table S4, Figure 5). To investigate the extent of concordance between inferences drawn from microsatellite data and from mtDNA, the mtDNA sequences were partitioned according to their sample site of origin into the geographically defined clusters and subclusters identified in the microsatellite analysis (see above; Table 3). We emphasize that, for analysis of the mtDNA sequences, this partitioning was strictly geographical. The most northerly subcluster (Na) had the highest number of haplotypes (31) and number of unique haplotypes (25) and the highest haplotype and nucleotide diversities (Table 3). Conversely, the most southerly subcluster, Sb, had the lowest values for all of these parameters. Only two abundant haplotypes (h1 and h6, both in Haplogroup R) were shared across all four geographical subclusters (Table S4). Representation of the two mitochondrial haplogroups was not equal in the different clusters/subclusters. Table 3 illustrates the low representation of Haplogroup W in Cluster S, and especially in Subcluster Sb (Bundaberg to Moreton Bay). In Torres Strait (Subcluster Na), the two haplogroups were roughly equally represented. Interestingly, Subcluster Nb (samples between Starcke River and Airlie Beach) contained significantly fewer representatives of Haplogroup R than expected (chi-square test, $p < .0001$) in comparison with Subcluster Na.

TABLE 3 Summary statistics for dugong mitochondrial sequence data arranged by mitochondrial haplogroup, geographical cluster and subcluster (as identified using microsatellite data).

Geographic cluster mtDNA subcluster	North Na	North Nb	North overall	South Sa	South Sb	South overall	All
n (total)	139	102	241	177	221	398	639
n (Haplogroup R)	79	12	91	137	217	354	445
n (Haplogroup W)	60	90	150	40	4	44	194
No. variable sites	36	23	37	30	24	31	45
No. haplotypes	31	12	38	15	7	18	47
Unique haplotypes	25	3	28	6	2	9	N/A
Haplotype diversity	0.877	0.829	0.924	0.765	0.551	0.670	0.851
Nucleotide diversity	0.0220	0.0142	0.0223	0.0161	0.0037	0.0100	0.0199
Average number of nucleotide differences	9.018	5.817	9.132	6.611	1.498	4.102	8.122

Note: n is number of individual dugongs; nucleotide diversity is per-site.

TABLE 4 Population structuring found by analysis of mtDNA control region sequences when partitioned into the four geographical subclusters identified by the STRUCTURE analysis of microsatellite data. Pairwise conventional F_{ST} values above the diagonal and Φ_{ST} values (distance method K2P + G) below the diagonal (Na – Torres Strait, Nb - Starcke River to Airlie Beach, Sa - Midge Point to Gladstone, Sb – Bundaberg to Moreton Bay) calculated in Arlequin. All values were significant ($p < .001$).

	Na	Nb	Sa	Sb
Na	—	0.138	0.173	0.289
Nb	0.297	—	0.161	0.306
Sa	0.164	0.590	—	0.068
Sb	0.493	0.849	0.157	—

Population structuring was identified in the mtDNA data, with pairwise comparisons indicating significant restrictions to gene flow between the main clusters identified with the microsatellite data (N and S; F_{ST} 0.191, $p < .00001$). The four subclusters were also significantly differentiated from each other (Table 4). The highest F_{ST} and Φ_{ST} values were between Subcluster Nb and Subcluster Sb, reflecting the very different proportions of each haplogroup represented. The analysis of molecular variance (AMOVA) also found significant results for comparisons among subclusters, within clusters, and within subclusters (Table 5). The failure to find significant differentiation between the main northern and southern clusters using AMOVA most likely relates to the low power to reject the null hypothesis of panmixia when a small number of populations are specified a priori (Fitzpatrick, 2009).

3.6 | Oceanographic modeling

Oceanographic modeling was conducted to identify possible explanatory mechanisms for the abrupt break between genetic clusters in the Whitsundays Islands region of central Queensland. Within this region, three seagrass hotspots have been identified from past seagrass presence/absence surveys in the region (Layer id: ea_nesp1:GBR_NESP-TWQ-3-1_JCU_Seagrass_1984-2014_Site-surveys, https://maps.eatlas.org.au) and these are located on the western side of Whitsunday Island (site 1 in Figure 6), at Shute Harbour (site 2) and at Airlie Beach (site 3). The oceanographic model showed that, in the absence of wind, most potential waterborne particles remain within the Whitsundays Islands region, with few escaping (Figure 6a). When this model is run with winds blowing from the south-east direction, again few particles drift beyond the Whitsunday Islands region (Figure 6b).

TABLE 5 AMOVA of the mtDNA control region sequences for the combined northern cluster (Subclusters Na and Nb) and southern cluster (Subclusters Sa and Sb). *P*-values were based on 1,000 permutations. The pairwise distance method specified was K2P + G. Note that, although a substantial percentage of the variation is among clusters, the number of populations specified is too low to achieve a significant result for F_{CT}.

Source of variation	*df*	Percentage of variation	*F*	*p*
Among clusters (north and south)	1	42.71	F_{CT} 0.427	$p = .325$
Among subclusters within clusters	2	13.80	F_{SC} 0.241	$p < .001$
Within subclusters	635	43.49	F_{ST} 0.565	$p < .001$

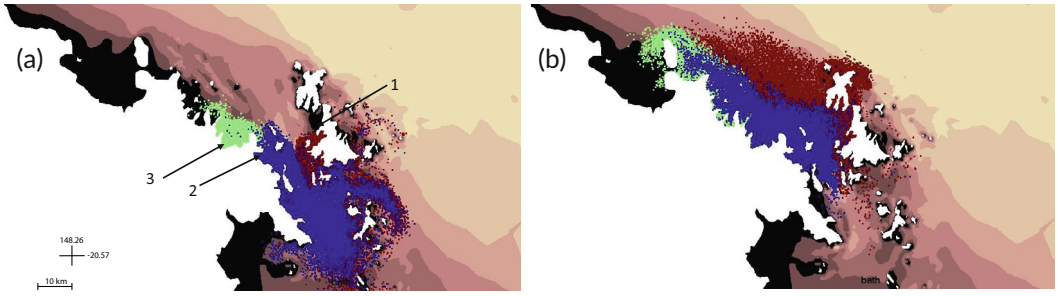

FIGURE 6 The predicted movement of potential waterborne particles emanating from the three color-coded seagrass meadows (site 1 - western side of Whitsunday Island (maroon), site 2 - Shute Harbour (blue), and site 3 - Airlie Beach (green)) in the Whitsundays Islands region (~20.32°S) after 184 hours (a) during calm weather conditions and (b) during the prevailing south-easterly winds. Land masses are shown in white with the change in ocean bathymetry shown as gray-scale contours (the actual values of the depth are shown in Figure S1).

4 | DISCUSSION

Analysis of the microsatellite genotypes from 293 individual dugongs and SNP genotypes from 43 dugongs sampled along the eastern Queensland coast consistently identified a genetic break in the Whitsunday Islands region of central Queensland, indicating the presence of at least two major genetically distinct populations of dugongs in Queensland. The relatively low levels of mixed ancestry and the small number of dugongs with cluster assignments contrary to their geographic location suggests low levels of dispersal across the Whitsunday Islands region. Since dugongs are a vagile species and in Queensland have been tracked making movements of up to 560 km (Deutsch et al., 2022b; Sheppard et al., 2006), such a profound separation of the two clusters occurring over a distance of less than 100 km was unexpected. The nature of the barrier to dispersal of dugongs in the Whitsunday Islands region is not obvious.

The population structuring of dugongs across the Whitsunday Islands region interrupts an overall pattern of isolation-by-distance. The distribution of dugongs along the eastern Queensland coast is largely limited to sheltered shallow coastal regions supporting seagrass meadows (Marsh & Saalfeld, 1989, 1990). Documented large-scale dugong movements have therefore tended to be strongly two-directional, i.e., north or south (Deutsch et al., 2022b; Sheppard et al., 2006; Zeh et al., 2016). Patterns of movement are less well known in areas in the northern Great Barrier Reef (GBR) region and Torres Strait where dugongs have been sighted more than 100 km from the nearest coast. The pattern of isolation-by-distance noted for the microsatellite data thus concords with the coastal distribution. In our study, geographical distance was identified as a more significant explanation of microsatellite genetic distance than sea-surface temperature (which is unlikely to be limiting in most of the area studied) or seagrass distribution (knowledge of which is incomplete). This contrasts with indications that dugongs might make small-scale movements in winter linked to sea temperatures at the high latitude limits to their range including Moreton Bay (Sheppard et al., 2006) and with a review of seascape-genetic studies (Selkoe et al., 2016) that suggested that sea temperature could be as influential as geography in explaining regional-scale population genetic structure of a number of marine mammal species (e.g., Amaral et al., 2012; Barceló et al., 2022; Fontaine et al., 2007; Pratt et al., 2022; Viricel & Rosel, 2014).

Past satellite-tracking data showed limited dugong movements across the region of the genetic break reported here. Fifty-two dugongs caught and tracked between Missionary Bay (18.2°S, near Cardwell; Figure 1) and Hervey Bay (25.2°S) had the potential to cross the Whitsunday Island region (20°S–21°S), based on a maximum possible movement distance of 560 km (Sheppard et al., 2006), yet none did so. It is possible that dugongs are traversing the Whitsundays region but have not yet been tracked doing so. The estimates of gene flow across the Whitsunday Islands region in this study were low with bidirectional migration estimates indicating greater movement from south to north. This low level of effective movement is lower than the genetic analysis estimates of a long term gene flow rate of 4%–5% per generation amongst dugong populations in south-east Queensland (Seddon et al., 2014). Targeted satellite tracking of numerous individuals from around the locality of the genetic break is required to confirm the degree to which dugongs move across the Whitsunday Islands region.

Why a genetic break is located in the region of the Whitsunday Islands is unclear. The high-resolution oceanographic modeling indicated the presence of the sticky water effect in this region, a phenomenon that might influence movements of dugongs and potentially other animals. In this sticky water scenario, although there may be substantial mean directional currents traversing a region, within that region (defined here in the Whitsundays by a complex matrix of reefs and islands) the currents are dominated by oscillating tidal flows, with little net movement (Wolanski & Spagnol, 2000). In the inshore waters of eastern Queensland, this effect is found only at the Whitsunday Islands region (Kingsford & Wolanski, 2019). Our modeling clearly shows the effect of the sticky water phenomenon on waterborne particles in the Whitsunday Islands region, with most particles remaining inside the region. The model showed that, by the time that they exit the Whitsundays, waterborne particles originating from the Whitsundays are highly diluted by a factor of 100:1 and probably also highly biodegraded because the water residence time is about 2 weeks. The sticky water effect may not physically inhibit dugong movements because they are large, strong swimmers. Nonetheless, the strong current and tidal mix might be disorientating to an animal for which

hydrodynamic reception plays a vital role in how it perceives its environment (Marshall et al., 2022). We hypothesize that the currents and tides in this area might inhibit the movements of dugongs traversing the Whitsunday Islands region. Further research is required to understand any effect of this phenomenon on dugong movement.

At least one other factor might be contributing to the genetic break identified here. Coles et al. (2009) modeled the likely spatial distribution of seagrasses in water deeper than 15 m in the GBR region, based on limited empirical point-source seagrass data and environmental variables including water depth, sediment characteristics and Secchi depth, an index of water clarity. Although dugong feeding trails have been recorded at depths to 35 m (Marsh et al., 2011), the importance of deeper water seagrass to dugongs in the GBR region is unknown and these predicted meadows were not included in our analyses. However, deeper water seagrass is reported to recover more quickly from disturbance than seagrasses in shallow water sites (Rasheed et al., 2014). Thus, offshore seagrass may be important for dugongs when their usual coastal feeding grounds are lost or degraded, including through the action of severe storms or cyclones and/or coastal flooding. Very strong spatial discontinuities have been identified in the modeling of offshore seagrass meadows in the GBR region (Coles et al., 2009; McKenzie et al., 2022). Seagrasses have been predicted to form extensive meadows in deeper water in a band running south from Princess Charlotte Bay (14.2°S, north of Starcke River; Figure 1) to 19.4°S (south of Townsville). Seagrass is then absent between 19.4°S and 22.4°S (between Clairview and Gladstone; Figure 1) before being predicted to occur again to the south. Thus, there is a break in the modelled distribution of offshore seagrass in the GBR that spans the region in which we identified the abrupt genetic break in dugongs, and it is possible that this seagrass discontinuity might be inhibiting north–south movements of dugongs offshore. Additional empirical data on seagrass distribution and dugong feeding behavior are required to test the role that offshore seagrass plays on determining dugong movements. Unfortunately, there are few comparative data on coastal movements from other species in this region; further studies might verify whether other (seagrass dependent/independent) species show similar patterns of restricted gene flow at this location. Another recent study of dugongs in southeast Asia suggested genetic isolation of dugongs in this area related to the disconnect in distribution of seagrass in the Strait of Malacca (Poommouang et al., 2021).

It is also interesting to speculate that cultural or social differences between the two main north and south dugong clusters may be driving the observed genetic structuring. The limited research undertaken to date is not suggestive of dugongs forming stable social groups (Roebuck, 2011), with only mother-offspring social relationships observed frequently. However, acoustic studies have revealed variations in vocal repertoires between spatially distinct populations of dugongs (Ichikawa et al., 2012), which may be indicative of cultural differences. In a recent review, O'Shea et al. (2022) conclude that socially transmitted knowledge is important in Florida manatees and possibly all sirenians.

In addition to the marked north–south Queensland genetic break, we also identified some indications of further population structuring, including subclusters in the microsatellite data with suggested boundaries in the vicinity of Starcke River and the Gladstone to Bundaberg region. The SNP data identified an additional third cluster without strong geographic basis. The presence of a gradual change in allele frequencies with strong isolation-by-distance patterns has been associated with STRUCTURE overestimating the number of clusters, with false subclusters being identified (Frantz et al., 2009; Perez et al., 2018). Conversely, the presence of true genetic structure can confound the estimation of isolation-by-distance, leading to the "cline versus cluster dilemma" (Guillot et al., 2009). The problem of cross-confounding of genetic clines and clustering estimates makes it challenging to identify the confounding factor and, given that 68% of studies on mammals ($n = 70$) in one review detected isolation-by-distance (Perez et al., 2018), this problem is substantial. We have followed a number of recommendations to identify support for the observed main genetic divide into the N and S clusters, including the use of the ΔK method of determining number of clusters and the identification of congruent patterns of population structure across analysis methods, which were helpful in the analysis of simulated populations (Frantz et al., 2009), as well as the use of both microsatellite and SNP genotyping data sets. We can expect greater accuracy and power from the genomic level data provided by SNPs for estimates of population parameters such as inbreeding, genomic diversity, and population differentiation, as seen in Gallego-García et al. (2021), and the similarity in our findings between markers might indicate low complexity of

population structure at the larger scale. However, adaptation and differential selection detected in genomic level analyses (e.g., Pratt et al., 2022) could influence patterns of genetic structure such as the third SNP cluster. The consistency of the genetic break at the Whitsunday Islands in all our analyses indicates that there is a reduction in gene flow across this region but, until appropriate analytical methods are available, we urge caution in management decisions taking account of the further subclustering identified in this study.

More historical patterns of dugong population movements are suggested by the mtDNA median-joining network (Martien et al., 2014). After sea levels rose following the last glacial maximum (LGM) and areas of suitable seagrass habitat expanded (Blair et al., 2014), dugong populations that were previously isolated from each other may have come into contact and interbred. Blair et al. (2014) suggested that dugongs were restricted to refugia such as the Coral Sea plateaus in the last glacial maximum (LGM). However, the margins of these plateaus would have been sheer limestone cliffs, rising from deep water and likely unsuitable for the growth of seagrasses and hence unlikely to support dugongs (Dr. R. Beaman, personal communication, January 2017). Limited shallow-water habitat refugia would have existed at that time along the Queensland coastline, possibly only at the southern end of what is now the Great Barrier Reef and around the mouth of the Fly River in the Gulf of Papua. With rising sea levels post-LGM, areas of suitable habitat expanded out from these refugia, but large parts of the northern GBR coastline would have remained unsuitable for dugongs until relatively recently. Following the flooding of the Torres Strait land-bridge (~7,000 years ago; Blair et al., 2014), dugongs representatives of Haplogroup W would have been able to colonize the eastern coastline of Queensland from further west or other regions in Papua New Guinea or Indonesia (Plön et al., 2019). Although the land-bridge contributed to periods of isolation, Plön et al. (2019) identified these as two of several deep mtDNA lineages in dugongs, globally. The low representation of Haplogroup R in mid-north Queensland, a portion of the coastline where Haplogroup W predominates, is puzzling. Further, the presence of haplotypes from Haplogroup W, particularly h22, to the north and south of the Whitsunday Islands supports past dispersal by females across this region. Nonetheless, we identified significant differentiation of the mtDNA sequences across the genetic breaks detected by the microsatellite data suggesting that barriers to dugong dispersal are also shaping patterns of mtDNA population structure.

At present, dugong management on the eastern coast of Queensland is largely conducted on a jurisdictional basis. The arrangements are separate (and very different) for Torres Strait (north of 10.68°S), the Great Barrier Reef Region (10.68°S to 24.5°S), and southeast Queensland (24.5°S to the Queensland/New South Wales border as detailed in (Marsh et al., 2011). Our analyses consistently identified a genetic break in the Whitsunday Islands region and highlights the need for improved cross-jurisdictional coordination. There are particular concerns about the dugongs along Australia's Great Barrier Reef coast between Cooktown (15.5°S, 145.2°E) and the southern border of the Great Barrier Reef World Heritage Area (24.5°S) due to apparent significant recent declines in dugong numbers in the Great Barrier Reef region south of Cooktown (Clark et al., 2021; Marsh et al., 2011, 2019). While the causes of these population declines remain unclear, suggestions include loss of habitat due to coastal development, fatal interactions with boats, fishing gear, and shark nets, as well as traditional hunting (Marsh et al., 2002). However, apparent regional declines could also be the result of temporary emigration due to the loss of seagrass meadows following cyclones and floods (Marsh et al., 2011; Preen & Marsh, 1995).

Along the eastern Queensland coast, we suggest that the two main distinct breeding units, north and south of the Whitsunday Islands, should be considered in designing monitoring and management of dugongs, recognizing that it is likely that there is at least some movement of dugongs across this region. Further local substructuring is expected. The Seddon et al. (2014) analysis of the southern-most Queensland dugong populations found weaker but significant genetic differentiation between two main breeding populations. Our microsatellite analysis found a candidate genetic break identified in the microsatellite data (subclusters Na versus Nb) that may be explained by the distribution of offshore seagrass (Coles et al., 2009) between Princess Charlotte Bay and Torres Strait. However, the lack of samples from this part of the northern GBR region, the uncertainty in the number of subclusters between microsatellite and SNP data, and the influence of isolation-by-distance patterns on clustering methods, mean that further investigations are required to determine the most appropriate design of dugong management arrangements.

Nonetheless, this study suggests that maintaining the movement corridors currently utilized by dugongs in each of the two main regions, separated by the Whitsunday Islands, should be a priority.

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AUTHOR CONTRIBUTIONS

Alexandra M. McGowan: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. **Janet M. Lanyon:** Conceptualization; data curation; funding acquisition; investigation; project administration; resources; supervision; writing – original draft; writing – review and editing. **Nicholas Clark:** Formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **David Blair:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; resources; visualization; writing – original draft; writing – review and editing. **Helene Marsh:** Conceptualization; writing – original draft; writing – review and editing. **Eric Wolanski:** Data curation; formal analysis; methodology; software; visualization; writing – original draft; writing – review and editing. **Jennifer M. Seddon:** Conceptualization; data curation; funding acquisition; investigation; project administration; resources; supervision; writing – original draft; writing – review and editing.

DATA AVAILABILITY

Sequences representing the mtDNA haplotypes identified are available in GenBank (Accession numbers: EU835761-EU835783, EU835785, EU835787, EU835793, EU835794, EU835800, EU835802, EU835805, EU835806, KJ944382, KJ944389, MT136732-MT136745). Microsatellite and SNP genotypes and SNP loci information are available at https://doi.org/10.48610/6735890. Sample location data are provided in the Supplementary Material.

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SUPPORTING INFORMATION

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