



Connecting the dots: Applying multispecies connectivity in marine park network planning

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ABSTRACT

Marine ecosystems are highly dynamic, and their connectivity is affected by a complex range of biological, spatial, and oceanographic factors. Incorporating connectivity as a factor in the planning and management of marine protected areas (MPAs) is important yet challenging. Here, we implemented a novel integrative framework that uses intraspecific genetic and genomic data for multiple marine species to characterise connectivity across a recently established South Australian MPA network. We generated connectivity networks, estimated cross-species concordance of connectivity patterns, and tested the impact of key spatial and oceanographic factors on each species. Connectivity patterns varied markedly among species, but were most correlated among those with similar dispersal strategies. Ordination analyses revealed significant associations with both waterway distances and oceanographic advection models. Notably, waterway distances provided better predictive power in all-species combined analyses. We extended the practical relevance of our findings by employing spatial prioritisation with Marxan, using node values derived from both genetic and geographic connectivity networks. This allowed the identification of several priority areas for conservation, and substantiated the initial decision to employ spatial distance as a proxy for biological connectivity for the design of the South Australian marine park network. Our study establishes a baseline for connectivity monitoring in South Australian MPAs, and provides guidelines for adapting this framework to protected networks elsewhere in the world.

1. Introduction

Ecosystem connectivity is an integral aspect of planning design in protected areas networks, as it affects the structure, function, and dynamics of populations and communities (Carr et al., 2003, 2017; Grummer et al., 2019). One important component of this is population connectivity, i.e., the dispersal of individuals between spatially separated populations (Treml et al., 2008; Cowen and Sponaugle, 2009). Population connectivity is highly relevant to both biodiversity conservation and fisheries management because it directly impacts demographic processes such as colonisation, recruitment, growth, and decline (Hastings and Botsford, 2006; Aiken and Navarrete, 2011). It also affects the distribution of genetic diversity, which can influence a population's evolutionary viability and adaptive resilience to changing environments (Hoffmann and Sgro, 2011; Frankham et al., 2017). Accordingly, connectivity is often listed in strategic commitments for

marine conservation planning (Balbar and Metaxas, 2019). Yet, this is not often translated into a measurable quantity suitable for integration with other spatially explicit information (Leslie, 2005; Magris et al., 2016), and connectivity surrogates such as geographic distance are often used in the design of marine protected areas (Leslie, 2005; DEH, 2008). This may overlook other important modulators of connectivity such as ocean circulation, distribution of traversable habitat, organisms' life histories and population sizes, and temporal fluctuations of any of these factors (Weeks, 2017; Balbar and Metaxas, 2019). Fortunately, biologically informed data are becoming increasingly available to researchers, improving prospects for data-driven decision making in spatial conservation prioritisation.

Genetic and genomic tools are particularly valuable for population connectivity assessments. Rather than relying on individual and potentially stochastic dispersal events, as for example in tagging or photographic recapture studies, genetic information has the advantage of

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capturing patterns of both short- and long-term demographic exchange. Moreover, since population genetic approaches provide a measurement of realised connectivity, they can be used to ground-truth predictive models for dispersal, for example, those combining distance and physical ocean circulation (Bracco et al., 2019; Wilcox et al., 2023). Ocean currents facilitate the passive dispersal of many marine species (Cowen and Sponaugle, 2009), and are also likely to affect population structuring of active dispersers due to their influence on local habitats and their prey (Möller et al., 2007; Hays, 2017). Oceanographic models, when combined with genetic data, might also allow forecasting of advective connectivity changes under future climate scenarios (Coleman et al., 2017), or project the flow of adaptive genetic variation into vulnerable populations (Boulanger et al., 2020). Successful integration of advection models and genetic approaches could therefore preemptively inform conservation prioritisation to maximise the resilience of marine species.

Population genetic and genomic datasets are accumulating for a variety of marine species and seascapes around the world (Riginos et al., 2016; Grummer et al., 2019). Likewise, genetic connectivity and population structure have been studied in a growing number of marine taxa (reviewed by Riginos et al., 2016; Teske et al., 2017; Jones et al., 2018). In Australia, such studies have typically focussed on single species,

limiting inferences about management of the wider ecosystem (Jones et al., 2018). However, combining datasets may allow for a broader understanding of patterns and relationships that are unapparent when analysing individual species separately. This has been explored in several previous studies of genetic connectivity, which have used data from multiple species sampled over a shared distribution to inform conservation (e.g., Kelly and Palumbi, 2010; Toonen et al., 2011; Drew and Barber, 2012; Cahill et al., 2017; Hanson and Fuller, 2019; Leiva et al., 2022; Benestan et al., 2023).

So far, a few studies have used multispecies connectivity estimates, enabling detection of shared breaks in connectivity to inform management units (Toonen et al., 2011; Drew and Barber, 2012), and providing feedback on MPA zoning changes (Leiva et al., 2022). In another study (Kelly and Palumbi, 2010), the authors tested a range of environmental correlates against connectivity for marine invertebrates but focused mainly on species-level differences, comparing overall genetic differentiation among species with different habitat requirements. Tools such as Marxan Connect (Daigle et al., 2020) are also allowing conservation planners to include connectivity metrics directly into spatial prioritisation algorithms. However, there remains scope for flexible methods for aggregating population connectivity data of multiple species into both spatial prioritisation frameworks and analyses alongside putative

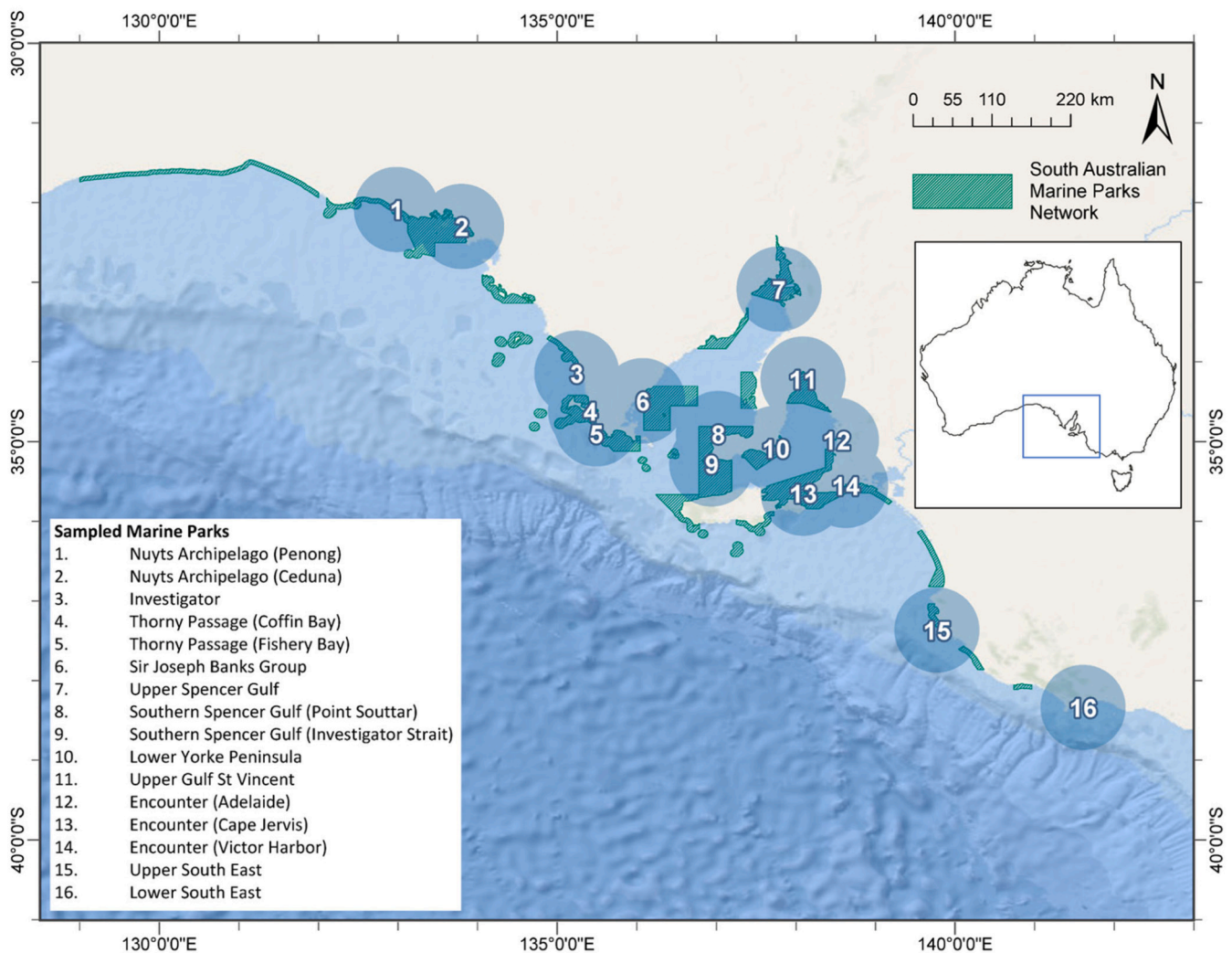


Fig. 1. Network nodes defined from aggregated data of five study species, *Delphinus delphis*, *Tursiops aduncus*, *Chrysophrys auratus*, *Siphonaria diemenensis*, and *Nerita atramentosa* sampled across the South Australian Marine Parks network. Inset shows the study region in the map of Australia. Green shaded regions correspond to boundaries of the South Australian Marine Parks Network 'General Managed Use' zones, accessed at: <https://data.sa.gov.au/data/dataset/marine-park-network-boundaries>. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

environmental drivers. Population-level (within-species) metrics of connectivity, when compared across multiple species, can help detect shared biological or geographical influences relevant across taxa. Meanwhile, identifying overarching connectivity patterns, including connectivity hubs, can be directly applied to MPA planning by pinpointing key regions that support connectivity for diverse taxa.

In this study, we took a meta-analytical approach to assess the connectivity of multiple species across the South Australian Representative System of Marine Protected Areas (SARSMPA). Established in 2009, the SARSMPA is a network of 19 multiple-use marine parks distributed across South Australia's bioregions (Fig. 1). A key biophysical design principle guiding the development of the SARSMPA was 'connectivity and linkages' (DEH, 2008). However, due to the inherent complexity of this concept, habitat inclusion across 'local, regional, and provincial' spatial scales was adopted by policy-makers as a surrogate for achieving connectivity within and between marine parks (DEH, 2008). While spatial metrics have been assumed as a pragmatic solution for policy implementation, there is growing recognition that targeted empirical studies are now required to effectively monitor and evaluate connectivity in this region and to test these initial assumptions about MPA network adequacy (Bryars et al., 2017; Jones et al., 2018).

This study addresses a key evaluation question in the Marine Parks Monitoring, Evaluation and Reporting Program (Bryars et al., 2017): "to what extent have marine park strategies contributed to the maintenance of ecological processes?", with connectivity being a crucial component of these processes. Specifically, we sought to address the gap in fundamental knowledge about population connectivity among South Australian MPAs, using metrics that are relevant to long-term population persistence, and which can be incorporated into broader inferential and decision-making frameworks. To this end, we re-analysed existing genetic and genomic datasets in a novel integrative framework to assess population connectivity patterns across the SARSMPA. This included the relative variation among species with actively and passively dispersing life history types. We then evaluated relationships between multispecies connectivity and hypothesised environmental influences, including waterway distances and simulated estimates of advection connectivity. Finally, we applied these results to identify priority conservation areas for maintaining intraspecific genetic connectivity, and outline opportunities to extend our framework under alternative sampling designs. This framework can be readily adapted to marine protected networks elsewhere in the world as suitable intraspecific genetic or genomic data become available. The continued integration of biological and physical data will be invaluable in improving spatial conservation planning and monitoring of marine ecosystems, especially in the face of climate change and other anthropogenic pressures.

2. Methods

2.1. Cataloguing and integrating existing genetic and genomic datasets

We selected available genetic and genomic datasets for which species' ranges and respective sampling schemes covered a broad region of the SARSMPA, with >3 South Australian sampling localities. This was further narrowed down to include only the two most common marker types used in population genetic analyses, microsatellites, and single nucleotide polymorphisms (SNPs). While SNPs generally have greater precision because they originate from a larger number of genomic regions, relatively high concordance is expected for estimates of genetic diversity and population structure between these marker types (Zimmerman et al., 2020). For microsatellites, we used the full, quality-filtered, genotype datasets described in the original publications (Teske et al., 2015, 2016). Unlike microsatellites, which are assumed to be selectively neutral, SNPs can be neutral or adaptive. Given that variation under local environmental selection may bias population demographic inferences, we used quality-filtered SNP datasets from which putatively adaptive markers had already been removed (as described in Barceló

et al., 2021, Bertram et al., 2022, Pratt et al., 2022, Bertram et al., 2023).

From the above requirements, we identified suitable high-quality datasets for five species (Fig. 2, Table 1). These included two iconic and legally protected cetaceans (the common dolphin, *Delphinus delphis*, and the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*), a commercially, culturally, and recreationally valuable teleost (Australasian snapper, *Chrysophrys auratus*), and two abundant and ecologically important intertidal invertebrates (Van Diemen's siphon limpet, *Siphonaria diemenensis*, and the black nerite, *Nerita atramentosa*) (Fig. 2, Table 1). Although these species provide only a snapshot of the diversity of connectivity patterns expected across our study region, they encompass both active dispersal strategies (bottlenose dolphins and common dolphins, herein 'active dispersers'), and advection-driven larval dispersal strategies (nerites, limpets, and snapper, herein 'larval' dispersers). Although snapper has a relatively long pelagic larval stage, our categorisation is an oversimplification because the species is also known to move during juvenile and/or adult stage (for details see Bertram et al., 2022, Bertram et al., 2023). Our study taxa include key species for MPA design in South Australia because of their priority status in conservation management plans and fishery stock assessments.

Based on the localities described in the original publications, we defined sixteen study network 'nodes' across South Australia (Fig. 1), with coverage in 11 of 19 SARSMPA General Managed Use zones. These zones delineate the outer boundaries of each park in the network, and while permitting recreational and some commercial activities, serve as managed areas within which marine park zones of higher protection are nested (Baker, 2004). Since sampling was not originally tailored to a multispecies approach (a limitation common to other datasets worldwide), our approach was limited by incomplete overlap of species' sampling localities. We chose to retain all unique intra-species sampling localities within the study region (Supplementary Fig. 1) but aggregated adjacent inter-species localities (<100 km apart) into geographically averaged 'nodes' to allow for combined analyses, which were labelled according to MPAs in proximity. This strategy relies on the assumption that spatially explicit variables have at least some influence on network connectivity, and that this influence will affect nearby localities more similarly than distant localities. For this reason, we ensured that no known biogeographic breaks occurred between aggregated sites (Teske et al., 2017). For some species, genetic data were available from outside of South Australia, but the major differences in interstate sampling ranges could also introduce taxonomic bias in multispecies network analyses (i.e. a node might be identified as important for network connectivity despite only being relevant to the single taxon sampled there). We therefore excluded those potential nodes, with the exception of Portland (Node 16). Although this node is located in the state of Victoria, it was sampled for four of the five species, and was expected to provide data relevant to the nearby but sparsely sampled Lower South East bioregion.

2.2. Spatial analyses of connectivity across and within the marine parks network

Neutral genotype data (pre-processed in the original studies) was used to quantify population differentiation for each species on a node-specific basis, as well as pairwise among nodes (population-specific F_{ST} and pairwise F_{ST} , respectively). Population-specific (in this case, node-specific) F_{ST} estimates the uniqueness of the ancestry at each node relative to the broader dataset or metapopulation (Weir and Hill, 2002). This statistic was calculated independently for each study species using the *betas* function in HIERFSTAT 0.5–10 (Goudet, 2005) using R (R Core Team, 2019), which can be applied to both SNP and microsatellite data. In contrast, pairwise F_{ST} estimates differentiation between pairs of population samples (nodes) resulting from population structure (Weir and Hill, 2002), and is therefore useful for exploring patterns of divergence across networks. Pairwise F_{ST} was calculated using EDENetworks (Kivelä et al., 2015), further described below. A number of indices of



Fig. 2. Study species, left to right. Top: *Delphinus delphis* (common dolphin), *Tursiops aduncus* (Indo-Pacific bottlenose dolphin). Bottom: *Chrysophrys auratus* (Australasian snapper), *Siphonaria diemenensis* (Van Diemen's siphon limpet), *Nerita atramentosa* (black nerite snail). Images by authors or used with permission.

Table 1

Sampling information and population genetic differentiation for five species included in the meta-analysis of South Australian Marine Parks network connectivity.

Species	Taxon class	Data source	Markers	N sites	N indivs	Dispersal	F_{ST} range (& mean)
<i>Delphinus delphis</i> (common dolphin)	Mammalia (mammals)	Barceló et al. (2021); Barceló et al. (2022)	SNPs ($n = 14,799$)	5	126	Lifelong, active, potentially year-round	0.013–0.043 (0.028)
<i>Tursiops aduncus</i> (Indo-Pacific bottlenose dolphin)	Mammalia (mammals)	Pratt et al. (2022)	SNPs ($n = 8,081$)	10	117	Lifelong, active, potentially year-round	0.035–0.146 (0.090)
<i>Chrysophrys auratus</i> (Australasian snapper)	Actinopterygii (ray-finned fishes)	Bertram et al. (2022); Bertram et al. (2023)	SNPs ($n = 10,916$)	7	270	Larval dispersal up to 30 days, subsequent sub-adult dispersal, decrease in adulthood	0.007–0.034 (0.021)
<i>Siphonaria diemenensis</i> (Van Diemen's siphon limpet)	Gastropoda (snails)	Teske et al. (2016); Teske et al. (2017)	Microsats ($n = 13$)	7	280	Larval dispersal 1–2 months	0.009–0.046 (0.027)
<i>Nerita atramentosa</i> (Black nerite)	Gastropoda (snails)	Teske et al. (2015); Teske et al. (2017)	Microsats ($n = 10$)	9	373	Larval dispersal ~4 months	0.005–0.013 (0.009)

SNP = single nucleotide polymorphism (genomic marker); Microsat = microsatellite (genetic marker); N sites = number of South Australian localities sampled; N indivs = total number of individuals; F_{ST} = fixation index representing pairwise genetic differentiation among localities (nodes); the scale ranges from 0 (no genetic differentiation) to 1 (complete genetic differentiation).

differentiation have been proposed as alternatives to F_{ST} for markers with high mutation rates, such as microsatellites (e.g., G'_{ST} , D and other indices). For the two microsatellite datasets used here (nerites and limpets), both the overall pattern of very low differentiation across the entire sampled region and the number of pairwise comparisons that were significant were very similar using either F_{ST} , G'_{ST} , or D (details and statistical comparisons in Teske et al., 2015; Teske et al., 2016). This indicates that F_{ST} is an adequate index for our comparative study, which includes microsatellite and SNP datasets. We point to the literature (e.g., Whitlock, 2011) for additional information about the choice of an index of differentiation.

To assess the extent to which patterns of connectivity were either shared or unique among the five species, we used a 'genogeographic clustering' method (Arranz et al., 2022) to capture relationships between genetic variation and geographic distance along the South Australian coastline for each species. Linearised coastline distances represented the shortest route between a starting point (here, the westernmost Node 1: Nuyts Archipelago Penong), and all other original (unaggregated) sampling localities while following the coastline. This measure could reflect migration paths of species with nearshore habitat preferences, which have been documented in some populations of bottlenose dolphins (Hoelzel et al., 1998; Zanardo et al., 2016; Pratt et al., 2022), and adult snapper (Bertram et al., 2022). Linearised coastline

distances were first calculated in ArcMap (ESRI, 2011) by using the vertex *snap* function to snap sampling coordinates to the nearest segment of the Australian Shoreline layer (Geoscience Australia), and calculating the length of all segments between the starting point and each sampling locality (total length of 2236 km). We then used 'genogeographic clustering' (Arranz et al., 2022) in R, which began by plotting linearised coastline distances against node-specific F_{ST} values. Curves were then fitted to the data points using maximum likelihoods to characterise each species' spatial trends, and were represented as colour maps depicting variation in genetic divergence along the coast. As advised by Arranz et al. (2022), this step was adapted to suit a linear coastline rather than a closed loop (island) coastline by omitting the triple-cycling and penalty steps from the original code. Fitted curves were scaled and centred, then clustered across species to identify similarities in spatial patterns. Parametric bootstrapping (1000 replicates) of species clustering was used to find the best species clusters, and to assess statistical significance of joins and splits (further described in Arranz et al., 2022).

2.3. Generation and analysis of connectivity networks using a graph theory approach

We used a network approach to summarise patterns of population

connectivity structure for (a) a combined “*all species*” dataset and (b) for the three most divergent species groupings identified by the genogeographic clustering analysis. First, raw genotype files (SNPs and microsatellites) were imported into EDENetworks to build population-based networks for each species. Nodes (connection points) corresponded to those defined from the aggregated sampling localities, while edges (links among nodes) were calculated as species-specific pairwise F_{ST} values (Reynolds distance, Reynolds et al., 1983). We exported the resulting species-specific edge values as distance matrices, which were used to produce each combined network (the *all species* network, plus three divergent cluster networks). For each of those desired networks, we independently scaled, centred, and averaged species-specific edge values (distance matrices) of the relevant species. The resulting combined matrices were then re-imported into EDENetworks for analysis. For each combined network, we derived corresponding thresholded networks; a threshold being the maximum pairwise distance considered as providing an effective link between nodes, with all links of larger distances therefore removed. We chose the maximum threshold below percolation, that is, the point at which a connected network would fragment into smaller components. Given the generally high dispersal ability of the species included in this study, the chosen threshold (proxy dispersal kernel limit) is likely lower than real-world dispersal limitations for these species. However, these thresholds provide an overview of the strongest and weakest pathways in each network, clarifying which nodes are likely to become disconnected if overall connectivity is reduced, and which may act as pathways between less connected regions. We calculated network characteristics and node values for each of the combined thresholded networks and produced circle plots using the R package CIRCLIZE (Gu et al., 2014).

2.4. Spatial and oceanographic connectivity models

To assess the relative concordance of spatial distance and oceanographic factors with genetic differentiation across the network, we tested correlations between pairwise F_{ST} and explanatory variables of interest (direct waterway distances, coastline distances, latitudinal distances, and ocean advection connectivity estimates), all calculated as pairwise values among all nodes. Direct waterway distances refer to the shortest route between each pair of nodes without crossing the land, and were calculated using the *viamaris* function in MELFU-R (<https://github.com/pygmyperch/melfuR>). Coastline distances refer to the shortest route between each pair of nodes while travelling along the coastline (converted from linearised coastline distances, described in Section 2.2). Latitudinal distance was calculated as the difference (in decimal degrees) in latitude between node pairs, which was included since it could have indirect effects on marine dispersal potential (Álvarez-Noriega et al., 2020).

Pairwise advection connectivity between nodes was estimated using the Connectivity Modelling System 1.1 (Paris et al., 2013) to integrate the Ocean General Circulation Model for the Earth Simulator 2 (OFES2; Sasaki et al., 2020). We used a resolution of 0.5° of the 2D velocity fields (eastward and northward) at 5 m depth, from 1994 to 2014. The resulting connectivity matrices show how many particles (e.g., larvae) released from each node are expected to settle within the same or another sampling node. We created four matrices representing each season. For each model, we released 1000 particles per node per day during the three-month seasonal period (a total of 1,800,000 particles per node per model). The particles were advected for at least 30 days before they could settle, and up to 150 days before they were considered dead, approximating the range of passive larval durations of the three study species with planktonic larvae (~30 days for *C. auratus*, ~30–60 days for *S. diemenensis*, ~120 days for *N. atramentosa*, Table 1). The particle locations were recorded every 3 h, whereupon it was determined whether they had settled or died. A particle was considered settled when, for the first time, its location intersected within the 1° semicircle surrounding a release site. Because the number of ‘settled’

particles differed by several orders between nodes, estimates were corrected to their natural logarithm. Following the methods of Teske et al. (2015) implemented in our study region, we subjected simulation results to a stepping-stone model of dispersal, by which pairwise advection connectivity was defined as the total number of migrants between each pair of nodes after four successive reproductive cycles. Although these models were not tailored for actively dispersing dolphins, the advection connectivity was still used in subsequent regressions against active dispersers because of growing evidence (details in the Discussion) that meso- and fine-scale patterns of ocean circulation predict population connectivity in these species, even after controlling for the effects of spatial geographical distance.

We used redundancy analyses (RDAs) in VEGAN (Oksanen et al., 2019) to test relationships between these variables and the genetic differentiation between nodes (pairwise F_{ST} , as used in the network analyses). Since RDAs do not handle missing data, and not all nodes were sampled for all species, we first used a principal component analysis of incomplete data (INDAPCA, Podani et al., 2021) to find the first significant principal components (PCs) of genetic variation. Separate RDAs were then performed for respective environmental variables, where environment acted as an explanatory variable, and genetic PCs acted as a response variable. As with the network analyses, this was performed for a combined *all species* dataset. We repeated analyses for the best-performing models using species subclusters identified by the genogeographic analysis. ANOVAs (function ‘*anova.cca*’) were used to assess the significance of each model with 1000 permutations.

2.5. Conservation prioritisation of MPAs

To translate our findings into practical conservation guidance, we applied the genetic connectivity results to spatial prioritisation analyses using the conservation planning tool Marxan (Ball et al., 2009), incorporating connectivity into a hypothetical prioritisation scenario in the form of an opportunity cost (suggested by Beger et al., 2014, Andrello et al., 2022). Since our study occurred in an existing MPA network, we chose a scenario where managers might seek to increase protections within existing boundaries, for example by increasing the coverage of habitat protection or sanctuary zones. This involved treating individual park boundaries (corresponding to the 16 network nodes) as planning units, with prioritisation among these existing managed zones. However, a similar approach could be implemented for the design of new MPA networks or modification of existing boundaries with either a finer-scale sampling method (e.g. if shared sampling sites (nodes) occur more frequently than the intended boundaries), or by interpolating genetic differentiation values (e.g. sensu Duforet-Frebourg and Blum, 2014, Wilcox et al., 2023) prior to network analysis.

Three alternative cost layers were created from connectivity network betweenness values, which are effective at representing areas important to a network’s global connectivity. However, alternative node values (e.g. degree centrality, subgraph centrality) may be valuable if the interest is to prioritise connectivity within local subsets of the network (Benzi and Klymko, 2014). The first used betweenness values from the *allspecies* network analysis, assigning an approximately equal cost to each of the five species (20 %). Since representation was uneven between species clusters (3 larval versus 2 active dispersers), a second cost layer was based on a ‘balanced’ dataset, in which betweenness values from the *active dispersers* network analysis and the *larval dispersers* network analysis were averaged, thus assigning an equal (50 %) weighing to each cluster rather than to each species. For comparative purposes, the third cost layer included betweenness values from the *geographic* network analysis based on direct waterway distances among nodes. The betweenness connectivity values for each of the three layers were normalised to between 0 and 1, and inverted ($1 - x$) to convert values to a positive cost (i.e. the cost of prioritising a node of low connectivity as a lost opportunity for prioritising a node of high connectivity). Each cost layer was added to a separate Marxan planning unit input file (pu.dat),

with ID corresponding to the relevant node, and an additional planning unit input was created with no costs.

To provide a realistic example of the application of these cost layers in a planning scenario alongside other priorities, we generated a ‘conservation features’ layer for prioritisation based on local presence of threatened fauna species. Note that, although based on real observation data, the conservation features layer was not optimised to meet any specific planning goals in this system, since this has been more thoroughly addressed in other studies (e.g. Kirkman, 2013; Lieberknecht et al., 2010). Species lists were obtained for each SARSMPA segment corresponding to one of our study nodes using NatureMaps 3.4.1 (DEW, 2017) Fauna Tools - > Create Simple Species Lists, manually selecting MPA boundaries, and filtering for State or Nationally rated threatened species. For the Marxan input (spec.dat), ID was based on individual species, conservation targets were uniform (prop 0.2), and species penalty factors were also uniform (spf 3). The number of observations for each species was included in the planning unit versus species feature file (puvspr.dat).

Marxan prioritisations were generated independently for each cost layer, each using 1000,000 iterations and 100 replicates in run mode 1 (apply simulated annealing followed by iterative improvement). Each prioritisation was performed with no cost threshold, then for comparative purposes, at two thresholds stricter than the initial cost results. Although we recognise that it is not strictly possible to set a meaningful ‘budget’ for relative connectivity values, such a comparison can still be

useful to illustrate sensitivity of the result to cost penalties.

3. Results

3.1. Spatial connectivity along the network for a range of taxa

Based on the available species’ datasets, we found reasonably high connectivity across the SARSMPA (Fig. 3). The lowest population genetic structure (and therefore highest connectivity) was observed for *larval dispersers*; this was reflected by comparatively low pairwise F_{ST} values (Table 1). This was most pronounced in nerite snails (average F_{ST} = 0.009), followed by snapper (0.021), limpets (0.027), common dolphins (0.028), and bottlenose dolphins (0.090).

Spatial patterns of connectivity were most divergent between *larval dispersers* and *active dispersers*. Genogeographic clustering (Fig. 4A; Supplementary Fig. 2), based on node-specific F_{ST} values, produced dendrogram groupings with common dolphins and bottlenose dolphins together on one branch, and nerite snails, limpets, and snapper on the other. When average values of each cluster were mapped along the South Australian coastline (Fig. 4B), the active-dispersing dolphin species appeared to have higher connectivity in open stretches of coast compared to gulf waters and embayments. In contrast, *larval dispersers* tended to have high connectivity in the centre of the sampling range, especially around the southern reaches of the gulfs. However, despite these trends, associations between no pairs of species were statistically

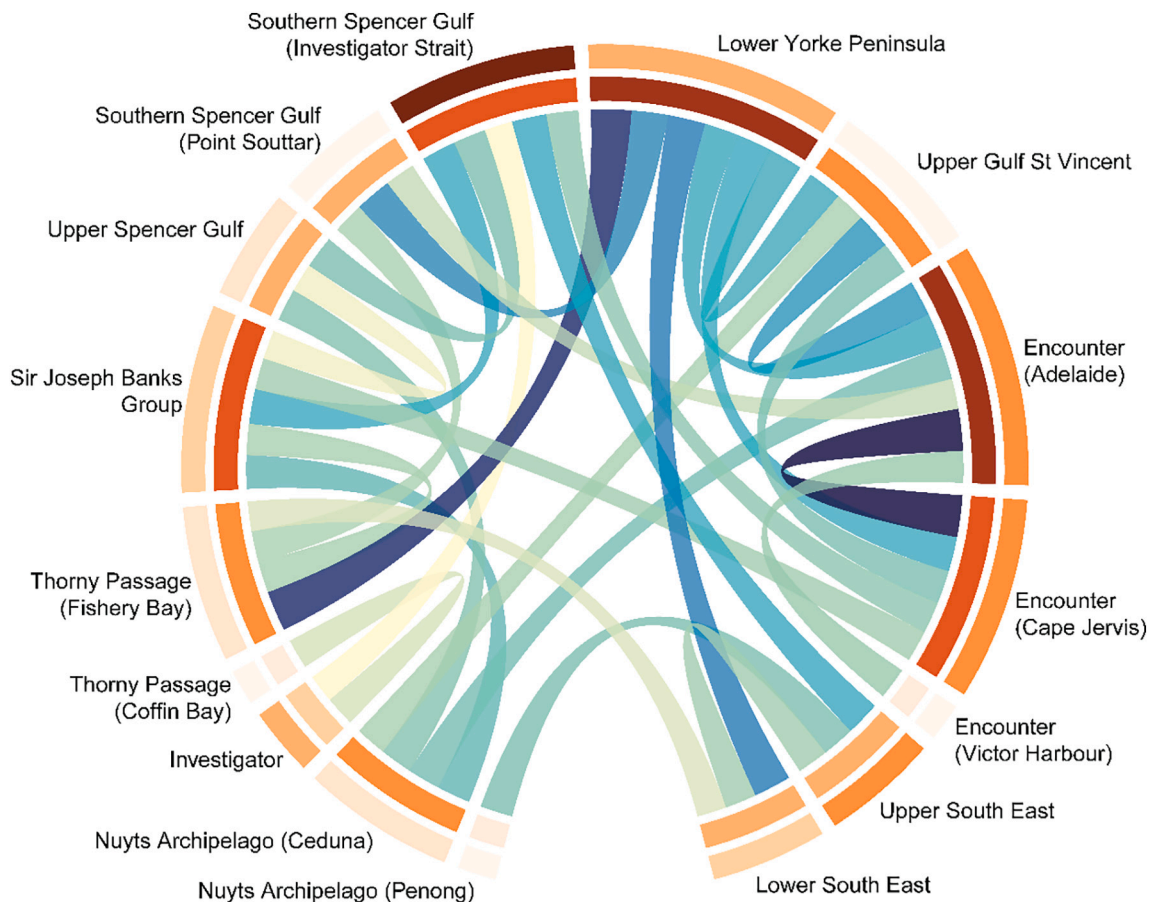


Fig. 3. Average connectivity network for all species combined (*Delphinus delphis*, *Tursiops aduncus*, *Chrysophrys auratus*, *Siphonaria diemenensis*, and *Nerita atramentosa*) among sampled marine parks, showing the maximum distance threshold for a fully connected graph. For edges (links in the network), relative pairwise connectivity among nodes is indicated by the degree of shading of the links, with the lightest (yellow) indicating lowest connectivity, and the darkest (navy) indicating the highest connectivity. On surrounding tracks, relative node values are represented by the degree of shading of the orange tracks, with lightest orange indicating the lowest values, and darkest orange indicating the highest values. The outer track represents betweenness centrality (i.e., the node's importance in forming a pathway between less connected subclusters), while the inner track represents node degree (the total number of links at maximum distance threshold). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

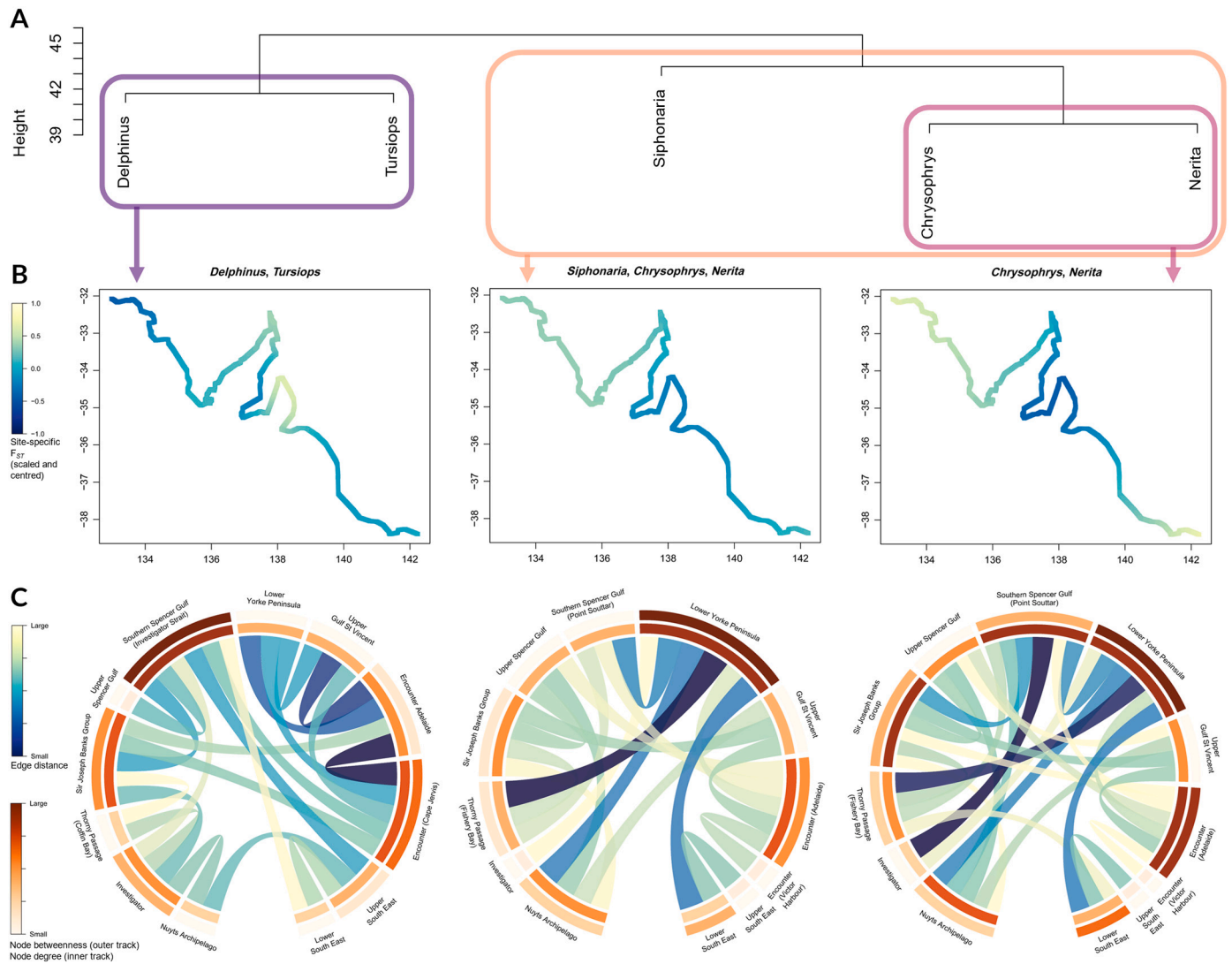


Fig. 4. (A) Species clustering based on spatial variation in node-specific genetic differentiation (F_{ST}); (B) average node-specific genetic differentiation (F_{ST}) for each species cluster in relation to position along coastline, with lighter yellow indicating regions of greater differentiation/uniqueness; and (C) networks of average connectivity among sampled marine parks per species cluster, showing minimum distance threshold for a fully connected graph. For edges (links in the network), relative pairwise connectivity among nodes is indicated by the degree of shading of the links, with the lightest (yellow) indicating lowest connectivity, and darkest (navy) indicating the highest connectivity. On surrounding tracks, relative node values are represented by the degree of shading of the orange tracks, with lightest orange indicating the lowest values, and darkest orange indicating the highest values. The outer track represents betweenness centrality (i.e., the node's importance in forming a pathway between less connected subclusters), while the inner track represents node degree (the total number of links at maximum distance threshold). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significant ($p = 0.482\text{--}0.597$), and siphon limpets were relative outliers within the larval-dispersing cluster. This suggests that despite some shared trends, there also remains a substantial degree of idiosyncrasy in connectivity patterns of individual species.

3.2. Network characteristics

At the maximum threshold below percolation (fragmentation of the network), the *all species* dataset network contained 16 nodes (localities), 28 edges (links among localities), and an average node degree (number of connections per node) of 3.5 (Fig. 3, Supplementary Tables 1 & 2). The clustering coefficient, reflecting substructure in the network, was 0.29 (where 0 = no substructure and 1 = total substructure). The greatest node degrees were observed for the Lower Yorke Peninsula and Encounter (Adelaide) nodes, which each had six strong connections to other nodes. Nodes with only a single strong connection (a node degree of 1) were Nuyts Archipelago (Penong), Thorny Passage (Coffin Bay),

and Encounter (Victor Harbor). Also of interest were nodes with high betweenness centrality values, which included Southern Spencer Gulf (Investigator Strait) (38.2), Encounter (Cape Jervis) (19.4), Encounter (Adelaide) (18.9), and Upper South East (17.5).

We also conducted network analyses for active and passive dispersal clusters identified by the genogeographic clustering (Fig. 4C). These networks each contained only 12 nodes due to less sampling coverage within species subsets. For *active dispersers* (dolphins), a thresholded network was produced with 17 edges, an average node degree of 2.83, and a clustering coefficient of 0.31. Southern Spencer Gulf (Investigator Strait) had the greatest node degree of 6, while the nearby Upper Spencer Gulf had the lowest node degree of 1. Since limpets were relatively outlying among *larval dispersers*, we analysed subsets with and without their inclusion (snapper, nerite snails, and limpets; versus snapper and nerites only). The *full larval group* had fewer connecting edges than the *reduced larval group* (18 vs 24), a lower average node degree (3 vs 4), and less clustering (0.21 vs 0.47). Both networks had

maximum node degrees of 6. Lower Yorke Peninsula had the highest node degree and betweenness centrality in both full and reduced larval groups. This was the only node with six connections in the full group, however in the reduced group, three other nodes also had node degrees of 6, namely Encounter (Adelaide), Southern Spencer Gulf (Point Souttar), and Sir Joseph Banks Group. Lowest node degrees for both groups were in Encounter (Victor Harbor) and the Upper South East, as well as Investigator in the full larval group.

3.3. Spatial and oceanographic relationships with empirical connectivity

We found that genetic connectivity was significantly correlated with both spatial distance and advection connectivity estimates, with differing extents depending on the species subset. For *all species*, direct waterway distance was the best predictor of population connectivity, whereby connectivity declined, and population structure increased, with increasing distances. This relationship accounted for 18.5 % of variation of genetic PC1 ($p < 0.001$; Fig. 5 (upper), Supplementary Table 3). Spring advection was also a relatively good model (associated with 14.9 % variation, $p < 0.001$, Fig. 5 (lower)). While considering these distance and advection variables together could potentially improve predictive power, we also found high autocorrelation between the two (-0.58 , Supplementary Fig. 3), indicating that combining them could artificially inflate the strength of the models. When considering species by their dispersal clusters, we found that both spatial and advection models were most effective at predicting genetic connectivity in the *active dispersers* (dolphins), compared to any other species cluster. The strongest associations were with the spring advection connectivity

model which, associated with 36.8 % of observed genetic variation ($p < 0.001$), is likely to have produced the strong performance of this advection model in the abovementioned *all species* RDA. Direct waterway distance was the next best model, associated with 33.3 % of variation ($p < 0.001$). For the *larval dispersers*, direct waterway distance was the only variable significantly associated with genetic connectivity (8.1 % of variation, $p = 0.043$). The advection model with the greatest explanatory power was autumn (1.5 %, $p = 0.386$), however this was also the variable most highly correlated with distance, which could explain the stronger effect.

3.4. Spatial conservation prioritisation

Incorporating any of the connectivity cost layers into the Marxan prioritisation scenarios resulted in a change to the combination of PUs identified as the ‘best solution’, which initially selected eight of the 16 parks when cost was not included (Supplementary Table 4). Interestingly, in runs with unthresholded cost layers, the combination of nodes in the best solutions were identical for the three alternative cost layers (all species equal, life histories balanced, or spatial proximity). In all of these runs, Node 5 (Thorny Passage: Fisheries Bay) was replaced by Node 9 (Southern Spencer Gulf: Investigator Strait) as part of the best solution. For several of the nodes, selection frequencies were consistently 100 % among runs with no cost and with unthresholded cost layers (Fig. 6, Supplementary Table 5). Total prioritisation costs were 5.5 (spatial), 5.8 (species equal) to 6.1 (balanced life histories). Selection frequencies became more variable when cost thresholds were introduced, and there were greater discrepancies among prioritisations under

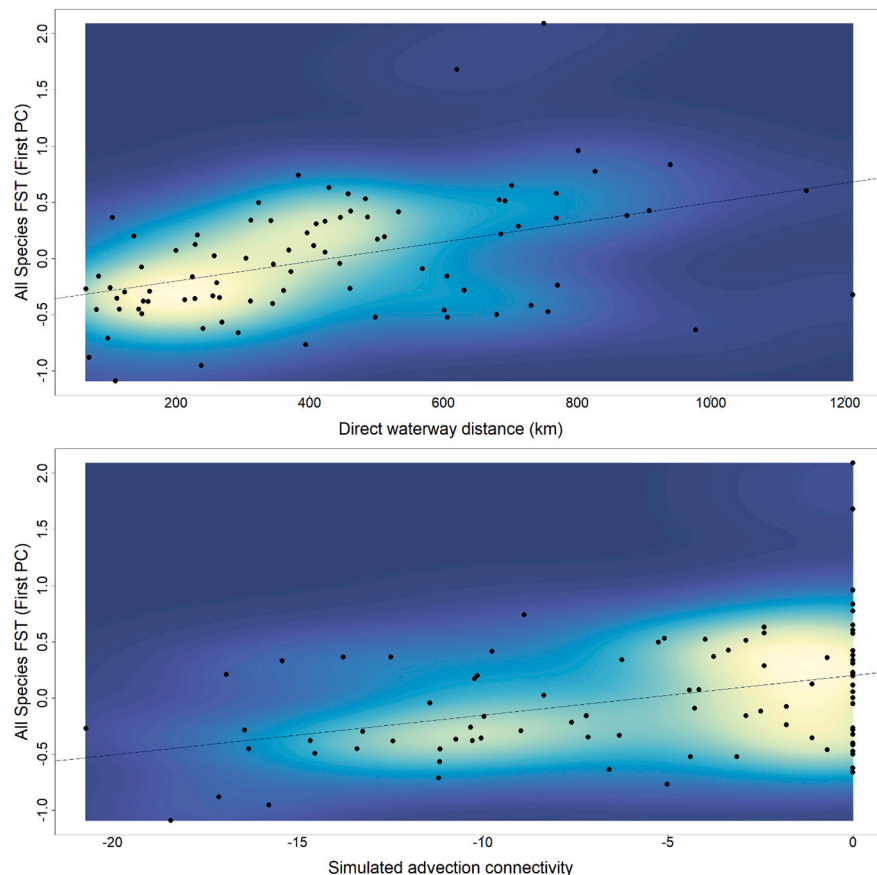


Fig. 5. Relationships between multispecies population differentiation and possible explanatory values, with scatterplots showing the line of best fit under a linear regression. Background shading corresponds to two-dimensional kernel density estimation of observations. Population differentiation is based on first principal component of pairwise F_{ST} among South Australian localities (nodes) for integrated genetic data from the common dolphin (*Delphinus delphis*), bottlenose dolphin (*Tursiops aduncus*), snapper (*Chrysophrys auratus*), siphon limpet (*Siphonaria diemenensis*), and nerite (*Nerita atramentosa*). Top: against direct waterway distances (km), $r^2 = 0.185$, $p < 0.001$. Bottom: against the best fitting advection connectivity model (spring, steppingstone), $r^2 = 0.149$, $p < 0.001$.

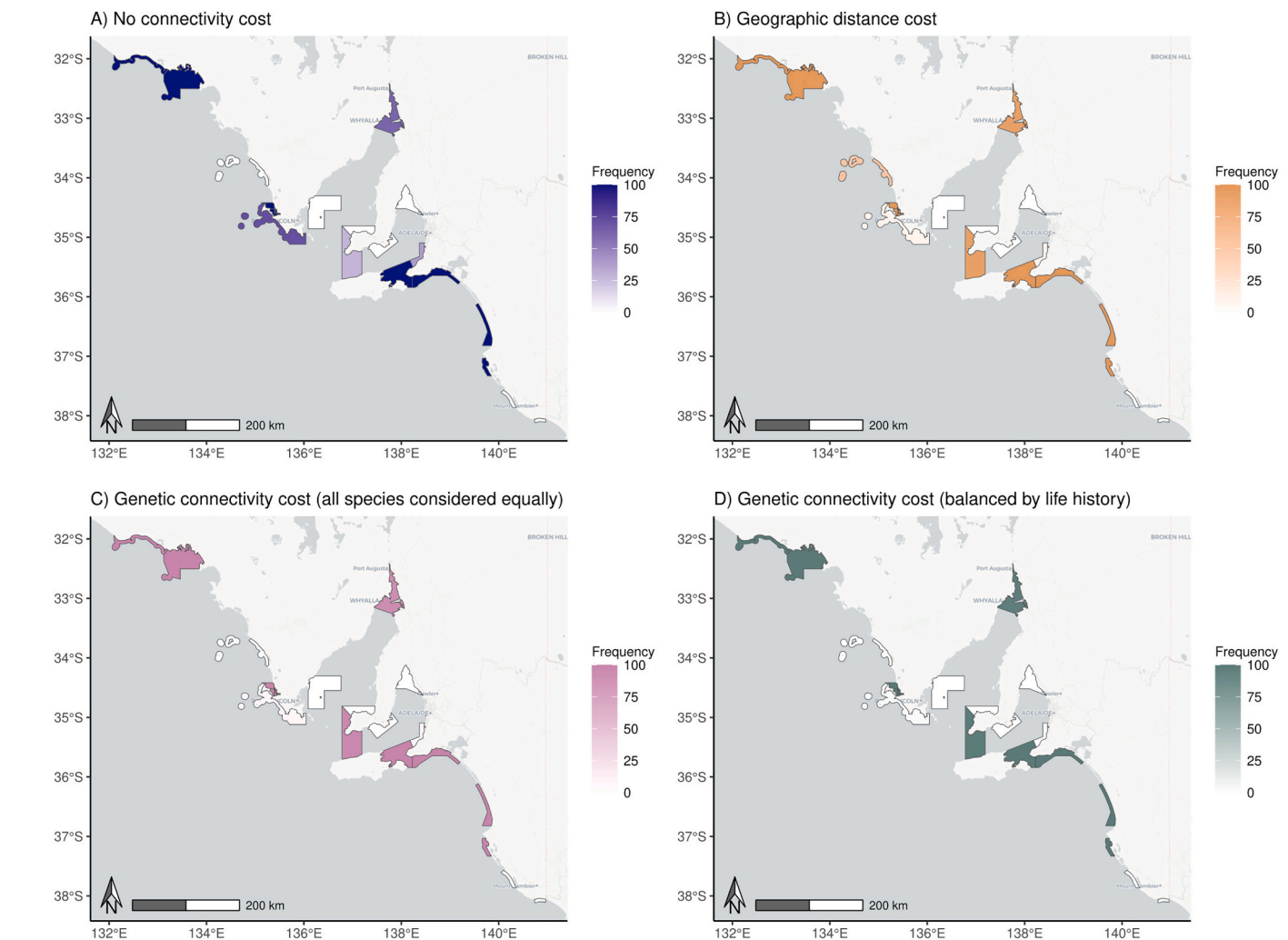


Fig. 6. Selection frequency of planning units (SARMPA marine park segments) using Marxan under 1,000,000 iterations and 100 replicates, in a hypothetical prioritisation scenario based on threatened species observation data. Results using various cost layer are presented, based on inverse node ‘betweenness’ values of distance-based connectivity networks. Cost layers were generated from connectivity networks based on A) (none included), B) direct waterway distances, C) genetic differentiation, with each species given equal weighting, and D) genetic differentiation, with weightings balanced between “larval dispersers” and “active dispersers”.

different cost layers in terms of both selection frequencies and best solutions. It is important to note that stricter thresholds sometimes resulted in solutions with fewer overall nodes, which may actually contradict efforts to increase overall connectivity.

4. Discussion

4.1. An approach for integrating genetic connectivity into MPA network planning

Our study presents an integrative approach to incorporate population connectivity in the planning and assessment of Marine Protected Area (MPA) networks. Focused on the South Australian Representative System of Marine Protected Areas (SARMPA), our case study leveraged population genetic data from multiple species with shared or nearby sampling localities to identify areas of shared importance for connectivity across the region. We found significant associations between connectivity and environmental factors, with waterway distances providing the best predictive power in combined-species analyses. This helps to validate the initial design assumptions of the SARMPA, which relied on spatial proxies of connectivity, and suggests that marine park strategies are likely contributing to the maintenance of ecological

processes in this system. Our findings extend previous multispecies connectivity research (e.g. Kelly and Palumbi, 2010; Toonen et al., 2011; Drew and Barber, 2012; Leiva et al., 2022) by aggregating and integrating multispecies connectivity metrics into broader analytical frameworks, including association testing against potential environmental correlates and spatial prioritisation alongside other conservation features using Marxan.

By conceptualising the sampled MPA zones as nodes in a network, we were able to evaluate their relative contributions to regional connectivity within the system. This evaluation encompassed measures of connectivity for all represented species and also allowed us to identify species clusters with greater spatial similarity of connectivity patterns. These clusters were only weakly associated, yet notably, there was a closer alignment of connectivity patterns among species with similar dispersal strategies, of either primarily active dispersal or primarily passive larval dispersal. This underscores the importance of selecting data from taxa that adequately represent the diversity of various life history traits when prioritising population connectivity in spatial conservation planning, and the need to balance any conflicting requirement among taxa.

A few previous studies have also assessed concordance of population connectivity across multiple species in marine areas, though generally at

the level of all available datasets, rather than specific subclusters. Drew and Barber (2012) used migration analyses of pooled mtDNA data of five Fijian reef fishes, but did not find consistent regional patterns among species. In contrast, Toonen et al. (2011) tested the significance of shared genetic breaks among localities for 27 diverse marine species, identifying four locations where species were more likely to share a break than randomly expected; in this case equivalent to a break identified in more than half the surveyed species. While the larger number of focus species may have improved detection, a similar result was produced in a more recent study of just five species (nemerteans, annelids and a sponge) using COI mitochondrial haplotypes (Leiva et al., 2022). Although focussed on the categorical existence of breaks in connectivity rather than on relative connectivity values across a spectrum, these examples also support the idea that important influences on connectivity may be shared among otherwise disparate taxa. This is potentially promising in the context of protected area network planning, since fewer conflicting priorities could result in fewer trade-offs to individual species' connectivity requirements if incorporated into spatial prioritisation frameworks like Marxan.

4.2. Connectivity within the MPA network

High effective network connectivity across all taxa across >2,000 km of coastline was consistent with general expectations for long-range dispersers (Waples, 1998), which could describe all included species. However, the Southern Spencer Gulf (Investigator Strait), Southern Spencer (Point Souttar), and the Lower Yorke Peninsula were the most important hubs of connectivity across *all species* networks. These nodes not only had the greatest number of strong connections with other nodes, but were also ranked highly for betweenness centrality, indicating their potential for gene flow relay between more disconnected areas (Kivelä et al., 2015). The two nodes provided links to the less connected gulf waters, and had relatively strong connectivity with distant MPAs, including the westernmost Nuyts Archipelago (for *larval dispersers*) and easternmost Upper South East and Lower South East (for all dispersal groups). Since the Investigator Strait represents a transition zone between gulf waters and pelagic (open) waters, this area may also represent high connectivity between inshore and offshore communities (Scientific Working Group, 2011). The existence of two MPAs in this area, including five sanctuary zones, is therefore positive for the maintenance of ecological connectivity across the SARSMPA network. A focus on monitoring and compliance should be a priority in this part of the network to maximise the protection of representative habitats and species.

High connectivity values may be influenced by hub nodes' orientation at the centre of a sampling range; however, this did not appear to apply to gulf waters, despite their relative longitudinal centrality. Lower average connectivity of the gulfs compared to surrounding nodes was consistent with influences of front formations at the gulf entrances, which is thought to allow accumulation of high densities of fish larvae in Investigator Strait during warmer months, but limits passive dispersal into the above gulf regions (Bruce and Short, 1990; Fowler et al., 2000). Gulf waters and embayments have been associated with higher site fidelity and residency in dolphins (Bilgmann et al., 2007; Möller et al., 2007; Fruet et al., 2014; Passadore et al., 2018). This may be a contributing factor in the particularly low connectivity of the *active dispersers* group between gulfs and the surrounding stretches of coastline. The stronger network clustering of *active dispersers* was also consistent with high site fidelity in the gulf waters. At network thresholds above percolation (i.e., if the weakest links in the network were to be removed), network breakdown would likely first occur between the two gulf-associated subclusters. In the passive advection models generated for each season, gulf nodes also had lower than average connectivity, which may reflect a mechanistic link between genetic and biophysical findings.

4.3. Environmental correlations and potential drivers of connectivity

We hypothesised that patterns of genetic connectivity would be associated with variations in geographic distance and oceanographic circulation, which was supported by strong associations with direct waterway distance and spring advection connectivity for the *all-species* dataset. However, at this level, advection models did not improve predictions over distance alone. We also found that the best explanatory variables were not shared among life history groupings (*active dispersers* versus *larval dispersers*). This is consistent with their divergent clustering in the genogeographic analysis and again highlights the importance of adequately representing divergent taxa in spatial planning.

Unexpectedly, we found that advection connectivity better predicted the connectivity of *active dispersers* than *larval dispersers*. Given that advection models were approximated from life history considerations of the snapper, limpet, and nerite, we hypothesised that advection models for these species might outperform predictions based on distance alone. We were interested in testing the ability of generalised projections to explain biological variation, since detailed life history information is absent for many marine invertebrates and species data used in biophysical models are often broad or even hypothetical, (e.g., Magris et al., 2016; D'Aloia et al., 2017). The underperformance here for *larval dispersers* could potentially relate to under-parameterisation of the model, and we would therefore recommend favouring species-specific advection models to maximise precision if the data is available (sensu North et al., 2009). However, mismatches between even species-specific biophysical models and genetic differentiation are not uncommon (Jahnke and Jonsson, 2022), and the underperformance could alternatively relate to difficult-to-characterise factors such as spatiotemporal variations in habitat characteristics, mating and recruitment success, or barriers in the intervening matrix (Hedgcock, 1994; Banks et al., 2007; Teske et al., 2015). These factors have been among the hypothesised drivers of 'chaotic genetic patchiness' sometimes observed in marine larval dispersers (Johnson and Black, 1982; Broquet et al., 2013; Eldon et al., 2016).

Equally interesting was the strong explanatory power of the spring advection model for the *active dispersers*' connectivity, despite its design for larval predictions. Although these findings could be considered counterintuitive by some, strong associations between population connectivity and meso- and fine-scale oceanographic processes have been reported for multiple active dispersers around the world (Luschi et al., 2003; Bilgmann et al., 2007; Möller et al., 2011; Amaral et al., 2012; Rodríguez-Zárate et al., 2018; Barceló et al., 2022; Pratt et al., 2022). For instance, a global study of common dolphins (Amaral et al., 2012) showed that differences in sea surface temperature, primary productivity and water turbidity across oceanographic interfaces better explain population connectivity than geographical distance alone. On the east coast of Australia, connectivity in common dolphins is better explained by the presence of three distinct coastal water masses than by spatial distance or biogeographic barriers (Möller et al., 2011). Along our study region, variation in current velocity, sea surface temperature and salinity due to mesoscale oceanographic circulation, seasonal upwellings, and on-shelf circulation are key factors influencing genetic differentiation and adaptive divergence between populations of both bottlenose (Pratt et al., 2022) and common (Barceló et al., 2022) dolphins. For sea turtles, biophysical modelling has shown that currents and dynamic ocean features (e.g. eddies) have a remarkable influence on movements to and between feeding grounds (Luschi et al., 2003) and provide different cost-benefit solutions and selective pressures during both the mating and migration periods (Rodríguez-Zárate et al., 2018). These studies point to the roles of coastal oceanographic processes in modulating population connectivity in active dispersers and influencing their patterns of local adaptation, feeding, reproductive and other behavioural specialisations.

Overall, the idiosyncrasies among species appear to have limited the generalisability of broad biophysical modelling estimates. However,

including more species would increase the representativity of multi-species connectivity estimates, and possibly improve statistical power to detect relationships between species clusters and generalised advection models by reducing the effect of stochastic events (e.g. [Liggins et al., 2013](#)). For now, we would encourage the use of species-specific information to inform larval dispersal models whenever possible. And, since advection models are being increasingly applied to connectivity estimates based on general dispersal traits rather than empirical data about included species (e.g. [Jonsson et al., 2016](#); [Bray et al., 2017](#); [Roberts et al., 2021](#)), we further encourage calibration of such models with information about the realised genetic connectivity of local species ([Faillietaz et al., 2018](#); [Bode et al., 2019](#)).

4.4. Spatial prioritisation planning

We found that connectivity affects the planning unit selection frequency and best solutions when incorporated into Marxan prioritisation as a cost value alongside other biodiversity values. In all runs using unthresholded connectivity costs, the tool was more likely to prioritise planning units identified as ‘connectivity hubs’, while still solving the minimum set problem using the same number of PUs. This supports the idea that incorporating connectivity as a cost alongside other conservation features may help to identify solutions that strike a balance between conserving species or habitats of high ecological importance while maintaining or improving landscape connectivity ([Beger et al., 2014, 2022](#); [Andrello et al., 2022](#)).

The high level of consistency among these runs when using alternative cost layers (equal species, balanced life histories, or geographic distance) was interesting given the incomplete explanatory power of isolation-by-distance on genetic differentiation in the RDAs. While geographic distance alone evidently cannot provide a precise quantification of biological connectivity, consistency in spatial prioritisation scenarios suggests that it may still be a valuable heuristic in conservation planning and management efforts when biological data is unavailable. Since genetic connectivity estimates were not available during the initial design of SARMPA, the pragmatic choice of planning habitat inclusion across ‘local, regional, and provincial’ spatial scales ([DEH, 2008](#)) is fairly well supported here. However, it’s worth noting that the results produced by different cost layers are likely to differ across a range of conservation feature targets, which were not within the scope of this study to test. Additionally, irreplaceability of planning units could limit the flexibility of possible solutions, and is likely to have applied to at least two sites in this study due to limited distributions of some conservation features (threatened species). Since inflexibility of PUs can lead to trade-offs with costs ([Levin et al., 2015](#)), it’s important to thoroughly interrogate the responsible observation data in applied planning studies to ensure that irreplaceability is not being inferred from observational errors or sampling biases.

Another consideration for input parameters is the inclusion of cost thresholds. Since the node-based connectivity values used in this study are relative and are not necessarily additive among sites, it was not possible to directly budget for specific levels of connectivity ([Beger et al., 2022](#)). However, we still chose to test a small sample of cost thresholds, since these might highlight trade-offs with the included conservation features (e.g. [Cameron et al., 2008](#)). We found that increasingly strict cost thresholds resulted in a greater divergence of solutions produced under different cost layers, which is intuitive if conservation priorities were obscuring modest differences among cost layers. We also found that stricter cost thresholds were effective in reducing total connectivity costs, however it’s critical to note that this was sometimes achieved by simply dropping a planning unit from the best solution, rather than by replacing high-cost planning units (low connectivity nodes) with low-cost planning units (high connectivity nodes). Since higher cost planning units don’t actually reduce connectivity in their own right (and likely still provide some benefit to connectivity), simply excluding them in order to fit cost thresholds runs

counter to the aims of the process. We therefore suggest against using cost thresholds to determine best solutions unless there is a very clear reason for doing so and the implications are well understood. In such a case, it might be helpful to adjust conservation feature targets to achieve a minimum number of PUs (perhaps by assigning a dummy ‘species’ with equal value in all PUs and a strong penalty factor for not achieving minimum coverage).

Finally, it is important to be able to balance costs, not just against conservation features, but within cost layers. For instance, although we found that best solutions were equivalent for the ‘equal species’ and ‘balanced dispersal clusters’ cost layers, there was still variation in the selection frequencies across replicate runs. Due to the differences in connectivity patterns established among life history subclusters, and their slightly uneven sampling representation, we suggest that the cost layer with ‘balanced’ representation of both *active dispersers* and *larval dispersers* should provide the least bias. It becomes more challenging in cases where additional unrelated costs must be incorporated (for example monetary costs), especially since they are likely to be measured in different units. [Cameron et al. \(2008\)](#) illustrate workable options for this, either applying multicriteria methods to standardise cost units by weight before combining them into a single cost index, or, alternatively, running prioritisations for each opportunity cost and then combining solutions into a single weighted sum. The choice of a specific weighting scheme will be highly dependent on the context, goals, and constraints of the system in question, which have been reviewed under different applications by [Ban and Klein \(2009\)](#).

4.5. Limitations and further recommendations

This study was designed to capitalise on existing genetic information spanning an MPA network. However, an important limitation was the number of datasets available from this region, which we acknowledge increases the risk of taxonomic or life history-related biases, especially at nodes with incomplete overlap of sampling efforts. Multiple analytical steps were taken to reduce possible biases; however, the distinctness of species-specific connectivity patterns suggests that a broader representation of species may be needed to fully capture the range of connectivity profiles. Further, more intensive sampling could strengthen statistical power for inferring environmental influences on species clusters, even if general trends remain consistent with those reported here. Our recommendations for future studies therefore include maximising both the number and variety of taxa and the overlap of sampling localities, ideally with an understanding of whether missing node data are due to previous sampling strategies or genuine absence. If enough funding is attainable, it may be possible to supplement these data with sampling tailored to address the deficiencies identified in a particular region, as well as gaps in biological data necessary for biophysical model parameterisation (e.g. [North et al., 2009](#); [Liggins et al., 2013](#); [Bode et al., 2019](#)).

This study addresses a specific case where marine parks were already established; however, a similar approach could be used in the initial planning designs with a few considerations. Conceptualising sampling localities as nodes is useful in that it allows network analysis, but it does not provide information distributed across a geographic matrix. To allow assessment of the entire area, interpolation can be used to estimate a finer resolution of connectivity-related conservation values, for example as by [Duforet-Frebourg and Blum \(2014\)](#), [Wilcox et al. \(2023\)](#). Efforts to enhance collaboration among researchers, curators, and data providers should further facilitate the compilation of standardised, multi-species genetic datasets to provide broader coverage across planning regions.

Although the opportunity for incorporating genetic connectivity into planning strategies for the initial SARMPA design was limited, our results support the appropriateness of the chosen proxies in the planning framework. The current distribution of Marine Parks is therefore expected to help maintain ecological processes associated with

connectivity, supporting ecosystem resilience. As outlined by Bryars et al. (2017), a Before-After-Control-Impact design would be optimal for assessing the ongoing contribution of marine park strategies to ecological functioning. The results of this study act as an important baseline, but cannot inform about temporal changes since the establishment of the SARSMPA, and ongoing monitoring and evaluation should be a continued priority. Additionally, while the results support the usefulness of spatial proxies in connectivity planning, there remains great scope to extend connectivity assessments for a more comprehensive understanding of spatial, temporal, and biological influences on linkages within this network, and marine connectivity more broadly. In the face of climate change and increasing anthropogenic pressures, continued integration of biological and physical data will be invaluable to the sustainable management of marine ecosystems.

CRedit authorship contribution statement

Katie Gates: Writing – original draft, Methodology, Formal analysis. **Jonathan Sandoval-Castillo:** Methodology, Formal analysis. **Andrea Bertram:** Data curation. **Eleanor A.L. Pratt:** Data curation. **Peter R. Teske:** Data curation. **Luciana Möller:** Supervision, Investigation, Funding acquisition, Data curation, Conceptualization. **Luciano B. Beheregaray:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data supporting this study are derived from the following publicly available sources:

<https://figshare.com/s/683409860163e2d08e75>.
<https://doi.org/10.6084/m9.figshare.19100609>.
<https://doi.org/10.6084/m9.figshare.22339921>.
<https://doi.org/10.5061/dryad.n9v91>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110759>.

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