

# REPORT

## ASSESSING AND FORECASTING MULTISPECIES CONNECTIVITY ALONG THE NETWORK OF MARINE PARKS IN SOUTH AUSTRALIA

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15<sup>th</sup> August 2022 (revised November 2022)

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## **Executive summary**

Connectivity is affected by a complex range of biological and oceanographic factors. Here, we assessed multispecies connectivity across SA marine parks by integrating existing genetic and genomic datasets from taxa with varying life histories. Further, we evaluated potential spatial and oceanographic influences on connectivity and their relevance under climate change. We found that connectivity varied significantly among all included species, but patterns were more similar among species with shared life history strategies. Of 16 sampled localities, we found that sites within Encounter, Lower Yorke Peninsula, Southern Spencer Gulf, and Sir Joseph Banks Group Marine Parks had the greatest number of strong connections within the network. Southern Spencer Gulf and Lower Yorke Peninsula were perhaps the most important connectivity hubs, given high betweenness values indicating their functions as links between more disparate population clusters. We found that population genetic differentiation (i.e., reduced connectivity) across all species was closely associated with spatial distance, affirming the importance of proximity as a metric for planning and evaluations of MPA networks. We also found strong associations with oceanographic advection models. However, these models did not have better predictive power than spatial distances in multispecies analyses. This finding may indicate the need to incorporate more in-depth information about oceanographic influences for each study species. The results of the present study should act as a baseline for ongoing assessments and further support the usefulness of spatial proxies in connectivity planning.

## Introduction

Ecosystem connectivity is an integral aspect of planning design in protected areas networks, affecting the structure, function, and dynamics of populations and communities (Carr et al. 2017, Grummer et al. 2019). As such, it is one of the biophysical design principles established to guide the development of the South Australian Representative System of Marine Protected Areas (SARSMPA), which aims to maintain ecological processes and contribute to the long-term ecological viability of marine and estuarine systems in South Australia (DEH 2008, Bryars et al. 2017). An understanding of ecosystem connectivity is also necessary to inform ongoing adaptive management and can be considered under key evaluation questions (KEQs) in the Marine Parks Monitoring, Evaluation and Reporting Program (MER; Bryars et al. 2017). These include KEQ 2, “to what extent have marine parks strategies contributed to the maintenance of ecological processes?”; and KEQ 3, “to what extent have marine parks strategies contributed to enabling marine environments to adapt to impacts of climate change?” However, focussed, broad coverage studies of connectivity have so far been limited across the South Australian Marine Parks Network (see review by Jones et al. 2018), making both planning and evaluation of management strategies difficult.

While connectivity can describe the transport of any items between areas of a network, population connectivity, the focus here, refers to the dispersal of individuals between spatially separated populations or subpopulations (Tremblay et al. 2008, Cowen and Sponaugle 2009). This is of primary concern for 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). Population connectivity also permits the spread of genetic diversity, affecting evolutionary viability and adaptive resilience to changing environments (Hoffmann and Sgro 2011, Frankham et al. 2017). The dynamic nature of population connectivity makes it a complicated concept to observe or incorporate into marine park strategies (Jones et al. 2007, Sale et al. 2010), and SARSMPA design principles have largely relied on spatial scales as a surrogate for measurable connectivity (DEH 2008). However, many different approaches are emerging to improve the

characterisation of marine connectivity patterns. Some of the most powerful and promising include genetic modelling, oceanographic modelling, and the integrated analysis of the two.

Ocean currents facilitate the passive dispersal of a large number of marine species (Cowen and Sponaugle 2009) and are likely to affect population structuring of active dispersers due to influences on local habitats and their prey (Möller et al. 2007, Hays 2017). Connectivity patterns may therefore be better reflected by ocean advection models than by simpler measures of spatial proximity (e.g., Xuereb et al. 2018). However, since connectivity may also be affected by other aspects of local biogeography, empirical observations are required for ‘ground-truthing’ or validating advection connectivity estimates in regions of interest (Siegel et al. 2003, Kool et al. 2013). Where this is possible, oceanographic models can also be projected to incorporate information about future climate scenarios (Coleman et al. 2017). This could provide a critical understanding of connectivity changes and outcomes for demographic resilience in a warming climate. Genetic and genomic tools are of great value here, enabling empirical measurement of population structure and connectivity for species sampled across multiple localities. Rather than being limited to individual and potentially stochastic dispersal events (e.g., tagging studies, etc.), genetic information also has the advantage of capturing patterns of both short- and long-term demographic exchange. While genetic connectivity and population structure are being studied in a growing number of South Australian marine taxa, these have typically focussed on a single study species, and with limited individual coverage of the SARMPA (Jones et al. 2018).

To address these gaps, we took a meta-analytical approach to assess the connectivity of multiple species along the South Australian network. We re-analysed existing genetic and genomic datasets in an integrative framework to provide information about connectivity patterns across SARMPA, relative variation among life history types, and the possible relevance of spatial and oceanographic factors.

## Objectives

The objectives of this report were to characterise and map multispecies connectivity across the SARSMMPA, including 11 of 19 Marine Parks. Meta-analysis of available population genetic and population genomic datasets using graph theory provides broad coverage of the state-wide network, including the majority of representative bioregions. Further, we aimed to provide statistical evaluations of potential geographic (i.e., spatial) and oceanographic effects on connectivity across the network, and discuss implications for ecosystem function and resilience. This includes key evaluation questions (KEQ) listed in the South Australian Marine Parks Monitoring, Evaluation and Reporting Plan (Bryars et al. 2017):

- KEQ 2: To what extent have marine parks strategies contributed to the maintenance of ecological processes?
- KEQ 3: To what extent have marine parks strategies contributed to enabling marine environments to adapt to the impacts of climate change?

## Methods

### *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 SARSMPA, with >3 South Australian sampling localities. This was further narrowed to include only the two most common marker types used in population genetic analyses; microsatellites (genetic markers), and single nucleotide polymorphisms (SNPs; genomic markers). While SNPs have greater precision in many applications, high concordance is generally expected for estimates of genetic diversity and population structure between these markers (Zimmerman et al. 2020), enabling us to take advantage of both data types. For microsatellites, we used the full datasets described in the original publications (Teske et al. 2015, 2016, Teske et al. 2017). For SNP data, there is an assumption that variation of genotypes among individuals can be either neutral (i.e., having no effect on fitness), or adaptive (i.e., affecting fitness or survival, and influenced by natural selection). Given that variation under local environmental selection may bias demographic inferences, we used datasets from which putatively adaptive variants had already been removed (as described in Barceló et al. 2021, Pratt et al. 2022, and Bertram et al. 2022).

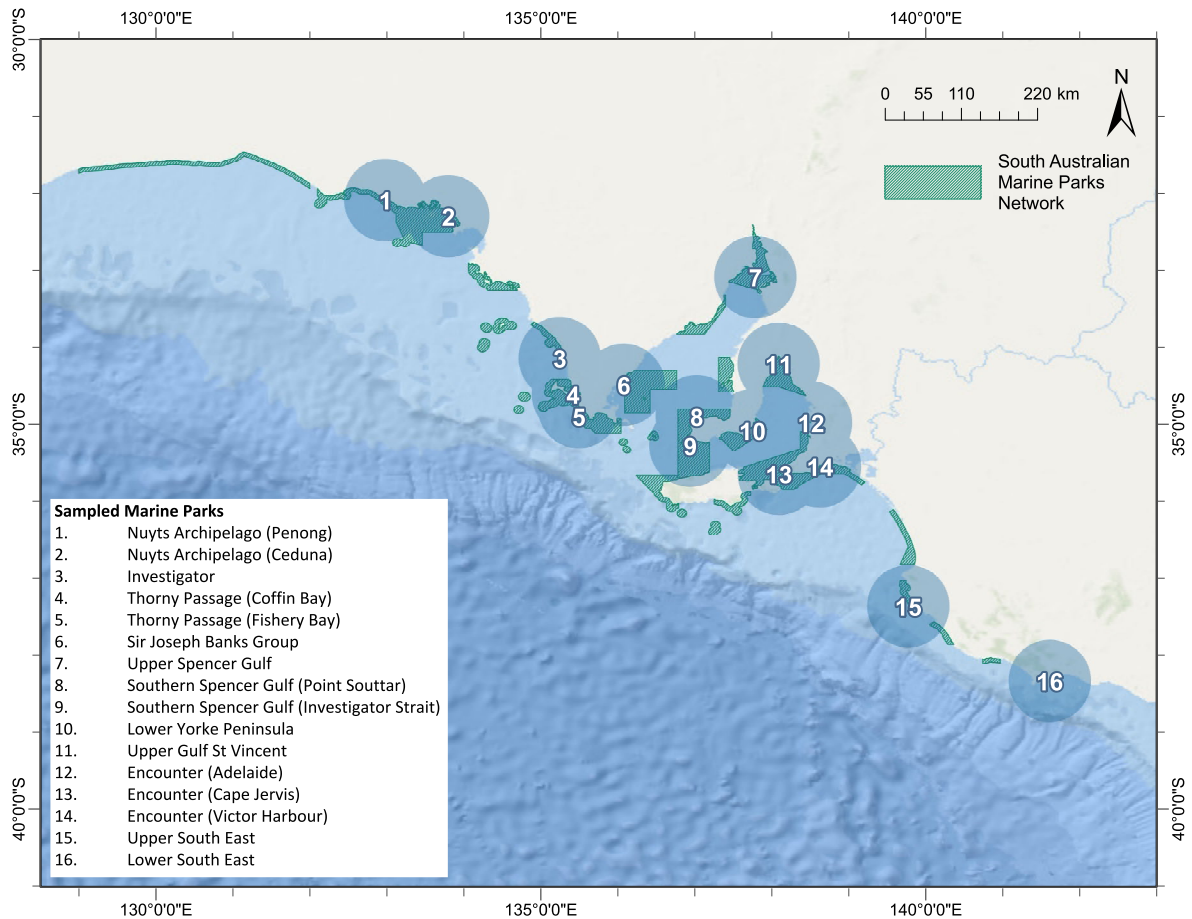
Data selection criteria were met for five high-quality datasets for species previously studied in the Molecular Ecology Lab at Flinders University (MELFU) (Table 1). Outside of these, we did not find publicly available genetic datasets with both sufficient accompanying information (e.g., location data) and at an appropriate sampling scale. Species included were two iconic and legally protected cetaceans (the common dolphin, *Delphinus delphis*, and the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*), a commercially and recreationally valuable teleost (snapper, *Chrysophrys auratus*), and two ecologically important intertidal invertebrates (the siphon limpet, *Siphonaria diemenensis*, and the black nerite, *Nerita atramentosa*) (Figure 1).



**Figure 1.** Study species, left to right. Top: *Delphinus delphis* (Common dolphin, image: CEBEL), *Tursiops aduncus* (Indo-Pacific bottlenose dolphin, image: CEBEL). Bottom: *Chrysophrys auratus* (Australasian snapper, image: David Harasti), *Siphonaria diemenensis* (Van Diemen's siphon limpet, image: Museum Victoria), *Nerita atramentosa* (black nerite snail, image: Luciano Beheregaray).

From the datasets, we defined sixteen sampling sites across South Australia (Figure 2). We based these on sites described in original publications, retaining unique intra-species sampling localities (Supplementary Figure 1), but aggregating proximal inter-species localities to allow for combined analyses. The localities have coverage in 11 of 19 General Managed Use Zones, and are also likely to reflect connectivity processes affecting Sanctuary Zones at a macro level. Not every included sample was collected from within SARSMPA zoning, however we expect that the increased spatial coverage resulting from their inclusion should allow better detection of regional influences on marine park connectivity, especially when considered across multiple taxa. For some of the species, genetic data was also available from outside South Australia. While its inclusion could improve inferences about species-specific processes (addressed in the source publications), large differences in interstate sampling ranges could also introduce taxonomic biases when used for more general inferences. We therefore excluded these localities, with the exception of Portland (Locality 16). Fortunately, this site was sampled for four of the five species, and could provide data relevant to the nearby but sparsely sampled Lower South East.





**Figure 2.** Sampling localities across the South Australian Marine Parks network based on aggregated data from five species, *Delphinus delphis*, *Tursiops aduncus*, *Chrysophrys auratus*, *Siphonaria diemenensis*, and *Nerita atramentosa*.

### *Spatial analyses of connectivity across and within the marine parks network*

Genetic information was used to quantify population differentiation for each species on a locality-specific basis, as well as pairwise among sampling sites (locality-specific  $F_{ST}$  and pairwise  $F_{ST}$ , respectively). Locality-specific  $F_{ST}$  estimates the uniqueness of the ancestry at each locality, 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 (RC

Team 2019), which handles both SNP and microsatellite data. Meanwhile, pairwise  $F_{ST}$  estimates differentiation between pairs of localities resulting from population structure (Weir and Hill 2002), and is therefore useful for exploring patterns of divergence across networks. This statistic was already calculated for each species in the source publications, however, since it was an optional output of the network analysis using EDENetworks (Kivelä et al. (2015); further described below), we preferred to use these output values to improve analytical consistency among the study species.

To assess the extent to which patterns of connectivity were either shared or idiosyncratic among the included taxa, we used a ‘genogeographic’ clustering method (Arranz et al. 2022) to capture relationships between genetic variation and distance along the SA coastline for each species. Coastal distances were first calculated in ArcMap (ESRI 2011) by snapping sampling coordinates to the nearest segment of the Australian Shoreline layer (Geoscience Australia), and calculating the length of all segments between sampling sites. Then, using R code adapted from Arranz et al. (2022), coastal distances were plotted against locality-specific  $F_{ST}$  values. Curves were fitted to the data points using maximum likelihood to characterise each species’ spatial trends, and were represented as colour maps depicting variation in genetic divergence along the coast. Fitted curves were scaled and centred, and finally clustered across species to identify similarity of spatial patterns. Parametric bootstrapping (1000 replicates) of species clustering was used to find the best dendrograms (groupings) of similar species, and to assess statistical significance of joins and splits.

### *Generation and analysis of connectivity networks using a graph theory approach*

We used a network approach to summarise patterns of connectivity structure, including for a combined “*all species*” dataset, as well as for 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. In each network, nodes (connection points) corresponded to sampling localities, while edges (links among nodes) were calculated as

pairwise  $F_{ST}$  values (Reynolds Distance). We exported the resulting distance matrices, before scaling, centring, and averaging species values for each combined network. Resulting distance matrices were then re-imported to EDENetworks for analysis of the combined networks. We derived 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 just below percolation, that is, the point at which a connected network would begin to fragment into smaller components. Given the generally strong dispersal ability of the included study species, the chosen threshold is likely lower than real-world thresholds for these species. However, these thresholds provide an overview of the strongest and weakest pathways in each network, clarifying which localities may be likely to become disconnected if overall connectivity is reduced, and which may be likely to act as pathways between less connected regions. We calculated network characteristics and node values for each of the thresholded networks, and produced circle plots using the R package CIRCLIZE (Gu et al. 2014).

### *Spatial and oceanographic modelling of connectivity in the SARMPA network*

To assess the relative importance of spatial distance and oceanographic factors on genetic differentiation across the network we tested correlations between pairwise genetic differentiation and environmental variables of interest. First, we calculated pairwise values among all localities for spatial distance (direct waterway distances and coastal distances); latitudinal distance; and simulated estimates of advection connectivity (single dispersal event and steppingstone). Direct waterway distances refer to the shortest route between two sites without crossing land, and were calculated using the *viamaris* function in MELFUR (<https://github.com/pygmyperch/melfuR>). Coastal distances (described above for genogeographic clustering) represent the shortest route between two sites while following the coastline and might reflect migration paths of species with nearshore habitat preferences. Latitudinal distance was calculated as the difference (in decimal degrees) in latitude between locality pairs, and could have indirect effects on marine dispersal potential (Álvarez-Noriega et al. 2020). Finally, ocean circulation has a critical role in transporting passively dispersing species (Mileikovsky 1968, Roberts 1997), and

has also been associated with population structure of active dispersers such as dolphins and sea turtles, possibly due to influences on prey availability or thermal gradients (Bilgmann et al. 2007, Möller et al. 2011, Rodríguez-Zárate et al. 2018).

To estimate pairwise advection connectivity between localities, we used 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  $0.5^\circ$  of the 2D velocity fields (eastward and northward) at 5m depth, from 1994 to 2014. The resulting connectivity matrices show how many particles (e.g., larvae) released from each locality are expected to settle within the same or another sampling locality. We created four matrices representing each season (spring, summer, autumn, and winter). For each model, we released 1,000 particles per sampling site per day during the three-month seasonal period (a total of 1,800,000 particles per site 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 larval durations of the included study species (Table 1). The particle locations were recorded every 3 hours, whereupon it was determined whether they settled or died. A particle was considered settled when, for the first time, their location intersected with in the  $1^\circ$  semicircle surrounding a release site. Because values differed by several orders of magnitude among localities, estimates were corrected to their natural logarithm. Following the methods of Teske et al. (2015), 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 localities after four successive reproductive cycles.

We used redundancy analyses (RDAs) in VEGAN (Oksanen et al. 2019) to test relationships between these variables and the genetic differentiation among localities (pairwise  $F_{ST}$ , as used in network analyses). Since RDAs do not handle missing data, and since not all localities 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 component (PCs) of genetic variation. Separate RDAs were then performed for respective environmental variables, where environment acted as an independent/explanatory variable, and genetic PCs acted as a response. As with the network analyses, this was performed for a combined *all species* dataset. We also then repeated analyses for 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.

## Results

### *Spatial connectivity along the network for a range of taxa*

Based on the available species’ datasets, we found relatively high connectivity across SARSMPA (Figure 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), then limpets (0.027). Population structure was only slightly greater in common dolphins (0.028) but was substantially greater in bottlenose dolphins (0.090).

Not only did these magnitudes of genetic structure seem to differ with dispersal strategy, but spatial patterns of connectivity were also the most divergent between *larval dispersers* and *active dispersers*. Genogeographic clustering (Figure 4a; Supplementary Figure 2), based on locality-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 SA coastline (Figure 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, it is also important to mention that within these species’ clusters, associations between pairs of species were not statistically significant ( $p = 0.482-0.597$ ).

Siphon limpets were a particularly poor fit 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.

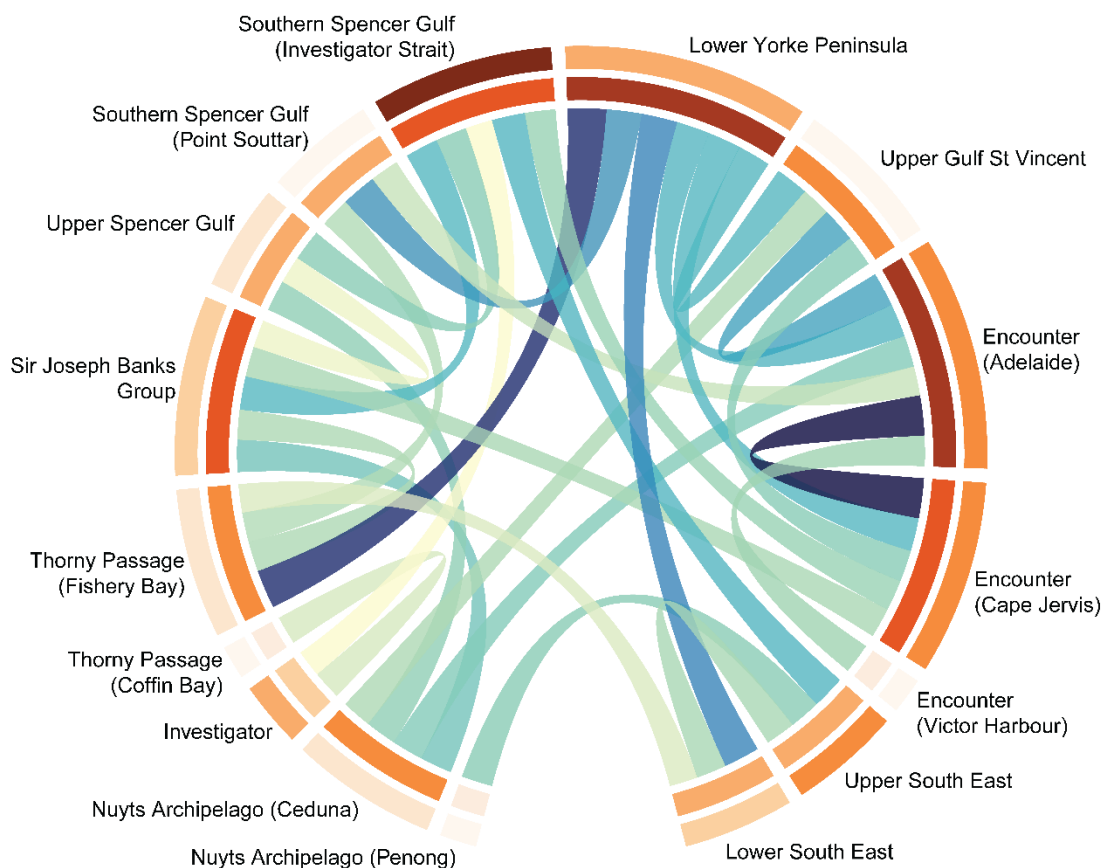
**Table 1.** Sampling information and population genetic differentiation for five species included in the meta-analysis of South Australian Marine Parks network connectivity. SNP = single nucleotide polymorphism (genomic marker). Microsat = microsatellite (genetic marker). N sites = number of SA localities sampled; N indivs = total number of individuals;  $F_{ST}$  = fixation index representing pairwise genetic differentiation among localities; scale ranges from 0 (no genetic differentiation) to 1 (complete genetic differentiation).

Species	Taxon class	Data source	Data type	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)	SNP	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)	SNP	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. (in preparation)	SNP	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)	Microsat	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)	Microsat	9	373	Larval dispersal ~4 months	0.005-0.013 (0.009)

### Network characteristics

At the maximum threshold below percolation (fragmentation of the network), network analysis for the combined *all species* dataset produced a network with 16 nodes (localities), 28 edges (links among

localities), and an average node degree (number of connections per node) of 3.5 (Figure 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 Lower Yorke Peninsula and Encounter (Adelaide) localities, 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 Harbour). 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). Betweenness centrality is defined as the number of shortest paths between other nodes which must pass through the node in question (Garroway et al. 2008), and can therefore indicate essential pathways linking subclusters in a network.



**Figure 3.** Average connectivity network for all species (*Delphinus delphis*, *Tursiops aduncus*, *Chrysophrys auratus*,

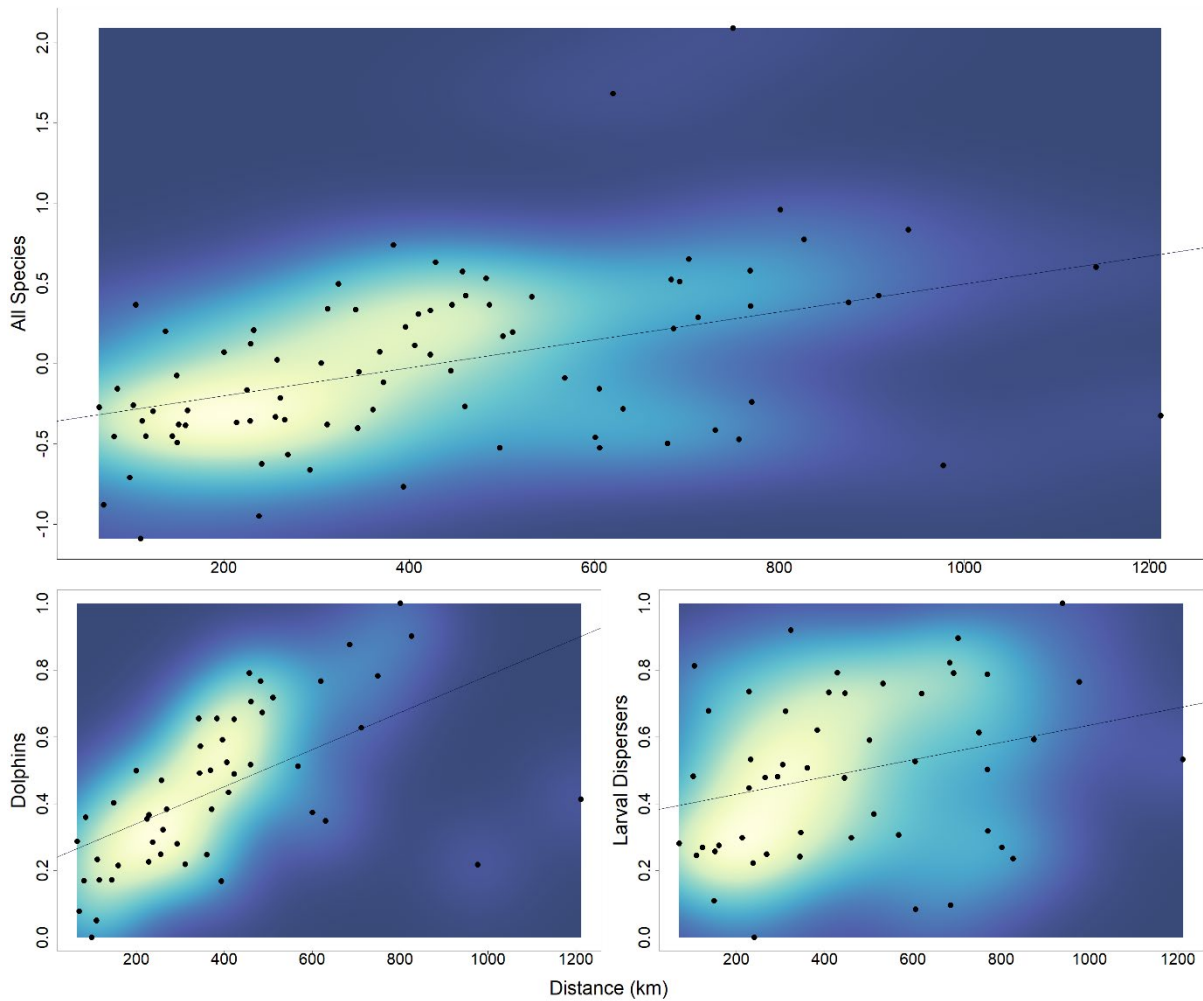
*Siphonaria diemenensis*, and *Nerita atramentosa*) among sampled marine parks, showing the maximum distance threshold for a fully connected graph. For edges (links in the network), relative pairwise connectivity among nodes is indicated by the degree of shading of the links, with the lightest (yellow) indicating lowest connectivity, and 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).

We also conducted network analyses for active and passive dispersal clusters identified by the genogeographic clustering (Figure 4c). Note that these networks each contained only 12 localities (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 locality with six connections in the full group, however in the reduced group, three other localities also had node degrees of 6 (Encounter (Adelaide), Southern Spencer Gulf (Point Souttar), and Sir Joseph Banks Group). Lowest node degrees for both groups were in Encounter (Victor Harbour) and the Upper South East, as well as Investigator in the full larval group.

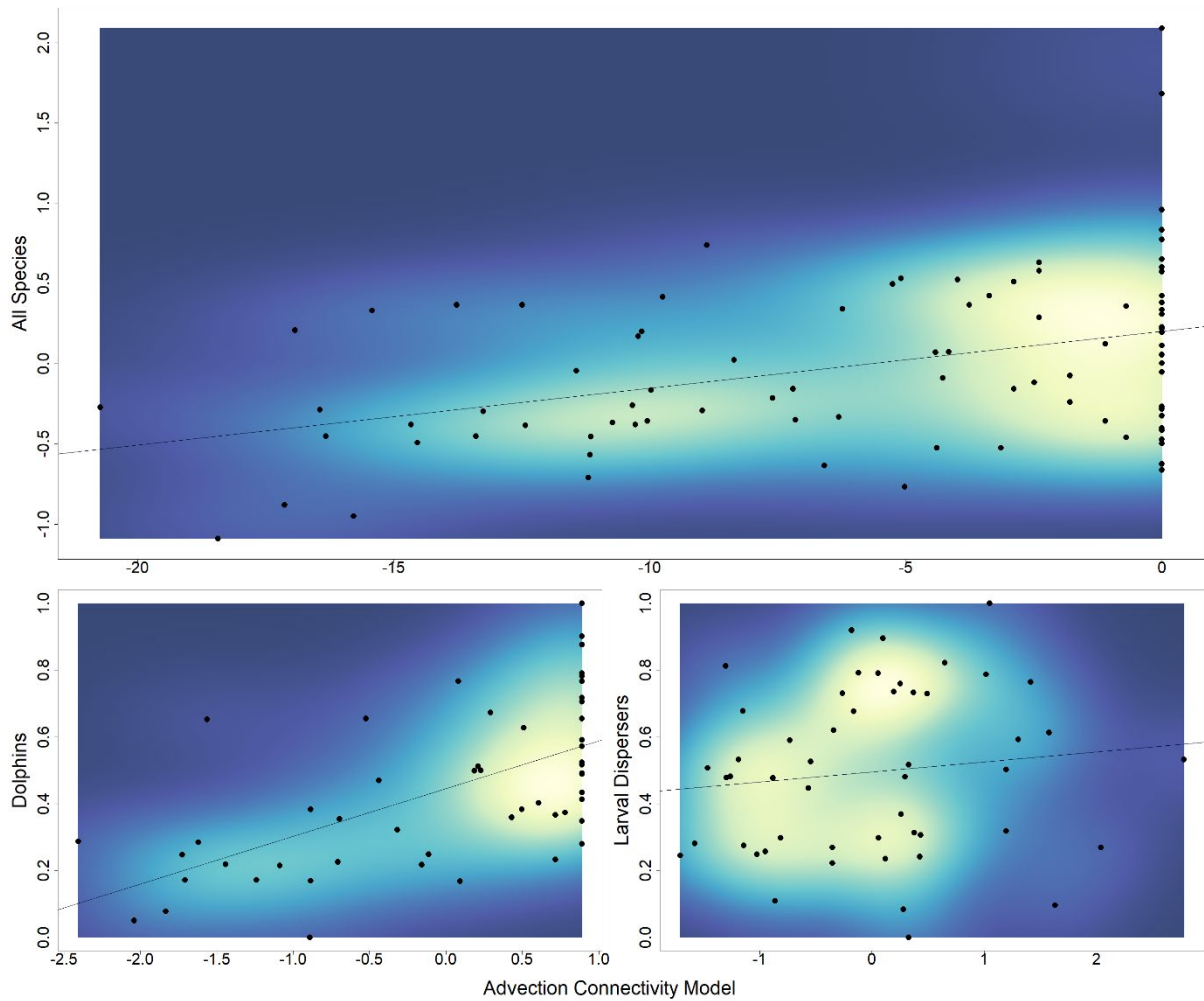




variation of genetic PC1, ( $p = <0.001$ ; Figure 5a, Supplementary Table 3). Spring advection was also a good model for predicting genetic connectivity (associated with 14.9% variation, ( $p = <0.001$ ); Figure 6a). While considering these distance and advection variables together could potentially improve predictive power, we also found high autocorrelation between the two (-0.58, Supplementary Figure 3), indicating that combining them could artificially inflate the strength of the models. When considering species by their dispersal clusters, we found that 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, associated with 36.8% of observed genetic variation ( $p = <0.001$ , Figure 6b), followed by direct waterway distances, associated with 33.3% of variation ( $p = <0.001$ , Figure 5b). For the *larval dispersers*, direct waterway distance was the only variable significantly associated with genetic connectivity (8.1% of variation,  $p = 0.043$ , Figure 5c). The advection model with the greatest explanatory power was autumn (1.5%,  $p = 0.386$ , Figure 6c), however this was also the variable most highly correlated with distance, which could explain the stronger effect.



**Figure 5.** Relationships between waterway distances (km) and population differentiation among South Australian localities, based on multispecies genetic values (first principal component of pairwise  $F_{ST}$ ). Scatterplots show line of best fit under a linear regression. Top, “All Species” ( $r^2 = 0.185$ ,  $p = <0.001$ ), includes integrated data from the common dolphin (*Delphinus delphis*), Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), snapper (*Chrysophrys auratus*), siphon limpet (*Siphonaria diemenensis*), and nerite (*Nerita atramentosa*). Bottom left, “Dolphins” ( $r^2 = 0.333$ ,  $p = <0.001$ ), includes data only from *D. delphis* and *T. aduncus*. Bottom right, “Larval Dispersers” ( $r^2 = 0.081$ ,  $p = 0.043$ ), includes data only from *C. auratus*, *S. diemenensis*, and *N. atramentosa*.



**Figure 6.** Relationships between best fitting advection connectivity models and population differentiation among South Australian localities, based on multispecies genetic values (first principal component of pairwise  $F_{ST}$ ). Scatterplots show line of best fit under a linear regression. Advection values are summed pairwise estimates (displayed negatively for ease of comparison with distance models, Fig. 4). Top, “All Species” ( $r^2 = 0.149$ ,  $p = <0.001$ ), shows spring advection, against integrated data from the common dolphin (*Delphinus delphis*), Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), snapper (*Chrysophrys auratus*), siphon limpet (*Siphonaria diemenensis*), and nerite (*Nerita atramentosa*). Bottom left, “Dolphins” ( $r^2 = 0.368$ ,  $p = <0.001$ ), shows spring, against data only from *D. delphis* and *T. aduncus*. Bottom right, “Larval Dispersers” ( $r^2 = 0.015$ ,  $p = <0.386$ ), shows autumn advection, against data only from *C. auratus*, *S. diemenensis*, and *N. atramentosa*.

## Discussion

### *Marine parks and the maintenance of ecological processes in SA waters*

Connectivity and linkage are essential for maintaining ecological processes in marine park networks, where they may help facilitate adaptation and resilience to environmental change. Assessments of 16 localities within 11 South Australian Marine Parks found substantial local variation in connectivity across the network and broad differences in connectivity patterns among individual species and dispersal phenotypes. Given the prior lack of data about multispecies connectivity patterns, this information provides a baseline for understanding the structure of South Australian Marine Park connectivity and for informing ongoing monitoring practices.

Effective network connectivity was high across all taxa, consistent with general expectations for long-range dispersers (Waples 1998). However, the Southern Spencer Gulf Marine Park (Investigator Strait locality) and the Lower Yorke Peninsula Marine Park (also in Investigator Strait) were perhaps the most important hubs of connectivity across all species networks. These localities not only had the greatest number of strong connections with other sites 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 localities provided links to the less connected gulf waters, and also 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 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 a 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 localities' orientation at the centre of a sampling range; however, this did not appear to apply to upper gulf waters, despite their relative longitudinal centrality. Lower average connectivity of the gulfs compared to surrounding localities 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). Meanwhile, gulf waters and embayments have also 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. 2018a). This may be a contributing factor in the particularly low connectivity of the *active dispersers* group between gulfs and the surrounding stretches of coastline. *Active dispersers*' stronger network clustering was also consistent with high site fidelity in gulf waters. At network thresholds above percolation (i.e., if the weakest links in the network were removed), network breakdown would likely first occur between the two gulf-associated subclusters.

#### *Environmental correlations and potential drivers of connectivity*

We hypothesised that patterns of genetic connectivity throughout SA would be associated with variations in 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. Moreover, we found that the best explanatory variables were not shared among life history subclusters (*active dispersers* versus *larval dispersers*). This suggests that idiosyncrasies among these groups (and potentially among comprised species) could limit the generalisability of oceanographic modelling for predictions in multispecies networks, at least within similar data constraints as seen here. Since advection models are being increasingly applied to connectivity estimates based on general dispersal traits rather than empirical data (e.g. Jonsson et al. 2016, Bray et al. 2017, Roberts et al. 2021), ongoing calibration with observational data may be required to ensure accuracy (Faillettaz et al. 2018).

Unexpectedly, we found that advection connectivity better predicted connectivity of *active dispersers* than *larval dispersers*. Given that advection models were approximated from life history considerations of the snapper, limpets, and nerites, we hypothesised that advection models for these species might outperform predictions based on distance alone. Their underperformance for *larval dispersers* could potentially relate to the lack of species-specificity of the models, or might instead be attributed to factors such as habitat suitability, temporal variation in recruitment, inappropriate spatial scale, or to unknown barriers in the intervening matrix (Hedgecock 1994, Banks et al. 2007, Teske et al. 2015). Equally interesting was the very strong explanatory power of the spring advection model for the *active dispersers*' connectivity, despite its design for larval predictions. However, this was also not an entirely novel finding; strong associations have previously been found between oceanography and dolphins' population divergence in southern Australia, with possible relevance to hydrological adaptation and feeding specialisations (Bilgmann et al. 2007, Barceló et al. 2022, Pratt et al. 2022). It is plausible that similar factors may be contributing to structure across current-driven habitat gradients here. Despite ongoing questions, a useful takeaway from the association analyses was the overall utility of distance as a metric for estimating broad patterns of connectivity across species of varying life histories. While there is room to improve predictive power for both current and future modelling, the results helps to affirm established planning and evaluation practices in the SARMPA, which have used spatial strategies as a surrogate for connectivity metrics within the network (DEH 2008).

### *MPA strategies and climate change adaptation*

Connectivity can promote adaptation and increase resilience to climate change in a number of ways. First, the exchange of genetic variation among populations or metapopulations can help to maintain local reservoirs of standing diversity; the raw material on which natural selection can act (Hendry and Taylor 2004, Nosil et al. 2019). Second, existing climatic variation across species' habitat ranges can lead to divergent regional adaptations, and some 'pre-adapted' genetic variations may spread quickly throughout the network if they become favourable under changing climates (Haldane 1948, Nosil et al. 2019). Finally, connectivity can simply permit individuals to relocate to more suitable conditions if they

have access to the required habitats. Recently, putative genetic adaptations in association with gradients in sea surface temperature across SA have been identified in both Indo-Pacific bottlenose dolphins (Pratt et al. 2022) and common dolphins (Barceló et al. 2022). However, since less dispersive dolphins resident to embayment habitats are considered more likely to be impacted by extreme heatwaves (Wild et al. 2019, Barceló et al. 2022), the capacity for gene flow and dispersal is particularly valuable. In the present study, network analyses indicated that the strongest link between dolphin population subclusters was between Encounter (Adelaide) and Southern Spencer Gulf (Investigator Strait). Without Marine Park zoning, dolphins in these regions are at increased risk from fisheries interactions, habitat degradation, coastal zone development, and human interference (Hamer et al. 2008, Passadore et al. 2018b, Barceló et al. 2021). Population depletion at these important nodes could have wide-ranging effects by reducing connectivity and adaptive genetic exchange between gulf systems, and thereby the wider network. Modelling oceanographic changes in future climate scenarios may help to pre-empt changes to connectivity pathways; however, a more immediate priority will be to refine understandings of the associations between oceanographic connectivity models and observed genetic structure.

### *Conclusions and future directions*

Assuming community compliance with marine park regulations, we can suggest that the current distribution of Marine Parks is expected to help maintain ecological processes associated with connectivity and climatic resilience. However, as outlined by Bryars et al. (2017), assessing the ongoing contribution of marine park strategies to ecological functioning will be best addressed by a Before-After-Control-Impact design. The results of this study can act as a useful baseline for ongoing assessments but cannot yet inform about temporal changes since the establishment of the SARSMPA, which should be a priority for future work. Moreover, while 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 the network. As genomic data become more cost-effective, we would recommend finer-scale sampling of a broader range of species and life histories, as well as longitudinal genomic monitoring of species



for which baseline data are already available. Further, comparisons among different zoning schemes, for example sanctuaries versus general use zones, will also allow more direct evaluation of Marine Park strategies.

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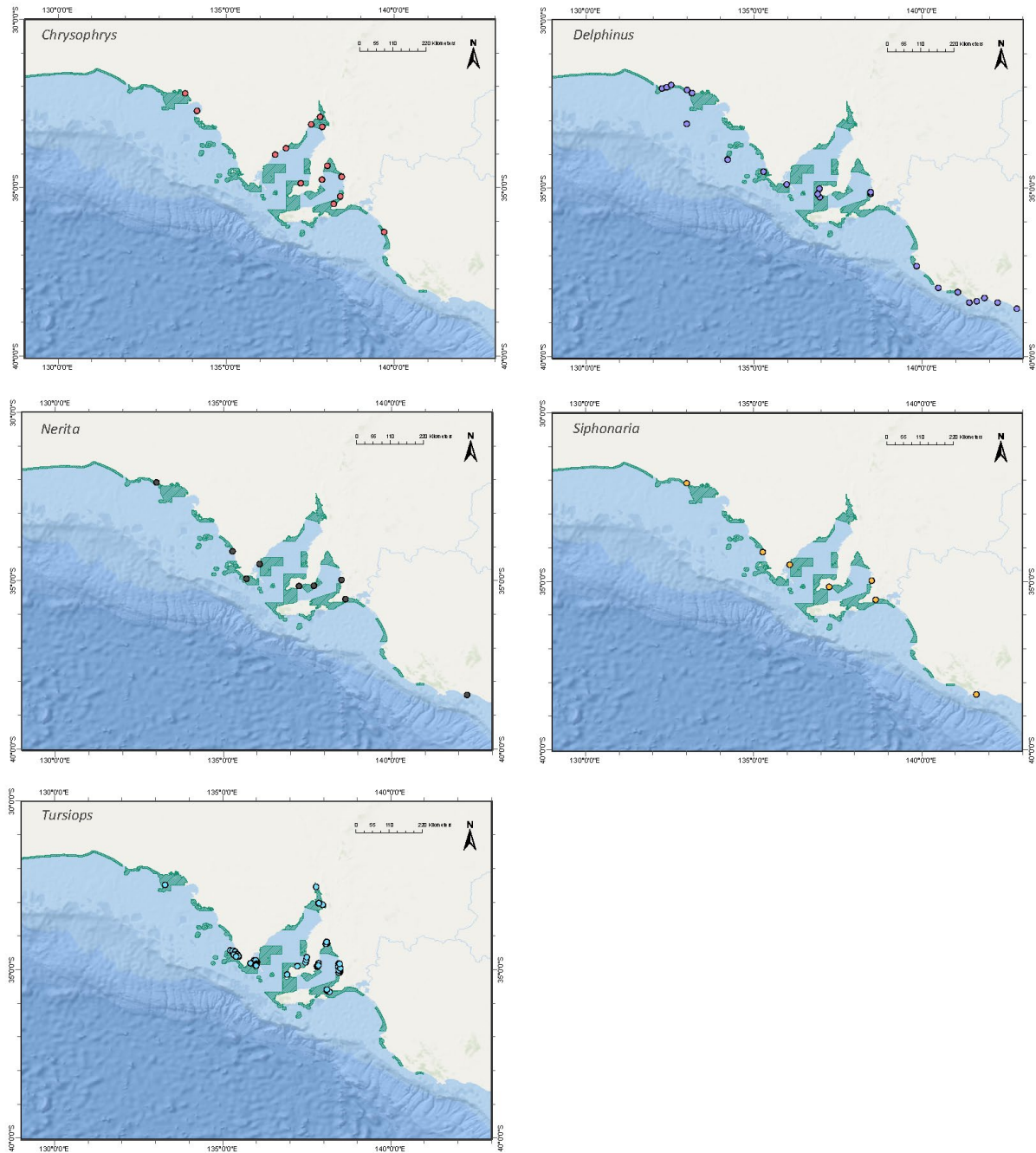
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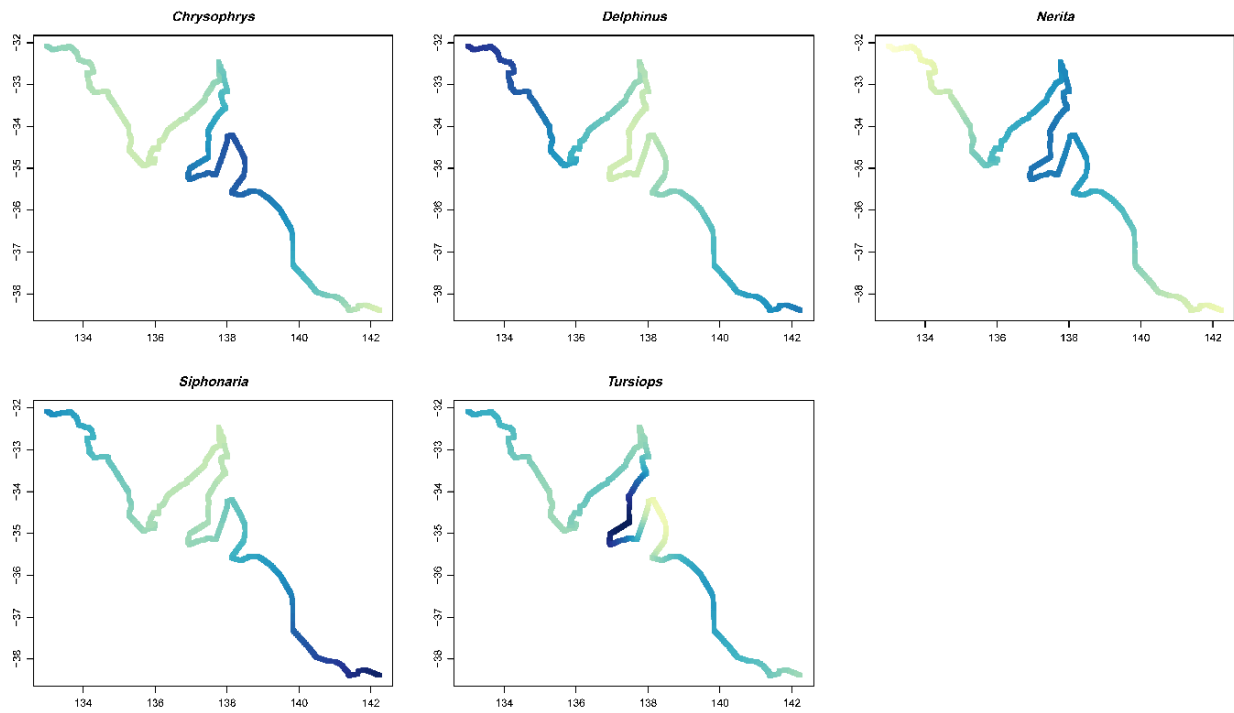
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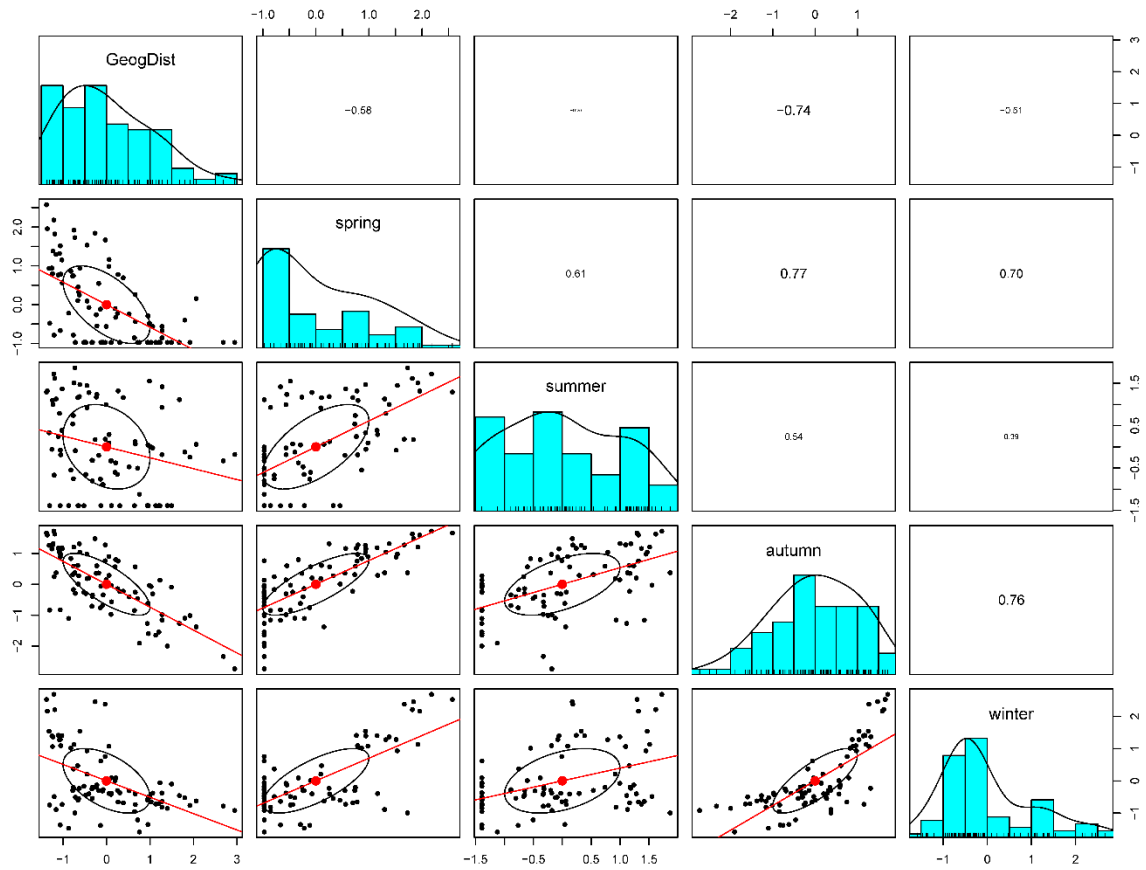
## Supplementary Figures



Supplementary Figure 1. Sampling localities, indicated by coloured circles, across the South Australian Representative System of Marine Protected Areas (SARSMPA) for five species, *Chrysophrys auratus*, *Delphinus delphis*, *Nerita atramentosa*, *Siphonaria diemenensis*, and *Tursiops aduncus*. SARSMPA General Managed Use Zones are indicated by green shading.



Supplementary Figure 2. Individual genogeographic maps for each species Average site-specific genetic differentiation ( $F_{ST}$ ) for each species cluster in relation to position along coastline, with lighter yellow indicating regions of greater differentiation/uniqueity.



Supplementary Figure 3. Proportion of autocorrelation among environmental variables used in RDAs. GeogDist = direct waterway distances. Seasons correspond to advection connectivity models calculated for respective three-month periods, based on the Ocean General Circulation Model for the Earth Simulator 2 (OFES2; Sasaki et al. 2020).



## Supplementary Tables

Supplementary Table 1. Characteristics of thresholded connectivity networks (main results, Figures 3 & 4), where  $d_{max}$  = maximum network distance (equivalent to percolation threshold),  $N$  = number of nodes (localities),  $E$  = number of edges (connections in the thresholded networks),  $\langle k \rangle$  = average node degree (average number of connections per node),  $k_{max}$  = maximum node degree (maximum number of connections of any node in network), and  $\langle c \rangle$  = clustering coefficient (scale 0-1).

	All species	Active Dispersers	Larval Dispersers	Reduced Larval
<b><math>d_{max}</math></b>	0.323	0.288	0.314	0.443
<b><math>N</math></b>	16	12	12	12
<b><math>E</math></b>	28	17	18	24
<b><math>\langle k \rangle</math></b>	3.5	2.83	3	4
<b><math>k_{max}</math></b>	6	6	6	6
<b><math>\langle c \rangle</math></b>	0.29	0.31	0.21	0.47

Supplementary Table 2. Node data for network analyses across 16 sampling localities in the South Australian Marine Parks network. Node degree = number of connections per node. Betweenness centrality = the number of shortest paths between other nodes which must pass through that node.

Locality	Node Degree				Betweenness Centrality			
	All species	Active Dispersers	Larval Dispersers	Reduced Larval	All species	Active Dispersers	Larval Dispersers	Reduced Larval
Nuyts Archipelago Penong	1	2	NA	NA	0.0	0.8	NA	NA
Nuyts Archipelago Ceduna	4	NA	4	5	5.4	NA	6.3	4.1
Investigator	2	4	1	2	14.0	8.3	0.0	0.0
Thorny Passage Coffin Bay	1	2	NA	NA	0.0	0.0	NA	NA
Thorny Passage Fishery Bay	4	NA	3	4	6.5	NA	3.0	4.6
Sir Joseph Banks Group	5	5	4	6	11.6	13.0	2.8	5.8
Upper Spencer Gulf	3	1	3	4	2.5	0.0	1.7	0.4
Southern Spencer Gulf Point Souttar	3	NA	3	6	1.0	NA	1.0	5.9
Southern Spencer Gulf Investigator Strait	5	6	NA	NA	38.2	26.0	NA	NA
Lower Yorke Peninsula	6	3	6	6	13.7	0.0	29.2	15.9
Upper Gulf St Vincent	4	3	3	4	1.4	0.0	1.7	0.4
Encounter Adelaide	6	4	5	6	18.9	3.2	16.3	14.1
Encounter Cape Jervis	5	5	NA	NA	19.4	14.8	NA	NA
Encounter Victor Harbour	1	NA	1	1	0.0	NA	0.0	0.0
Upper South East	3	3	1	1	17.5	2.8	0.0	0.0
Lower South East	3	2	2	3	9.0	0.0	10.0	10.0

Supplementary Table 3. RDA summary statistics for associations between environmental variables and first PCs of genetic variation for all species, and for species subclusters. For  $p$ -values, significance codes  $p < 0.001 = ***$ ,  $p < 0.01 = **$ ,  $p < 0.05 = *$

<b>Environmental variable vs all species connectivity</b>		<b>R<sup>2</sup></b>	<b>Adj R<sup>2</sup></b>	<b><math>p</math>-value</b>	<b>F</b>
<b>Distance</b>	Direct waterway	0.185	0.176	0.001 ***	19.33
	Coastal	0.115	0.104	0.001 ***	10.99
	Latitudinal	0.093	0.082	0.004 **	8.72
<b>Advection model</b>	Spring	0.149	0.139	0.001 ***	14.94
	Summer	0.033	0.021	0.102	2.88
	Autumn	0.113	0.103	0.002 **	10.86
	Winter	0.092	0.081	0.005 **	8.62
	Sum of seasons	0.103	0.092	0.002 **	9.72
<b>Environmental variable vs dolphin connectivity</b>					
<b>Distance</b>	Direct waterway	0.333	0.319	0.001 ***	24.93
	Advection model				
	Spring	0.368	0.355	0.001 ***	29.08
	Summer	0.266	0.251	0.001 ***	18.08
	Autumn	0.244	0.228	0.001 ***	16.10
	Winter	0.172	0.156	0.004 **	10.42
<b>Environmental variable vs larval disperser connectivity</b>					
<b>Distance</b>	Direct waterway	0.081	0.062	0.043 *	4.32
	Advection model				
	Spring	0.019	-0.001	0.353	0.93
	Summer	0.014	-0.006	0.434	0.69
	Autumn	0.015	-0.005	0.386	0.74
	Winter	0.036	0.016	0.191	1.81