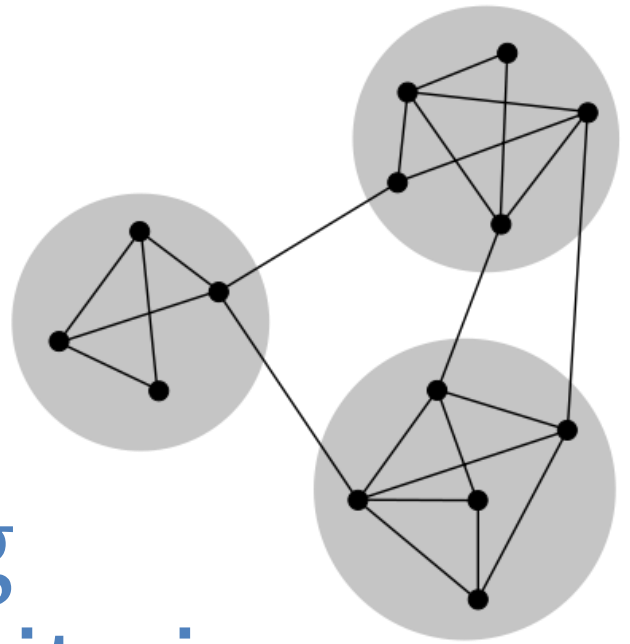

The University of Adelaide

Assessing connectivity in South Australia's Marine Parks Network

Report prepared for the Department of Environment Water and
Natural Resources



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1. Executive summary

This report and the associated literature database reviews existing studies relating to connectivity of marine species and habitats within South Australian waters. It was undertaken in response to a need for information to support an assessment of the adequacy and effectiveness of the South Australian state marine parks network. We found 131 studies that contained information of some relevance to aspects of connectivity in South Australian waters, however only six of these were specifically focussed on marine parks, and those that were focused on single species within single marine parks. This lack of focussed, broad coverage studies of connectivity and population structure across the marine parks network limits the utility of the available data for assessing questions of connectivity specifically related to the network.

In summarising the available literature, we have found data on 47 species relevant to the assessment of connectivity across the South Australian marine parks network. The majority of studies were on bony fish (teleost) and invertebrate species with commercial or recreational fishing value. There was a notable lack of studies on habitat forming species such as mangroves, seagrasses and macroalgae. There were only two multi-species studies, and few that combined multiple approaches in an integrated way (i.e. combining genetic, otolith, morphological, growth and/or bio-physical data); which is increasingly recommended in the broader literature on connectivity.

Based on our findings we have identified key knowledge gaps around the distribution of habitats, species life-history data (particularly for non-fished species) and an issue of scale mismatch; in that most studies either have broad coverage but poor spatial and temporal resolution, or have high resolution but over very limited spatial scales. In order to undertake a robust assessment of the connectivity of populations and habitats throughout the SA marine parks network, studies will need to be focussed at the scale of the network, but have high resolution. Such studies could provide specific information about connections within and between parks, across the entire network. As such, we have made recommendations that future work be multidisciplinary and combine broad scale (well-resolved) bio-physical modelling approaches with genetic and tracking (telemetry and bio-markers) data to simulate validated, whole-of-network connectivity patterns. These types of assessments are complex, and it is not feasible that they be undertaken for all species, therefore some prioritisation and generalisation will be required in order to highlight key species, or life-history ‘types’ to focus future work on.

2. Introduction

2.1. Connectivity

The movement of individual organisms has a strong influence on their species' population structure and dynamics. The term 'connectivity' can refer to the extent to which populations of the same species in different areas are linked by exchanges of individuals (Palumbi 2003). It can also refer to the movement of individuals or materials (e.g. organic matter) between areas of the same or different habitats (Olds et al. 2012). In the context of marine parks, sites can be viewed as connected if organisms move between them; if they are used by different life stages of the same species; or if materials (e.g. sources of carbon) that support the food web are moved between them (DEH 2008). A network of marine protected areas should therefore aim to maximise connectivity between designated sites to support ecological function and productivity (Palumbi 2003).

Populations of marine organisms are generally structured such that separate sub-populations are connected to each other through exchange of individuals to create a meta-population (Cowen et al. 2009; Calò et al. 2013). The level of connectivity between sub-populations defines the overall meta-population structure for a species within a given region. This structure affects many critical processes such as population dynamics (including the persistence of populations), local adaptation and resilience to disturbance or exploitation. As a result, connectivity between populations also has implications for the maintenance of biodiversity, community structure and ecosystem function, and is thus integral to the success of management measures such as marine protected areas (Palumbi 2003; Cowen et al. 2007).

For the purposes of this review, when we refer to connectivity of populations, we focus predominantly on *demographic* connectivity, which is the effect of dispersal processes on population growth, vital rates and the persistence of populations of marine species (Lowe et al. 2010). *Genetic* connectivity can also be important and is defined by Lowe et al. (2010) as "the degree to which gene flow affects evolutionary processes within populations". Whilst genetic connectivity is important, it can be misleading if not properly presented or understood. For example, individuals from one population may supply enough migrants to another population to prevent significant genetic divergence (i.e. the two populations would be *genetically* connected); however, the levels of migration may not influence population persistence and therefore are not *demographically* relevant (Palumbi 2003; Lowe et al. 2010).

Marine species populations have historically been considered demographically ‘open’ (i.e. highly connected) due to many of them having a pelagic and broadly dispersive early life history stage and a relatively sedentary adult life stage (for example most fish, invertebrates and macroalgae (Cowen et al. 2007). However, research over recent decades has demonstrated great variability and unpredictability in the structure of marine species’ populations. This structuring is due in a large part to biological traits (such as life history, dispersal capacity, habitat associations etc.) and oceanographic processes, which both influence connectivity between sub-populations over a variety of scales (Palumbi 2003; Palumbi 2004).

Connectivity of habitats may refer to connections between patches of habitat used by individuals (e.g. availability of key foraging habitats for mobile species (Grüss et al. 2011; Babcock et al. 2012); connections between areas of different habitats required during different life stages of a species (Gillanders et al. 2003; Nagelkerken et al. 2015; Weeks 2017); or connections between different types of habitat through trophic transfer (the movement of carbon or other nutrients between different habitats (Heck et al. 2008; Hyndes et al. 2014). Connectivity between habitats is affected by proximity and fragmentation/isolation of patches. The connectivity of fragmented landscapes is theoretically a function of distance between patches of suitable habitat and the characteristics of the habitat through which individuals/material moves between patches (the ‘matrix’). However, the effect of the matrix in marine systems includes both the habitat type *and* the physical water column properties (temperature, salinity, depth, hydrodynamics), which may assist or hinder the movement of individuals and materials. The connectivity of habitats is directly linked to demographic connectivity processes because dispersal and successful settlement of individuals (and subsequent reproduction or assimilation into the food web) will depend on the availability and accessibility of habitats and potentially the matrix that separates habitat patches.

2.2. The South Australian marine parks network

South Australian state waters are divided into eight marine bioregions, within which the Government of South Australia has developed the South Australian Representative System of 19 Marine Protected Areas (SARSMPA), which is part of the broader National Representative System of Marine Protected Areas (NRSMPA; Figure 1). The SA network was based on seven biophysical design principles, which include ensuring continuance of natural processes that are characteristic of the State's marine bioregions (DEH 2008) and, where possible, ensuring that connectivity was considered in a theoretical and/or surrogate manner, taking into consideration objectives such as linkages between habitats and bioregional zoning (DEH 2008).

The SA marine parks network covers an area of 26,655 km² (44 %) of State waters and 267 km² of coastal lands and islands (DEH 2008; Bryars et al. 2017a). The marine parks are multiple-use and have different levels of zoning throughout, which afford varying levels of protection and limits on the activities allowed inside each zone. The zones range from General Managed Use Zones (GMUZ, the lowest level of restriction, covering 30 % of the network area) through to Habitat Protection Zones (HPZ; 56 % of the total area), Sanctuary Zones (SZ; 5 % of the total area) and Restricted Access Zones (RAZ, the highest level of restriction, covering 1 % of the total area). In addition, there are different types of Special Purpose Area (SPA), which allow selected activities (such as shore-based recreational line fishing, transshipment, or harbour activities) that would otherwise be restricted as a consequence of the zoning (Bryars et al. 2017a; Bryars et al. 2017b).

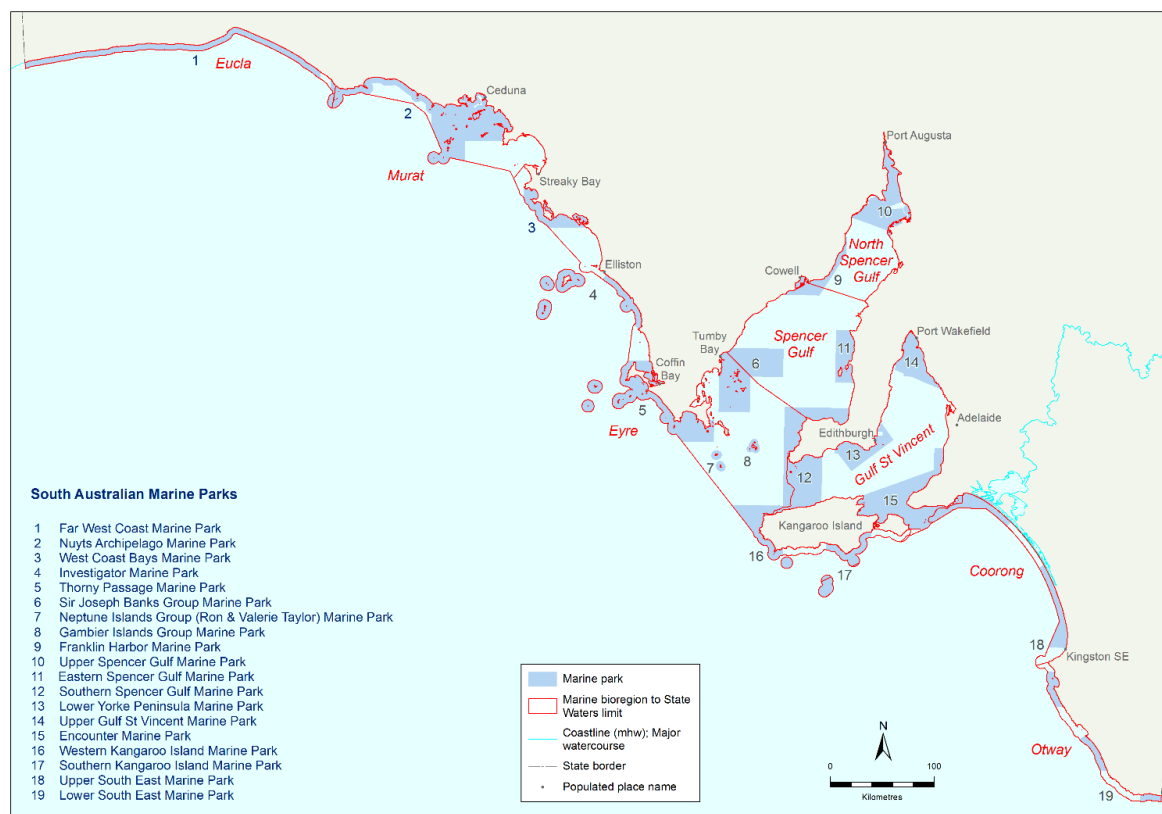


Figure 1 from Bryars et al. (2017b): Map of the bioregions and the outer boundaries of South Australia's network of marine parks.

2.3. Need

Assessing the spatial structure and dynamics of marine species populations, as well as seascape connectivity (connections between different types of habitats) is critical to assessing the effectiveness of the South Australian Representative System of Marine Protected Areas (SARSMPA). The Marine Parks Act 2007 requires that “the Minister must review a management plan at least once in every 10 years”. DEWNR are the responsible authority required to undertake this assessment, which must be completed within 10-years of the proclamation of the marine parks (i.e. by 2022).

The biological effectiveness of the marine parks network will be assessed by DEWNR using a range of indicators and measures including the marine parks design principles of: Comprehensiveness, Adequacy and Representativeness (CAR) (DEH 2008; Bryars et al. 2017b). To achieve comprehensiveness, the network of marine parks should have comprehensive coverage of the full range of ecosystems and habitats that are characteristic of South Australia's marine environment. Therefore, for comprehensiveness to be attained, each marine park should establish or improve the coverage of the full range of ecosystems and habitats occurring within each bioregion.

For the network of marine parks to be representative, it must reflect the biodiversity and variability naturally present in our marine environment. As there is still much to learn about the biodiversity of the marine environment, the ecosystems and habitat types that characterise the marine environment are included as a substitute or ‘surrogate’ for biodiversity. To achieve representativeness, the marine parks network was designed to include large, uniform areas of each of the ecosystems and habitats that are typically found in each bioregion (and their borders). By incorporating multiple marine parks within each bioregion, altogether the marine parks network should reflect and encapsulate the environmental variability within each bioregion. In turn, by developing marine parks within and across each bioregion the network of marine parks should represent the biodiversity and variability across the state.

For the marine parks network to be adequate, it should provide for the maintenance of the ecological viability and integrity of populations, species and communities. To create an adequate network of marine parks, selected areas must ensure the continuance of natural processes that are characteristic of the bioregion they are representing, which is inherently dependent on connectivity. For a marine park network to achieve adequacy, whole areas of representative habitats need to be encapsulated within marine park boundaries. Two of the main factors contributing to adequacy for marine park design are the size of marine parks and the connectivity within and between bioregions, parks and zones.

Connectivity is critical to safeguarding the integrity of ecological processes and viability, thus sustaining populations and habitats. As such ‘connectivity and linkages’ were also specifically noted as a biophysical design principle for the SARSMPA and the NRSMPA (DEH 2008) and will be an essential part of achieving its primary objective to “protect and conserve biological diversity and marine habitats..... and to assist in the maintenance of the ecological viability and integrity of populations, species and communities” (DEH 2008; Bryars et al. 2017b). Currently our limited understanding of connectivity throughout the SA marine parks network impacts on DEWNR’s ability to monitor and assess whether the network adequately provides for the connectivity and linkages underpinning viable populations and biodiversity from broad (national, state and bioregional) to fine (sanctuary zone) scales. This has been highlighted as an area where a review of existing literature and recommendations for targeted research would be valuable to support the CAR assessment of the network (Bryars et al. 2017b).

This report describes a desktop review, which assessed the current state of knowledge and highlights knowledge gaps around connectivity in the SARSMPA. We also summarise some of the potential

methods that can be employed to assess marine parks connectivity in the future. The report can be used by DEWNR to help focus marine parks research to fill key gaps in knowledge and prevent duplication of existing research. This will enable a more effective assessment of the network's overall adequacy into the future.

2.4. Objectives and scope

The objectives of this work were threefold:

- 1) To collate available information on connectivity that is relevant to the SA Marine Parks Program and deliver this information in the form of a database (in Excel), with PDF copies of all documents (and if relevant hyperlinks to online sources of information or data).
- 2) To prepare a section that summarises the current state of knowledge around connectivity, which may aid with DEWNR's assessment of the adequacy of the marine parks.
- 3) Based on the current state of knowledge, to focus the scope of future DEWNR-funded research and prevent duplication of previous studies in future DEWNR-funded research projects. This will be done by highlighting key knowledge gaps and making recommendations for addressing these using current best-practice methods for assessing connectivity of marine park networks.

3. Review of current knowledge

3.1. Overview

Through a comprehensive literature review, we have collated and synthesised 131 research papers, reports and theses containing information on 47 different marine species relevant to the assessment of connectivity across the South Australian Marine Parks Network (Table 1). The majority of studies were on bony fish (teleost) species (n = 43) with most of these studies being on commercial or recreational fishing value. Invertebrates (n = 26) and marine mammals (n = 17) were also relatively well represented groups, with a paucity of studies on macroalgae (n = 6) and multi-species assessments (n = 2). Survey methods (e.g. observations, fisheries catch data and tag-recapture) were the most commonly employed approach used in the reviewed studies (n = 46), followed by genetic assessments (n = 37). There were 16 studies that combined multiple approaches, such as using both bio-markers and acoustic telemetry (e.g. Fowler 2016 on snapper), or satellite telemetry and genetics (e.g. Rogers et al. 2015a on shortfin mako). One study, by Izzo et al. (2017), integrated genetic, otolith, morphological, growth and fishery data from a 60-year long dataset to determine population structure for the Australian sardine throughout Australian waters. Another recent study by McLeay et al. (2016) in Spencer Gulf coupled a biophysical model with fisheries data on western king prawn catch rates (i.e. relative abundances) and reproductive output to generate spatially resolved model estimates of the sources and sinks of larval recruitment.

Most of the studies we reviewed were not specifically focussed on the marine parks network and not all of them were equally informative. We discovered only six studies that were undertaken within SA marine parks, and just one of these which looked at multiple species (Edgar et al. 2009; Bryars et al. 2012; Rogers et al. 2014a; Teske et al. 2015; Bryars et al. 2016; Rogers et al. 2016). As a result, many studies were not ideal for the purposes of assessing marine parks connectivity. However, it has been possible to extract useful information from most studies, which demonstrates the possibility of applying research undertaken with a different primary focus to the marine parks connectivity question.

The following review is a summary of the main findings related to connectivity for each species based on the literature we have collated. Not all papers contained in the excel database are referred to in the text (for example if they did not contribute anything in addition to the references cited). There is also a high likelihood that there are unpublished studies and datasets being held by SA (and other) research, Government and management bodies, which we have not been able to include. Over 40 %

of the studies in our database have been published in or after 2013. This shows that marine species population structuring and connectivity are popular research areas and relevant studies are likely to continue to become available in the near future.

Table 1: Summary of the literature reviewed, detailing the number of studies collated, split by the methodological approach used and the type of organism studied. ‘Genetic’ approaches included mitochondrial DNA, microsatellite DNA, and allozymes. ‘Modelling’ approaches are those that incorporated some aspect of biophysical, oceanographic or larval transport modelling. Note that some studies used multiple approaches and were therefore included in the count for all methods that were relevant (meaning the sum of the method column sub-totals is greater than the overall number of studies). The full database of all relevant studies is provided in the excel file associated with this review document (‘Connectivity_database_v1.xlsx’, sheet name ‘Literature_database’).

Type of organism	Total number of studies	Methodology used						
		Tracking (satellite/GPS/acoustic tags)	Biomarkers (otolith, chemistry, stable isotopes/morphology)	Genetics	Lab-based experiments/controlled manipulation	Modelling (dispersal/hydrodynamics)	Survey/observations/tag-recapture	Review
<i>Seagrass</i>	12		1	4	4		4	1
<i>Macroalgae</i>	6			4	1	2	1	
<i>Marine mammal</i>	17	2		9		1	6	1
<i>Elasmobranch</i>	12	7	1	4			3	
<i>Teleost</i>	43	6	18	7		5	16	4
<i>Invertebrate</i>	26	2	1	7	2	6	10	3
<i>Multispecies</i>	2						2	
<i>Seabirds</i>	13	4	1	2		1	4	2
Total	131	21	22	37	7	15	46	11

3.2. Literature review

Habitat forming species (seagrass and macroalgae):

Sinclair et al. (2016) built hydrodynamic models of seed dispersal for *Posidonia australis*, which indicate relatively high levels of demographic connectivity between meadows surrounding two SA sites (Nora Creina on the south-east coast and north-eastern Kangaroo Island). This local and regional scale connectivity is maintained by floating fruit that acts to disperse seeds (see Figure 2). These theoretical connectivity model outputs could be validated using genetic approaches, which would provide information on the successful settlement, colonisation and reproduction of dispersing individuals (for example see Kendrick et al. 2017).

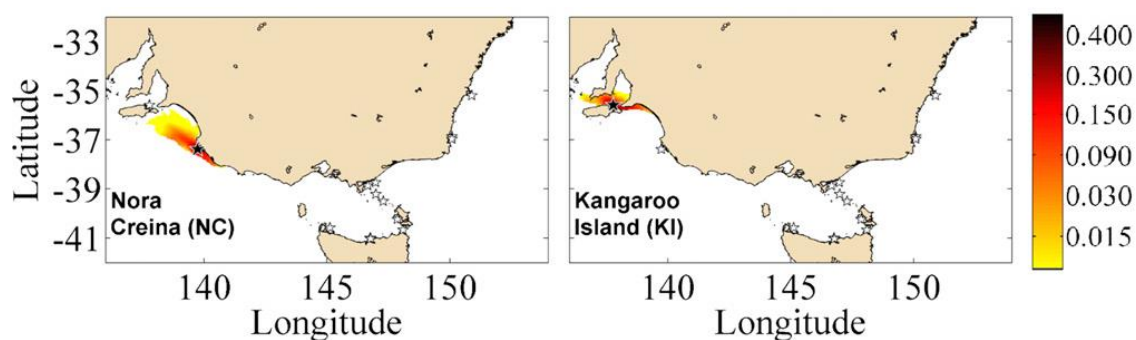


Figure 2 from Sinclair et al, (2016): Maps of *Posidonia australis* settlement probability based on hydrodynamic models of seed dispersal from two SA sites. *Journal of Biogeography*, 43, 2209–2222. © John Wiley and Sons Ltd, used under a creative commons license.

Ticli (2015) carried out the first study of genetic diversity, structure and connectivity of *Zostera muelleri* seagrass populations across the species' entire range in Australia. When looking across the whole range of the species, there was clear isolation by distance with populations from West, South and all of Eastern Australia showing genetic differences. Within South Australia isolation by distance was also detected. However, these finer-scale patterns were complex, with varying levels of genetic relatedness between sampled meadows in SA (Figure 3).

The importance of the availability of suitable physical habitat for recruitment of the seagrass *Amphibolis antarctica* was studied by Irving et al. (2014), who deployed artificial substrate to aid recovery of seagrass meadows in Gulf St Vincent. They found that recruitment of seagrass seedlings to artificial habitat patches (in this case sand/rubble filled hessian bags) declined with distance from established 'donor' meadows. It was also influenced by the weave of the hessian bags, what the bags were filled with (i.e. the 'substrate type') and their spatial arrangement (single bags retained more

seedlings than grouped bags) (Irving et al. 2014). Goodsell and Connell (2008) also found that the distance between patches of fragmented habitats (kelp holdfasts) had a negative relationship with connectivity. They also demonstrated an effect of the ‘matrix’ of habitats in between target habitat patches, showing significant differences in the assemblages of invertebrates colonising kelp holdfasts when there were different habitats in between them. Tanner (2006) found similar effects of matrix habitats on the invertebrate assemblages in seagrass patches in SA waters. The inference from these studies is that matrix habitat type influences successful movement, and thus connectivity between seagrass habitat fragments. These findings warrant further investigation as they suggest that parks containing patches of the same habitat type may need to be within a threshold distance of each other, and have favourable matrix habitats between them in order to facilitate successful movement events. However, the generality of these findings is uncertain, and the threshold distances between parks and the suitability of the intervening habitat matrices will be organism specific.

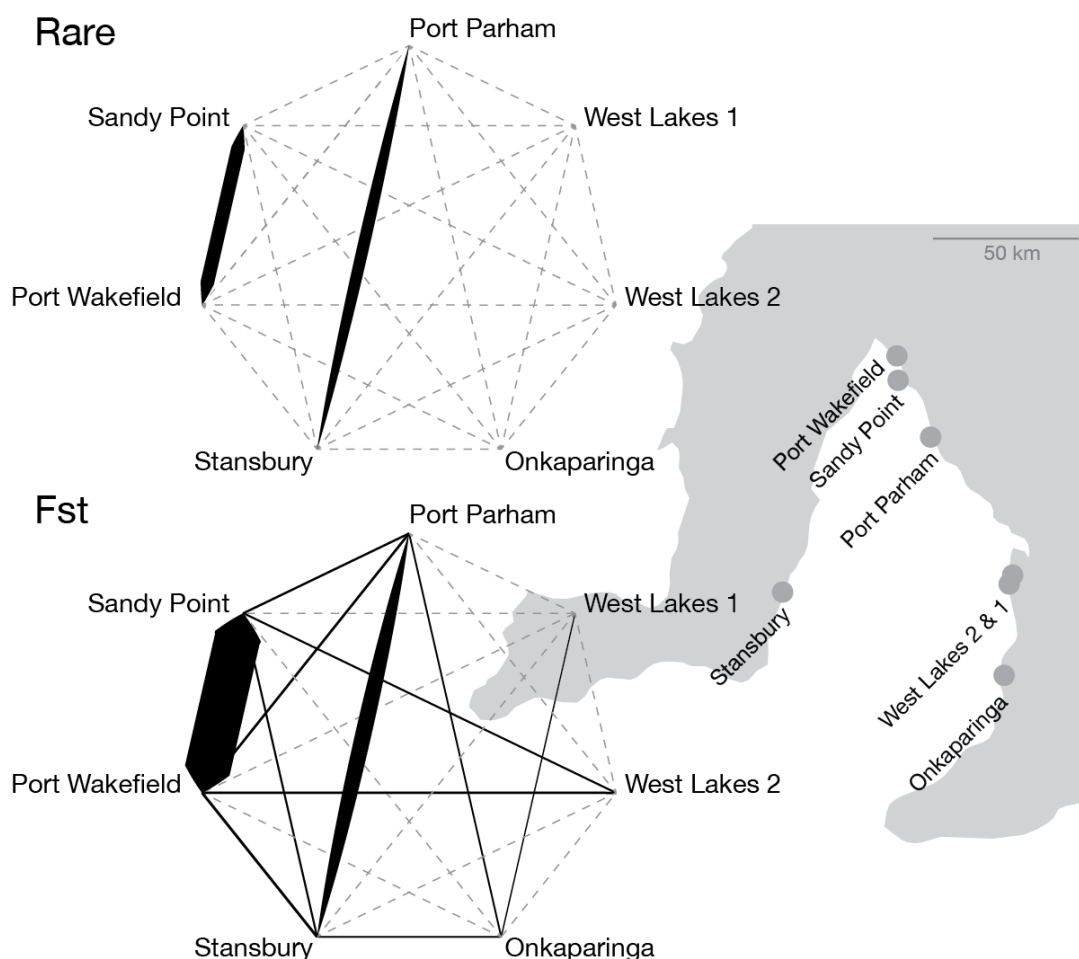


Figure 3 from Tigli, (2015): Diagrams of connectivity estimates for Gulf St Vincent populations of *Zostera muelleri*. Estimates are for number of migrants per generation (N_m) based on two different measures of gene flow: 1) Rare alleles and 2) F_{ST} . Line weight is proportional to N_m with solid lines showing estimated $N_m > 0.5$ (Rare) and > 1.0 (F_{ST}). The relationships between Stansbury–Port Parham and Port Wakefield–Sandy Point were statistically significant.

Coleman et al (2009) sampled kelp (*Ecklonia radiata*) at five populations in SA waters, ranging from Streaky Bay in the west, to Robe in the East. They found high levels of genetic structuring between populations at moderate (10s km) to large scales (100s km), with almost all sites being significantly different from each other (Coleman et al. 2009), suggesting that there is low genetic connectivity between them. Number of migrants per generation was estimated at ~ 1 across populations sampled in SA, based on an F_{ST} value of 0.211 (Coleman et al. 2013). The amount of genetic differentiation between pairs of populations was correlated with the geographic distance between them, despite the existence of the Flinders Current which was expected to act as an aid to dispersal (Coleman et al. 2009; Coleman et al. 2013). These results are likely to be reflective of the connectivity patterns between kelp populations on rocky reef habitats within the SA Marine Parks Network (i.e. a model of isolation by distance).

We have not found any literature on other key marine habitat forming species in SA, such as mangroves and saltmarshes. In terms of movement of materials and connectivity through trophic transfer, we have found one study in SA that demonstrates that animals living in both seagrass and mudflats were reliant on seagrass-derived carbon sources for food (Connolly et al. 2005).

Teleosts:

Most studies on teleosts that are relevant to connectivity have focussed on the stock structure of commercially important taxa (32 %), with comprehensive knowledge for a few of these species (see detailed below). There are also some studies on iconic species, or species of conservation concern, such as western blue groper (Bryars et al. 2012), harlequin fish (Bryars et al. 2016) and leafy sea dragon (Stiller et al. 2017). However, these studies are focused on the highly philopatric adult life stages and although these data are useful, they do not provide information on population connectivity (although see below for a description of the genetic relatedness of leafy sea dragons across SA from Stiller et al. 2017).

Izzo et al. (2017) investigated population structure of the Australian sardine (*Sardinops sagax*) across its entire Australian range using otolith structure and microchemistry. They found evidence of some separation between regions across Australia, although sub-structure between neighbouring groups was low, indicative of an overall meta-population throughout the entire species range. However, there was enough separation over large geographic distances for the authors to suggest that the species should be managed as four broad stocks: south western coast (off WA); Great Australian Bight and Spencer Gulf; Bass Strait and Port Phillip Bay (off Victoria and Tasmania); and eastern Australia (Izzo et al. 2017). At a finer scale, Izzo et al. (2012) also suggest some spatial structuring within the

GAB. The overall outcome of this work indicates that population structuring of the Australian sardine is complex and mixing between neighbouring populations can vary from year to year, but there is unlikely to be significant separation between sub-populations within SA waters (Izzo et al. 2017).

King George whiting have been shown to separate spatially on the basis of age with distinct SA spawning (offshore) and nursery areas (Gulfs) (Fowler et al. 2000; Fowler et al. 2003). These discrete locations are connected by predominantly south-to-north advection of larvae into the Gulfs (Fowler et al. 2000), followed by north-to-south movement of adults out of nursery areas into deeper waters offshore where they reside and spawn (Fowler et al. 2003). Tag recapture studies and age-class reconstructions using fisheries data inferred some level of east-west divergence, with Eyre and Yorke Peninsulas proposed as barriers to dispersal/movement (Fowler et al. 2003; Fowler et al. 2011). However, more recent genetic studies (using msatDNA and SNPs) show that genetic diversity does not vary significantly between populations or regions across the entire southern Australian range of the species. Although some distance-based differences in genetic similarity were detected at a large spatial scale (e.g. between WA and SA/Vic), overall estimates of the number of migrants between populations per generation were relatively high (11.146 ± 1.252), which suggests that genes are well mixed (Jenkins et al. 2016), although this does not necessarily mean that sub-populations are demographically connected. Current work being undertaken at SARDI and the University of Adelaide is investigating the connectivity of populations in SA using otolith microstructure and chemistry, as well as oceanographic modelling (as part of an FRDC-funded project).

Observational surveys and telemetry studies of the leafy sea dragon report a relatively small home range and strong site-fidelity in SA waters (Connolly et al. 2002a; Connolly et al. 2002b), indicating potential for demographically discrete sub-populations. This is supported by a recent genetic study by Stiller et al. (2017) which indicates substructure based on significantly different allele frequencies between many of the sampled bays in SA waters, with genetically distinct groups in Encounter Bay, on both shores of Gulf St Vincent, and in Spencer Gulf. This fine-scale population structuring indicates a high level of adult site-fidelity and self-recruitment in this charismatic species (Stiller et al. 2017), which suggests that populations contained within marine parks should be well protected. This is particularly the case for sanctuary and habitat protection zones, where the seagrass and rocky reef habitats that the species lives within are relatively undisturbed by human activities.

The marine parks network, particularly the sanctuary zones around rocky reefs, are also likely to offer significant benefits to other fish species with high site fidelity, which are threatened by human activities such as fishing and habitat degradation. Examples include the southern blue devil, harlequin

fish and western blue groper, which have been demonstrated to be strongly site attached and have small adult home ranges (< 50 m, < 200 m and < 1.1km respectively) that could be fully encompassed within marine park sanctuary zones (Bryars 2011; Bryars et al. 2012). Although it is known that these species are broadcast spawners with pelagic larval phases (Coulson et al. 2009; Bryars 2013; French et al. 2014), there are no data available regarding the details of larval dispersal (e.g. pelagic larval duration, spatial dynamics of dispersal) or the genetic and demographic connectivity of these species; so it is unclear how reliant they are on propagule dispersal or retention, or how well protected they are by the marine parks network throughout earlier life stages. Shepherd and Brook (2007) found that the habitat of juvenile and adult western blue groper did overlap, with both age classes being dependent on subtidal rocky ecosystems. However, there was a transition along depth and exposure gradients with juveniles found more commonly in shallower, sheltered locations; and adults dominant on rocky reefs in deeper, exposed locations. This indicates that, at a minimum, rocky reefs in both these settings need to be protected in marine parks in order to ensure protection of, and connectivity between, *potential* juvenile and adult habitats. However, further research is required to demonstrate the *realised* value of the existing marine parks network for the species. Examples of such studies include larval dispersal modelling, tagging juveniles to elucidate movements to final settlement habitats, and genetic connectivity studies between reef-attached sub-populations.

Combined genetic and natural tagging (otolith shape, structure and microchemistry) studies suggest some east-west structuring of mulloway populations in SA, with a separation of the fish in the south-east of the state (the Coorong estuary and surrounding coastal waters) from the far west of the state (Barnes et al. 2014; Barnes 2015), supporting an earlier otolith study by Ferguson et al (2011) that indicated some level of sub-structuring of populations within SA waters. There is limited evidence that fish sampled from Gulf St Vincent may be grouped with the south-eastern sub-population, and fish from the GAB region may be grouped with the western sub population (Barnes et al. 2014; Rogers et al. 2014a); however, the spatial resolution of these studies was not able to effectively delineate fine-scale structuring within SA waters and there appears to be occasional migration between these sub-populations (Rogers et al. 2014a). Satellite telemetry studies of adult mulloway in the State's Far West Coast Marine Park suggested that this park may provide some protection for the mature fish of this species for at least part of the year (Rogers et al. 2014a; Barnes 2015), however recreational fishing from the shore of this marine park is allowed year-round in some areas of the park (outside the sanctuary and restricted access zones), so the level of protection may be limited.

Early genetic studies of snapper indicated connectivity (i.e. no structuring) between eastern WA and SA and no sub-structuring within SA waters (Donnellan et al. 1996). This result was supported by

studies of adult movement using otolith chemistry, which suggested that fish sampled from along 2000km of the SA coast originated from only one or two nursery areas (and subsequently dispersed throughout SA waters to become resident in new regions) (Fowler et al. 2005). However, more recent work by Fowler et al (2016; 2017) showed regional differences in physical and chemical otolith characteristics (size, shape, chemistry), as well as population-based demographic characteristics (size at age, growth rates etc.) in different parts of SA. These results suggest that northern Gulf St Vincent and northern Spencer Gulf may be self-sustaining populations that do not receive any recruits from elsewhere, but are critical sources of recruits to many other regions in SA (Figure 4). The potential isolation of these northern Gulf areas, in terms of emigration, suggests that sanctuary zones in these regions could play an important role in protecting source populations whose export of recruits sustains the broader meta-population within SA waters (Fowler 2016; Fowler et al. 2017).

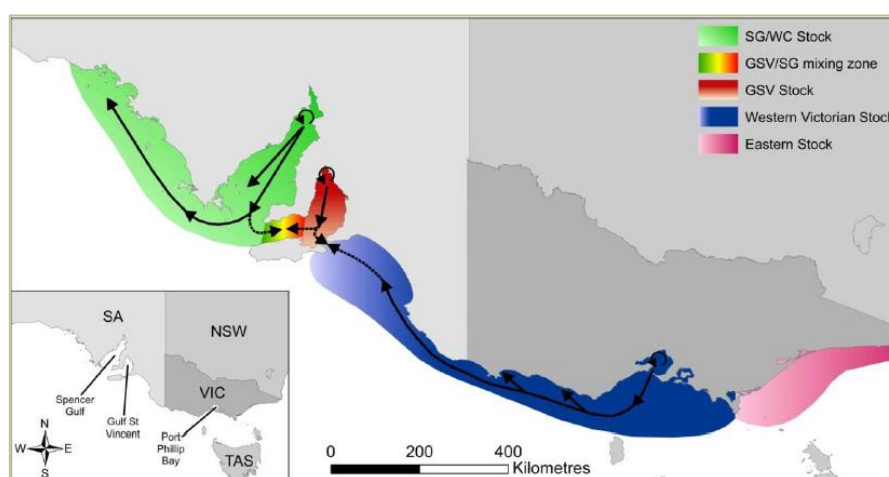


Figure 4 from Fowler et al (2016): Map of population structure and connectivity between sub-populations of snapper in coastal areas of eastern SA. Arrows show the direction of movement of recruits (emigration) from the three main nursery areas in northern Gulf St Vincent, northern Spencer Gulf and Port Phillip Bay in Victoria. © Fisheries Research and Development Corporation and South Australian Research and Development Institute, reproduced under a creative commons license.

Southern sea garfish populations in SA were demonstrated to be genetically different from those in Victoria, Tasmania and WA by Jones et al (2002). Further fine-scale spatial structuring was demonstrated within SA waters using both otolith chemistry (Steer et al. 2009) and stable isotopes (Steer et al. 2010). They showed that garfish in SA waters can be separated into 6 regional populations with varying levels of mixing: Northern Gulf St Vincent, South West Gulf St Vincent, Kangaroo Island, Northern Spencer Gulf, South West Spencer Gulf and the West Coast of Eyre Peninsula. In some locations it was possible to separate sites that were < 60 km apart based on the chemical signatures in the sampled fish otoliths (Steer et al. 2009).

Elasmobranchs:

Izzo et al (2016) used elemental analyses of bronze whaler shark vertebrae samples from Spencer Gulf and Gulf St Vincent to look at fine scale population structuring, over long and short timescales, within the sampled regions. They found some indication of small differences over short timescales (weeks to months) between samples from Spencer Gulf and those from Gulf St Vincent and other sampled regions. This suggests seasonal structuring, which may be related to pupping in Gulf waters (Izzo et al. 2016). Huveneers et al (2010) demonstrated that 43 % of (predominantly juvenile) bronze whaler and dusky sharks implanted with acoustic transmitters in northern Gulf St Vincent remained in the same region for over a year. Rogers et al (2013) also note that SA gulf waters are likely to be a significant habitat for juvenile dusky and bronze whaler sharks; they found that 75 % of those tagged by recreational anglers in these areas were juvenile, and that > 50 % of these were recaptured within 50 km of their tagging location. These results indicate medium-term residency for juveniles of these two species in Gulf waters. However, the elemental chemistry analysis of larger bronze whaler sharks showed strong evidence of connectivity across SA regions over the sharks' full lifetime (Izzo et al., 2016). This is supported by long-term tag-recapture data and telemetry studies on adult dusky and bronze whaler sharks, which report some long-distance movements within SA, as well as into WA, Victoria and Tasmania. (Goldsworthy et al. 2010; figures 5 & 6; Rogers et al. 2013). These studies highlight the potential importance of Marine Parks sanctuary zones in Spencer Gulf and Gulf St Vincent to young sharks of these two species (which are particularly vulnerable to overexploitation; Rogers et al. 2013), as well as the connectivity between Gulf waters and offshore areas within and outside SA (including connectivity through the NRSMPA).

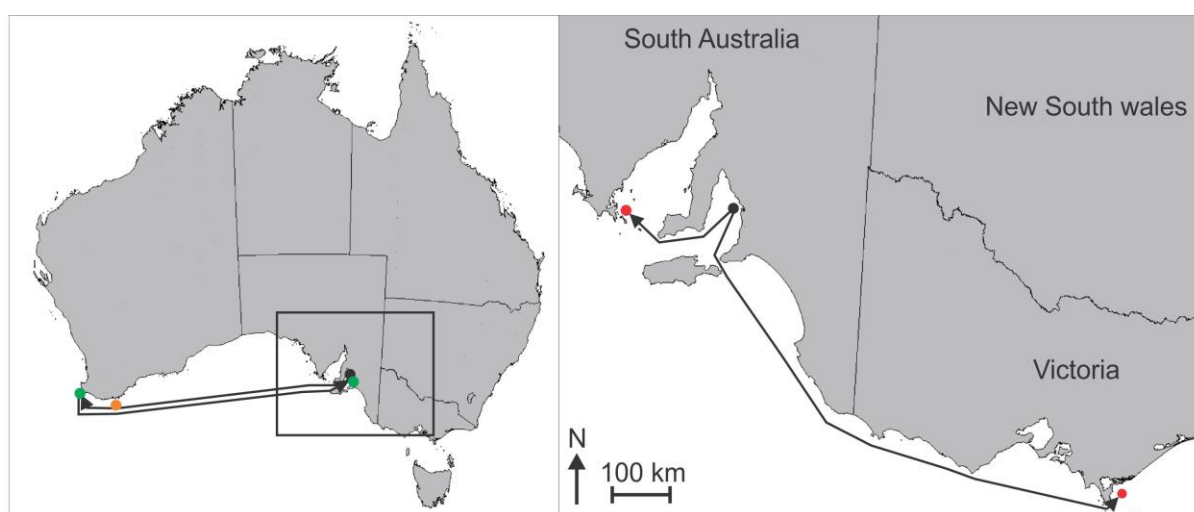


Figure 5 from Huveneers et al. (2014): Maps of movements of tracked sharks from tag attachment sites (black dots). Green dots (track) and orange dot (observation) = dusky (adult male). Red dot = dusky (adult female). Blue dot = bronze whaler (adult female). © South Australian Research and Development Institute, reproduced with permission.

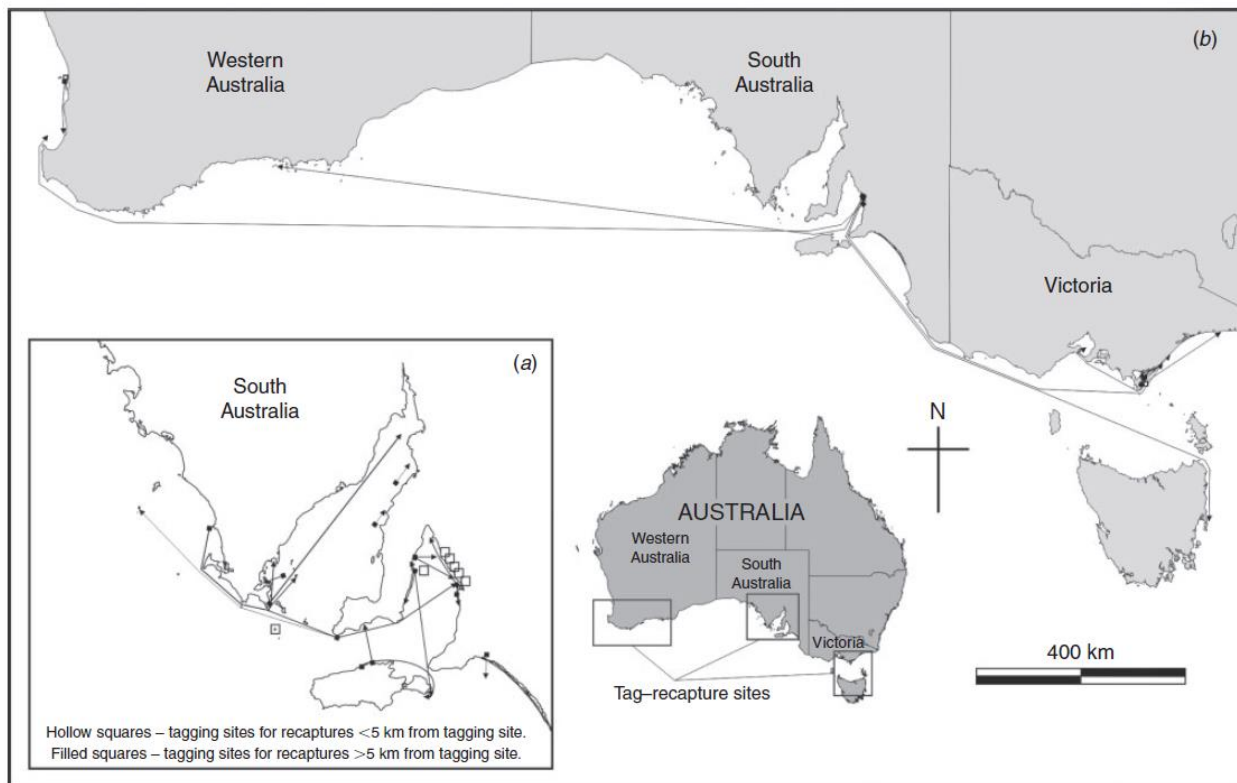


Figure 6 reproduced from Rogers P.J. et al. (2013) with permission from CSIRO publishing: Maps of reconstructed ‘movements’ of tagged and recaptured bronze whaler and dusky sharks (1977 – 2008). A) Regional scale movements of < 374 km within the Gulfs and GAB. B) Long-distance movements from SA to WA, Vic and Tas. Filled arrow head represent capture locations of sharks recaptured < 5km from the tag attachment sites.

School shark population structure was assessed at a broad-scale (global) level by Chabot et al. (2009) who found genetic separation between the populations around each continent. The population in Australian waters is genetically distinct from those in the waters around other Africa, North and South America and Europe, probably because of very low levels of trans-continental migration (Chabot et al. 2009). This study did not report structure between Australian sampled populations (based on 50 samples from across Australia & New Zealand), although this finer-scale analysis was not a stated aim of their research. Further research on school shark by Hernandez et al. (2015) found no population structuring within southern Australia, or between there and New Zealand, indicating broad-scale connectivity of populations across the Tasman Sea. Current PhD research at the University of Adelaide is investigating the location of pupping grounds and possible natal and nurse areas for school shark in SA waters using satellite tags and vertebrae chemistry (McMillian, unpublished data).

Juvenile shortfin mako sharks tracked from the Great Australian Bight showed an affinity for offshore areas around the mid-outer shelf zone, therefore are predominantly found outside the State’s coastal marine management area (but may potentially interact with offshore island Marine Parks and Commonwealth Marine Parks in the NRSMPA) (Rogers et al. 2015b). Some tracked individuals also

moved over long distances into the Coral Sea and across the Indian Ocean, with the greatest distance travelled being > 25,000 km (Rogers et al. 2015b). Mitochondrial and microsatellite DNA analyses on shortfin mako sharks show a high level of connectivity across Australian management jurisdictions and with South Africa and northern hemisphere populations (Rogers et al. 2015a). These combined results indicate that this highly migratory species, along with many of the other large shark species found in South Australian waters, will not be adequately protected by the state (or national) marine park networks because of their long-distance movements, which take them outside SA (and even Australian) waters. The picture is similar for blue shark; tracking data from 2015/16 demonstrate a preference for offshore waters in oceanic zones >1000 m deep (eastern and central GAB, Bonney upwelling and Tasman Sea) and long-distance movements, although some individuals did spend time (up to 14 %) within the Great Australian Bight Commonwealth Marine Reserve (Rogers et al. 2016). This indicates that ensuring the ongoing viability of these wide-ranging species is likely to be dependent on the implementation of both national (i.e. NRSMPA) and international recommendations around marine protected area network coverage. The IUCN's recent global targets for "30% of each marine habitat" to be set aside in "highly protected MPAs and other effective area-based conservation measures" by 2030 will be helpful in ensuring this (IUCN 2016).

White sharks have been demonstrated to use areas within and around the Neptune Islands Marine Park consistently, with acoustically tagged sharks showing residency periods of up to 10 days at a time (Rogers et al. 2014b; Rogers 2016); however, individual sharks are not resident in the area year-round. Five white sharks were tracked by (2016) from the Neptune Islands (a state Marine Park) and moved distances of between 9 and 1,931 km from the tagging site, using both the deep continental shelf slope and shallower habitats in northern Spencer Gulf. The use of shallow Gulf habitats at certain times of year is supported by acoustic tagging studies on white sharks that report detections in north-west and north-east Gulf St Vincent and Adelaide Metropolitan waters (Huvneers et al. 2014). Unfortunately, these studies do not report whether the sharks spent time in the Gulf Marine Parks. These results combine to suggest broad-scale connectivity of inshore and offshore habitats for this species in SA, supported by broader-scale research that demonstrated no population structure for white sharks within or between SA and WA (Blower et al. 2012). However, further detailed information about the species' movements and residency will be required to assess the adequacy of the Marine Parks Network for their protection while they are in SA waters.

Seabirds:

Goldsworthy & Page (2010) report a general lack of data on crested tern distribution and population structure/connectivity, with long term monitoring data only available (intermittently) from a single study site in SA (Troubridge Island in Gulf St Vincent) and no information on demographic or genetic connectivity. An earlier study of banded birds (from 18 colonies in SA) showed long-distance dispersal from banding locations (>2000 km); however, this study relied on recoveries of sick and wrecked birds which may have been carried some distance by currents (Waterman et al. 2003). Even so, it demonstrates the wide at-sea distribution of birds from SA colonies (Figure 7) and highlights the need for inter-annual tracking data that can elucidate habitat use of non-breeding birds and adults during inter-breeding periods and dispersal behaviour of fledged juveniles from the colony during their pre-breeding years. McLeay et al (2010) tracked adult crested tern movements during chick-rearing, when they are central place foragers who must return to the colony to provision chicks. The typical foraging trip was < 40km from the colony, although distances of up to 118 km were recorded. Figure 8 shows the tracks from tagged birds (McLeay et al. 2010) and indicates that approximately half of the foraging activity of the tracked birds during the breeding season falls within the Habitat Protection or General Managed Use Zones of the Lower Yorke Peninsula Marine Park, however foraging trips in southerly or easterly directions were not encompassed within the Marine Park boundaries.

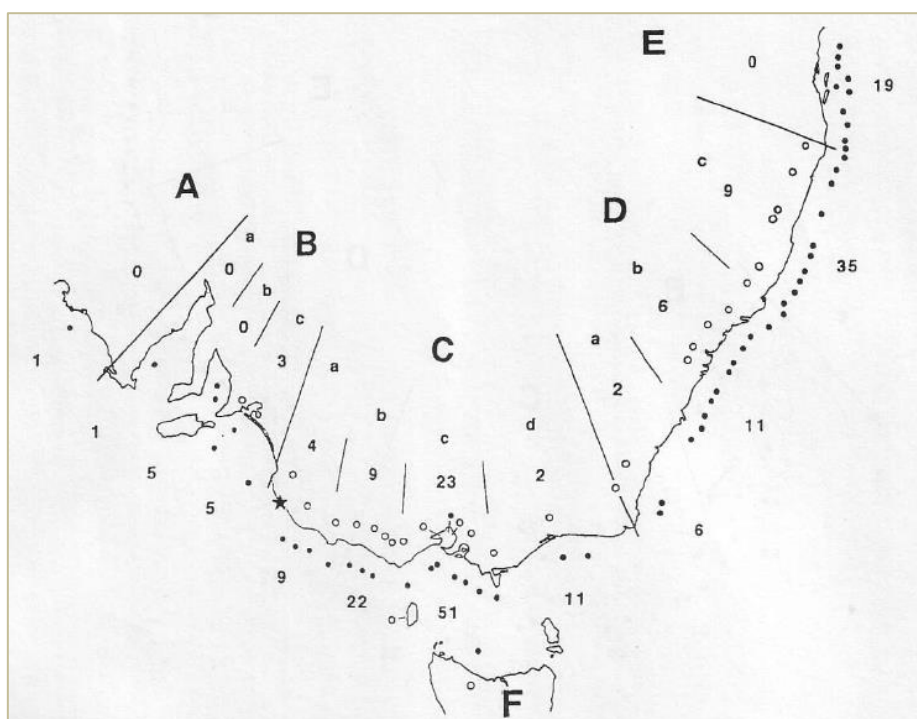


Figure 7 from Waterman et al. (2003): Locations of recoveries of dead or dying crested terns that were banded at Penguin Island in SA (indicated by a black star). Immature, one-year and two-year birds are shown by solid circles, and mature, three-year and older birds are shown by open circles.

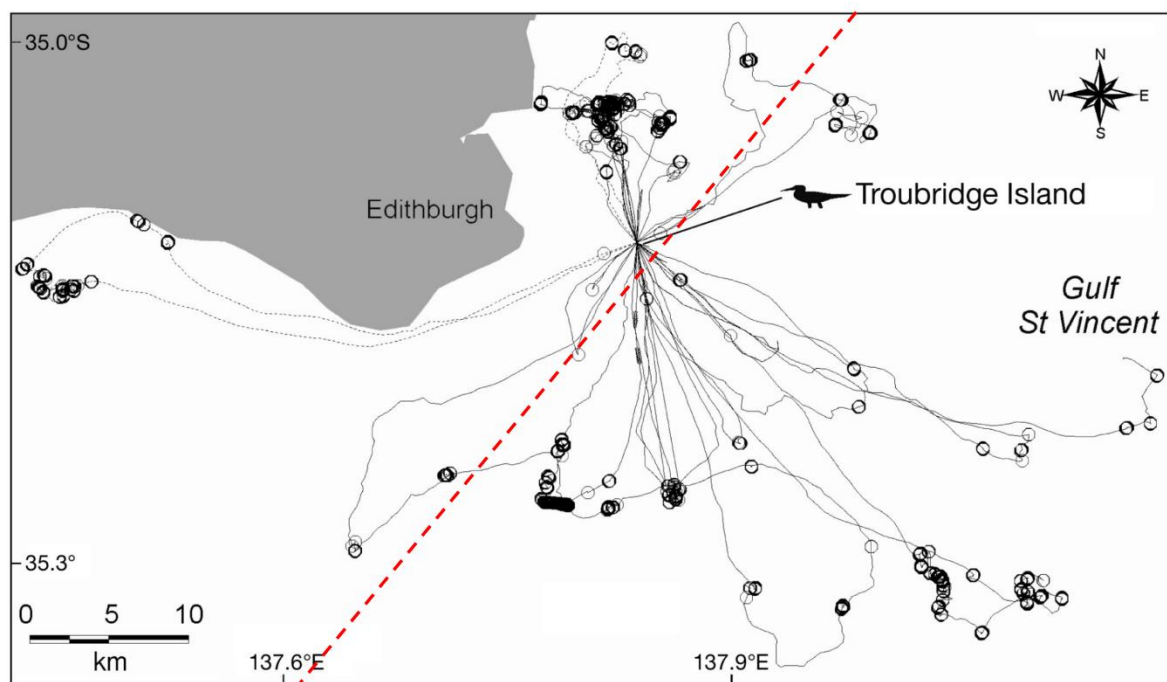


Figure 8 adapted from McLeay (2009): Crested tern foraging trips from Troubridge Island colony, tracked using GPS (N = 21 adult breeding birds). Circles indicate areas of concentrated foraging. Red dashed line indicates the approximate location of the outer boundary of the Lower Yorke Peninsula Marine Park (foraging areas inshore of this line are within the marine park Habitat Protection or General Managed Use Zones).

There are approximately 100 little penguin colonies in SA (DEWNR, 2016), several of which have seen severe population declines over recent years (Goldsworthy et al. 2010; Department for Environment 2016). Figure 9 shows the location of known colonies and indicates population sizes based on the most recent estimates (some of which may be based on decades-old data) (Department for Environment 2016).

Tracking of adult little penguins has been carried out from some breeding colonies: Granite Island (n = 10), West Island (n = 8), Troubridge Island (n = 18), Pearson Island (n = 12), Olive Island (n = 12) and Reevesby Island (n = 5) (Bool et al. 2007; Wiebkin 2012). This information alone is of limited use in inferring population connectivity as it focusses on a single life stage during a limited temporal period. However, these data can provide information on the level of protection afforded by the SA Marine Parks Network to adult birds during the chick-rearing season (see examples in Figure 10). It should be noted that currently only very small populations persist at the colonies on Granite and West Islands and in Kingscote and Penneshaw (Department for Environment 2016), therefore the tracking data from these colonies may no longer be relevant or representative.

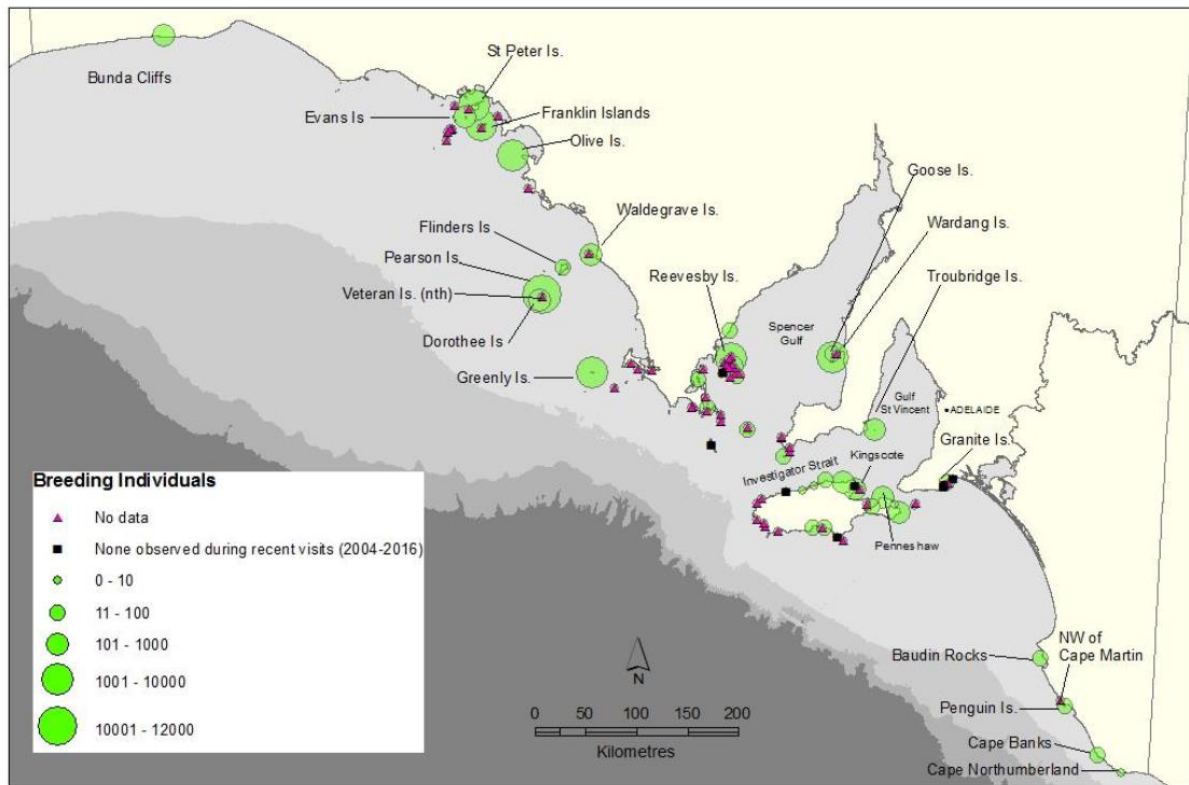


Figure 9 from DEWNR (2016): Distribution of little penguin colonies in SA with estimates of number of breeding birds. Black squares show locations where penguins were recorded historically, but were not observed in visits between 2004 and 2016. Population estimates are from the best-available data, which have varying levels of reliability/uncertainty.

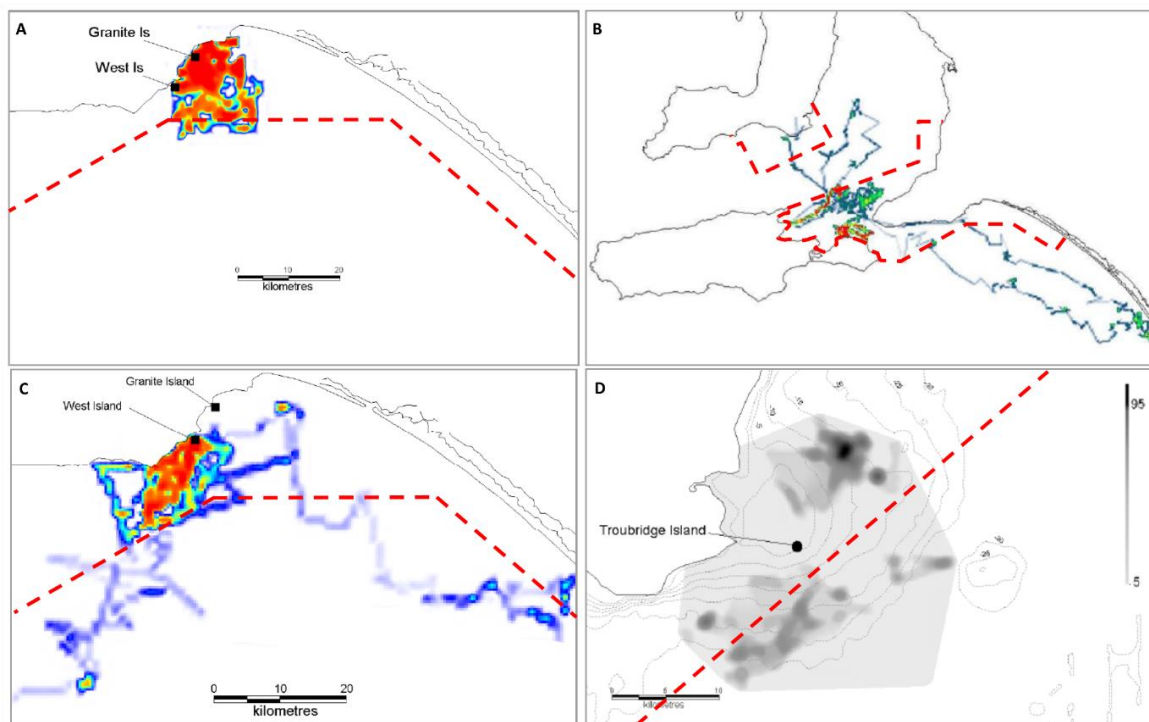


Figure 10 adapted from Bool et al (2007) and Wiebkin (2011): Density maps indicating the proportion of time that tracked breeding adult little penguins spent foraging in the waters around their colonies. A) Granite Island (n = 10); B) Kingscote and Penneshaw (n = 5); C) West Island (n = 8); and D)

Troubridge Island (n = 15). The red dashed lines show the approximate locations of the outer boundaries of relevant SA Marine Parks. © South Australian Research and Development Institute, reproduced with permission.

There is no evidence of phylogeographic structuring in Australian little penguin populations, which infers a high level of historical relatedness between colonies (Peucker et al. 2009). A broad scale study of the whole of south-eastern Australia provided evidence of some contemporary genetic differentiation between SA populations and populations in other states (Overeem et al. 2008). At a finer scale, only one population in SA (Troubridge Island) is genetically distinct from all others, suggesting that there is some genetic connectivity between most South Australian colonies. However, differences in morphological, behavioural and ecological traits indicate that natural selection due to local environmental conditions (water temperature, water depth and prey availability) influences the birds at each colony (separated by < 150 km) (Wiebkin 2012; Colombelli-Négrel 2016). The differences between morphological traits were greater between birds from colonies that were further away from each other (Colombelli-Négrel 2016). These results suggest a low level of demographic connectivity between the populations at different colonies, which may negatively affect their ability to recover from population declines.

Short-tailed shearwaters tracked using satellite transmitters during chick-rearing from two SA island colonies (Althorpe Island and St Peter Island) were shown to have two primary modes of foraging. The first was 'short' trips into waters 35 - 70 km from the colonies (Einoder et al. 2005), and the second was 'long' trips into the Southern Ocean – some going as far as the Antarctic ice front (Einoder et al. 2011). These results indicate that there are likely areas for foraging around the colonies which may be afforded some protection by the SA marine parks network (for these two colonies this would particularly be Western Kangaroo Island Marine Park, Southern Spencer Gulf Marine Park and also the South-west Commonwealth Marine Park). However, the interspersed 'long' foraging trips of > 1000 km means there are considerable periods when the birds are not using habitats within the network, even during the breeding period when they are central-place foraging from SA colonies (Einoder et al. 2005; Einoder et al. 2011).

Data on population structure and connectivity for other sea and shore bird species using SA waters are lacking.

Marine mammals:

Recent genetic studies using mitochondrial DNA (Campbell et al. 2008; Lowther et al. 2012) and microsatellite loci (Ahonen et al. 2016) show that populations of Australian sea lions are highly

structured at a fine scale in SA and that both males and females are strongly philopatric. Ahonen et al. (2016) found that at least 68% of the adults they sampled were at their natal colonies. These results indicate low dispersal and high levels of population structuring, which fits with the species asynchronous breeding behaviour at the different SA breeding colonies, but is somewhat surprising given their capability for long distance movements (> 350 km) (Ahonen et al. 2016). Lowther et al (2012) demonstrated individual foraging specialisation and discrete foraging habitats (using stable isotopes), and suggested that dispersal was limited by these behaviours. Genetic differentiation increased with distance between colonies (Campbell et al. 2008; Ahonen et al. 2016) and there was no evidence of exchange between WA and SA colonies (Ahonen et al. 2016; Figure 11). Despite the low overall connectivity, the study found moderate levels of contemporary migration between most colonies, with the exception of Lewis Island, which is a source of dispersing animals, but has not received many migrants over recent generations (Ahonen et al. 2016; Figure 11).

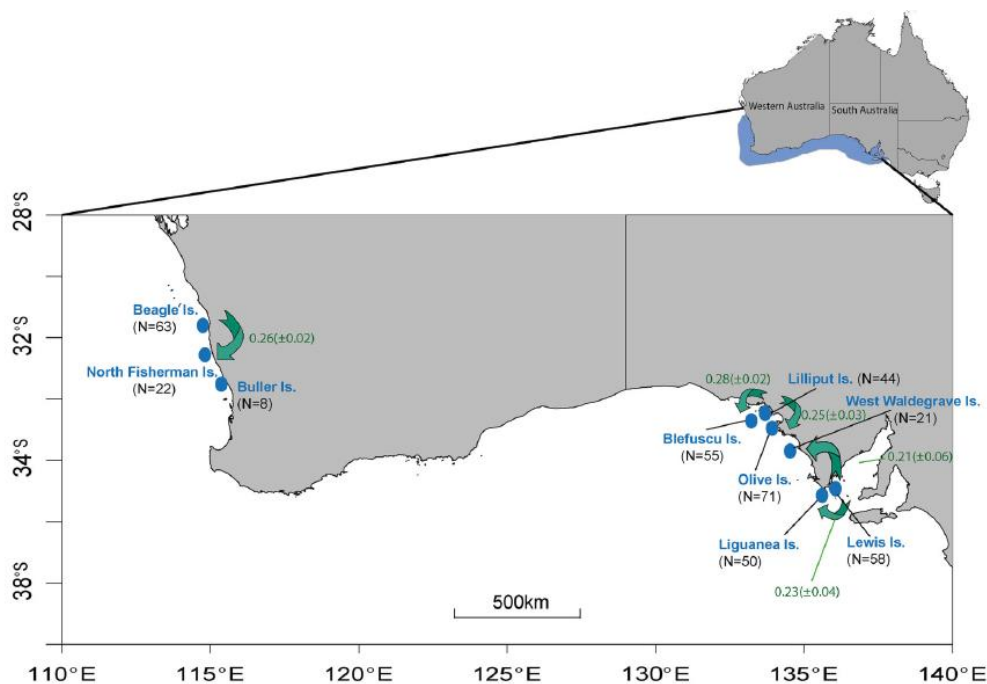


Figure 11 from Ahonen et al. (2016): Location of sampling sites for Australian sea lion DNA with number of samples from each location indicated. Green arrows and values show the direction and magnitude of contemporary movement between pairs of sites. © 2016 Ahonen, Lowther, Harcourt, Goldsworthy, Charrier and Stow. Reproduced under a creative commons license.

There are currently no published studies on the population structure or connectivity of long-nosed fur seals in SA waters although it is likely that some relevant data may be held by SARDI, collected as part of the Great Australian Bight research program. The outcomes of the multispecies tracking work associated with this program are likely to be very useful in terms of assessing connectivity in the marine parks network for mobile megafauna.

Studies on short-beaked common dolphins indicate no population structuring within SA waters (but indicate that SA populations are not well-connected with those in Tasmania). A high level of connectivity across SA is to be expected for this vagile species, which is often found aggregated into very large pods (Bilgmann et al. 2008). On the contrary, there is evidence for population structure in bottlenose dolphins in SA, evidenced by restricted gene flow (indicating a lack of contemporary connectivity) between populations in Spencer Gulf and in coastal areas to the west of the Gulf, separated by distances of 100s of km (Bilgmann et al. 2007). A finer-scale study of bottlenose dolphin residency along the coast of Adelaide found that there was a mixture of resident and visiting dolphins using these waters (Zanardo et al. 2016). This indicates that there is likely to be some connectivity between populations, at least within this region of Gulf St Vincent.

Attard et al. (2010) showed that there is a high level of connectivity in the wide-ranging blue whale, which is an annual visitor to SA waters that are influenced by the Bonney Upwelling. Individuals sampled within SA waters were also not genetically differentiated from those sampled in Victoria or WA, suggesting that there is a single mobile population feeding in areas of coastal upwelling along the southern coast of Australia (Attard et al. 2010). This level of connectivity and long-distance dispersal means that this species is unlikely to be adequately protected throughout its life-cycle by the SA Marine Parks Network, although they will potentially afford some protection at specific feeding grounds (depending on the zoning). There is no research that looks specifically at the connectivity of southern right whales in SA waters, although there are data on their distribution and offshore movements (3 tracked individuals) in the Great Australian Bight (Mackay et al. 2015a; Mackay et al. 2015b), as well as information suggesting an important calving area in Encounter Marine Park (Australian Government DSEWPC 2012). These studies indicate that there is a high level of occupancy of southern right whales (including mother and calf pairs) in the Far West Coast Marine Park, particularly around the Head of Bight and Yalata Beach nurse areas, during July – September (Mackay et al. 2015b; Figure 12 b, c & d). However, tracked individuals (N = 3) showed long-distance dispersal, moving outside State waters and indicating broad scale connectivity with areas under WA and Commonwealth jurisdiction (Mackay et al. 2015a; Figure 12 a). This long-range connectivity is also supported by (Bilgmann et al. 2014) who undertook inshore cetacean surveys as part of the Great Australian Bight Research Program from July – August 2013. Their results suggest that the inshore waters between Ceduna and Coffin Bay are used by whales transiting from feeding grounds to aggregation sites at the Head of the Bight and/or Fowlers Bay in the Nuyts Archipelago Marine Park, and may also occasionally be used for calving and nursing (Bilgmann et al. 2014).

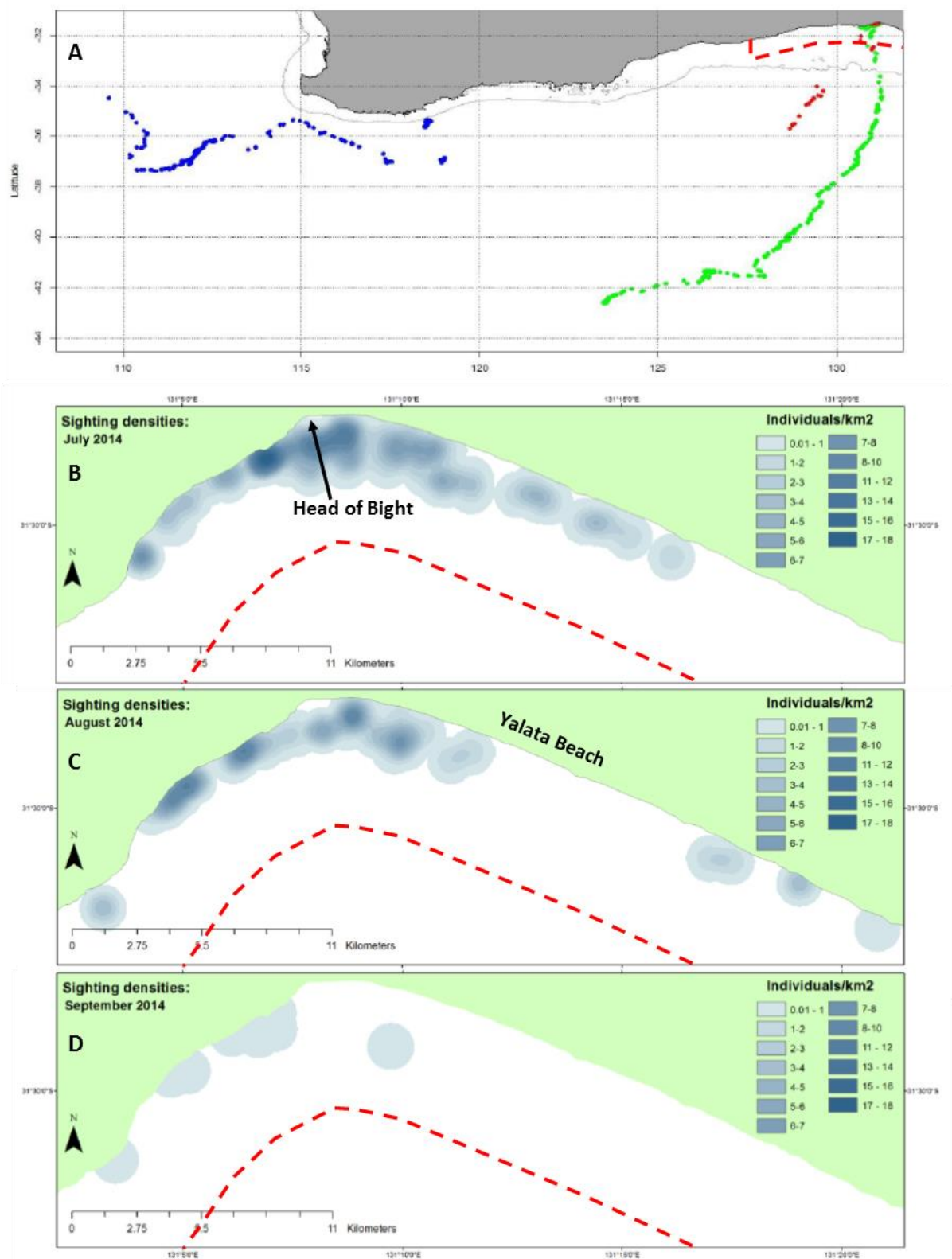


Figure 12 adapted from Mackay et al. (2015a) and Mackay and Goldsworthy (2015b): Maps of the abundance, distribution and movement of southern right whales in the Great Australian Bight. A) Tracks of 3 tagged adult female southern right whales, all accompanied by calves (deployed September–November 2014). B), C) & D): Kernel density plots showing the abundance and distribution of southern right whales (from aerial survey data collected July – September 2014). Red dashed lines indicate the approximate location of the outer boundary of the Far West Coast Marine Park. © South Australian Research and Development Institute, reproduced with permission.

Invertebrates:

Blue crabs are generally confined to three areas around the SA coast; northern Spencer Gulf, Gulf St Vincent and the west coast of Eyre Peninsula. These have been shown to be discrete sub-populations with limited gene flow, probably due to barriers to larval dispersal meaning that each population is predominantly self-sustaining (Bryars et al. 1999). Chaplin et al. (2001) present further evidence for genetic sub-structuring at a fine scale, with genetic differences (and hence low connectivity) between populations in different areas of Spencer Gulf. Given this apparent fine-scale population structuring and low connectivity, there is potential for Marine Parks in the Gulfs to adequately protect entire populations of blue crab. However, this would depend on the size and location of the Park and its coverage of critical habitats at varying depths. The distribution of blue crab larvae is largely unknown, although the genetic sub-structuring indicates self-replenishment (therefore local retention) of populations is common. Post-settlement juvenile blue crabs have a broadly similar distribution to the adults, but different specific habitat and depth preferences, actively selecting areas of specific intertidal seagrass (*Zostera* and *Heterozostera sp*) over other seagrass species, unvegetated intertidal areas or subtidal seagrass habitats (Svane et al. 2005). Svane and Cheshire (2005) reported several intertidal and shallow subtidal sites that supported particularly high abundances of juvenile blue crabs, these were areas around Port Broughton and Port Pirie in Spencer Gulf, and Barker Inlet in Gulf St Vincent. These details may be very useful in understanding the capacity for the Marine Parks in the Gulfs and western Eyre Peninsula to protect all life-stages of the species.

Teske et al. (2015; 2016) combined genetic and oceanographic dispersal modelling approaches to study the population structure of the intertidal molluscs black nerite and false limpet. This multidisciplinary approach found a signal of isolation by distance in both species sampled along the SA coast, attributed primarily to self-recruitment because of local and regional hydrodynamics (Teske et al. 2015; Teske et al. 2016). These results are surprising, given the long pelagic larval duration of the two species. For the false limpet, it was inferred that larval retention is promoted in areas where the continental shelf is wider and water movement is slower (Teske et al. 2016). The results of these two studies highlight the benefits of combining oceanographic modelling and genetic studies to infer realised/demographic connectivity in a meta-population. They have broad implications for other SA coastal broadcast spawning species (with limited larval mobility, but long larval duration), which may be assumed to be panmictic along the coast, but in fact can show significant isolation by distance due to oceanographic factors (Teske et al. 2015; Teske et al. 2016).

Research by Donnellan and Gillanders on giant Australian cuttlefish (unpublished) used samples from across southern Australia and combined multiple approaches to assessing population structure (microsatellite DNA, statolith chemistry and body morphometrics). They found evidence of five populations across the range of the species, including two in NSW; one that spanned Victoria; two in SA (one in southern Spencer Gulf and Gulf St Vincent, the other in northern Spencer Gulf); and one from western SA through to WA. Subsequent molecular analyses of samples show that there are two highly-resolved genetic clusters in SA waters, one occupying the northern part of Spencer Gulf, and another in southern Spencer Gulf and Gulf St Vincent (no samples were included from other areas of the SA coast) (Gillanders et al. 2016; Figure 13). Although the populations are clearly separated genetically, with evidence of hybridisation, their distributions overlap (Figure 13), indicating that genetic separation is maintained by behaviour (i.e. philopatry to breeding aggregations; Gillanders et al. 2016) and the species' limited dispersal abilities (Payne et al. 2013). The northern population is known to breed at the Point Lowly mass aggregation site and the southern population breeds elsewhere in Spencer Gulf or other coastal areas in SA. The Upper Spencer Gulf Marine Park clearly provides some protection for the northern population's mass breeding aggregation (around Point Lowly and Whyalla), however there is little known about the breeding sites of the southern population or the dispersal and habitat usage of either population outside of the breeding season. The northern part of Spencer Gulf, including the breeding aggregation site has also been protected under fisheries legislation (particularly the cuttlefish fishing exclusion zone), which is unrelated to the marine parks legislation and is likely to provide considerable protection for the species during breeding.

In contrast to the Giant Australian Cuttlefish, Doubleday et al. (2009) found evidence of high levels of connectivity over distances up to 1,500 km in the Maori octopus in SA, based on both genetic and morphometric analyses. This indicates that there is likely to be wide scale movement of this species in SA coastal waters; but with little information about specific movements or records of dispersal behaviour it is not currently possible to assess how well the Marine Parks Network protects this species.

Greenlip abalone have discrete populations between the southern states of Australia, as well as at a finer scale within SA waters (Miller et al. 2014), with greater isolation between reefs that are further away from each other (Figure 14). Miller et al (2014) also provide detailed descriptions of estimated numbers of migrants between pairs of sampled populations in SA, which will be very informative for assessments of marine parks adequacy for this species. Blacklip abalone have been shown to have similar levels of fine-scale population structure (low connectivity) in Tasmania (Miller et al. 2009). In South Australia, blacklip abalone have been separated into proposed discrete populations, over small

spatial scales (10s – 100s km) based on clear morphological differences, indicative of low connectivity due to limited larval dispersal (Saunders et al. 2009). Unfortunately, this study was limited in terms of spatial scale, only covering a section of the coast in the far southeast of the state (Saunders et al. 2009).

Based on these studies, it is likely that no-take sanctuary zones within SA's marine parks network that contain rocky reefs inhabited by abalone will provide high levels of protection to the species given the low connectivity between populations.

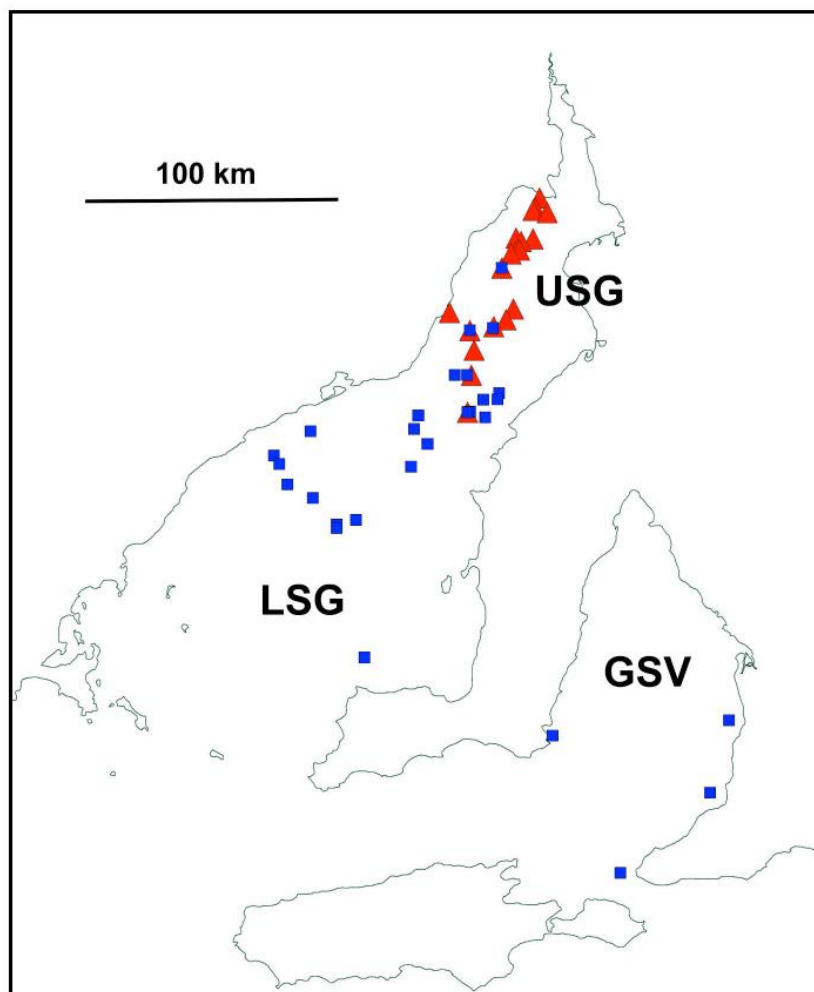


Figure 13 from Gillanders et al (2016): Map of the Gulfs region of the SA coast showing sampling locations of giant Australian cuttlefish with points coloured to indicate the discrete genetic clusters: red triangle = northern cluster, blue square = southern cluster. USG = upper Spencer Gulf, LSG = lower Spencer Gulf, GSV = Gulf St Vincent (samples from GSV represent multiple individuals). © Fisheries Research and Development Corporation, reproduced under a creative commons license.

Population sub-structuring in the sea urchin *Heliocidaris erythrogramma* was inferred by Beck and Styan (2010) using differences in patterns of colouration. They found clear phenotypic differences

between samples from the two South Australian Gulfs (red dermis) and samples from further east on the state's coastline (predominantly white dermis). These trait differences indicate population structuring, however further investigation would be required to confirm the demographic implications of these differences.

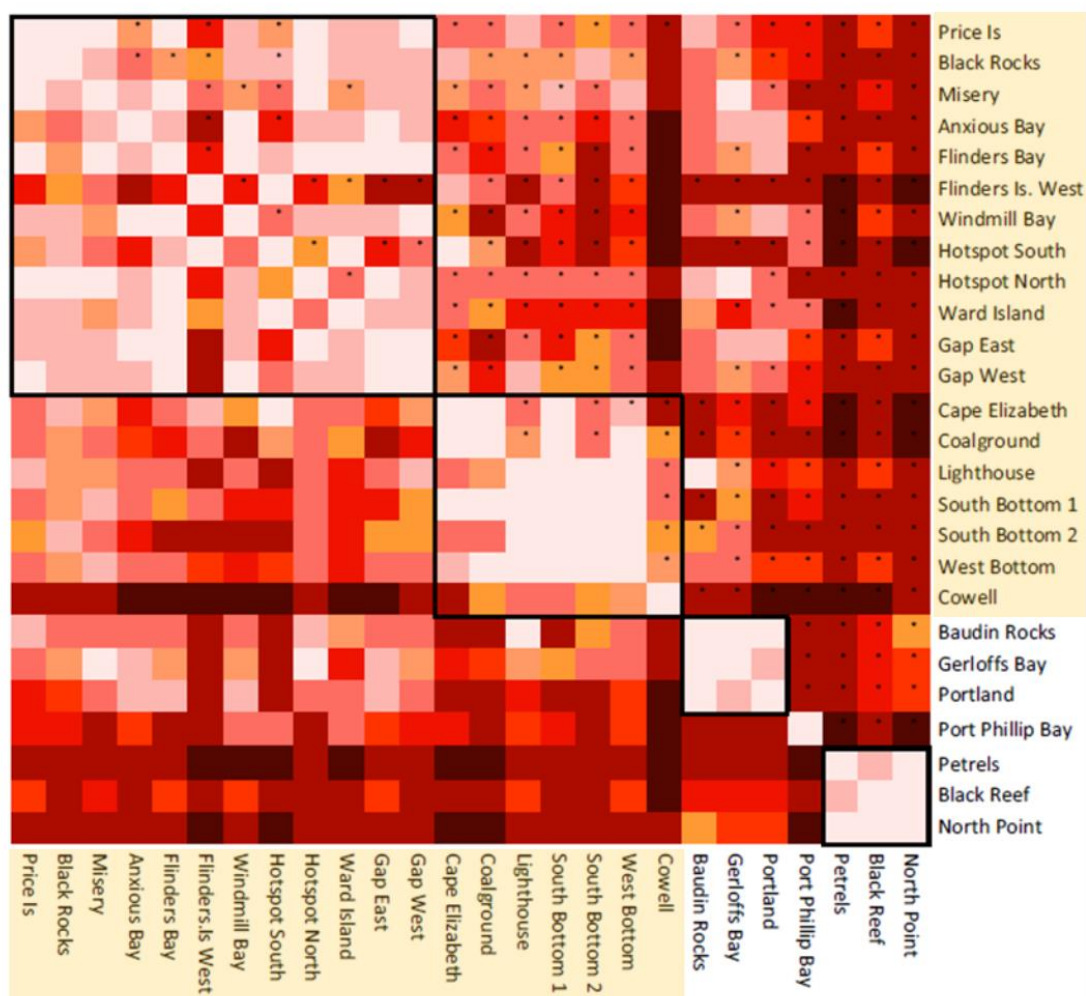


Figure 14 adapted from Miller et al (2014): Heat map showing pairwise genetic differentiation (based on Jost's D) among all populations of greenlip abalone sampled in south-eastern Australia. Highlighting around site names has been added to indicate SA sample sites. Black borders enclose biogeographic areas and asterisks indicate significant pairwise genetic differentiation. © 2014 John Wiley and Sons Ltd. Reproduced with permission.

Southern rock lobsters monitored in SA waters via a tag and release program between 1993 and 2003 ($n = 14,280$) were found to move variable distances in different areas, in a non-predictable way (Linnane et al. 2005). Most lobsters did not move over large distances, with 85 % within 5 km and 68 % within 1 km when they were recaptured (Linnane et al. 2005). However, there were areas in the south-east of the state where systematic offshore movements of < 20 km were recorded, and around Yorke Peninsula some individuals moved > 100 km (from inside to outside the Gleeson's Landing rock

lobster sanctuary). There were also age and sex-based differences in movement behaviour, with young females being most likely to move greater distances and to go longer before being recaptured than other groups (Linnane et al. 2005). This information is pertinent to any assessment of the ability of marine parks to effectively protect this species, which has been designated a marine parks program indicator species (see Bryars et al. 2017b). It is particularly notable that lobsters in inshore areas appeared to move greater distances than those initially captured further offshore (Linnane et al. 2015).

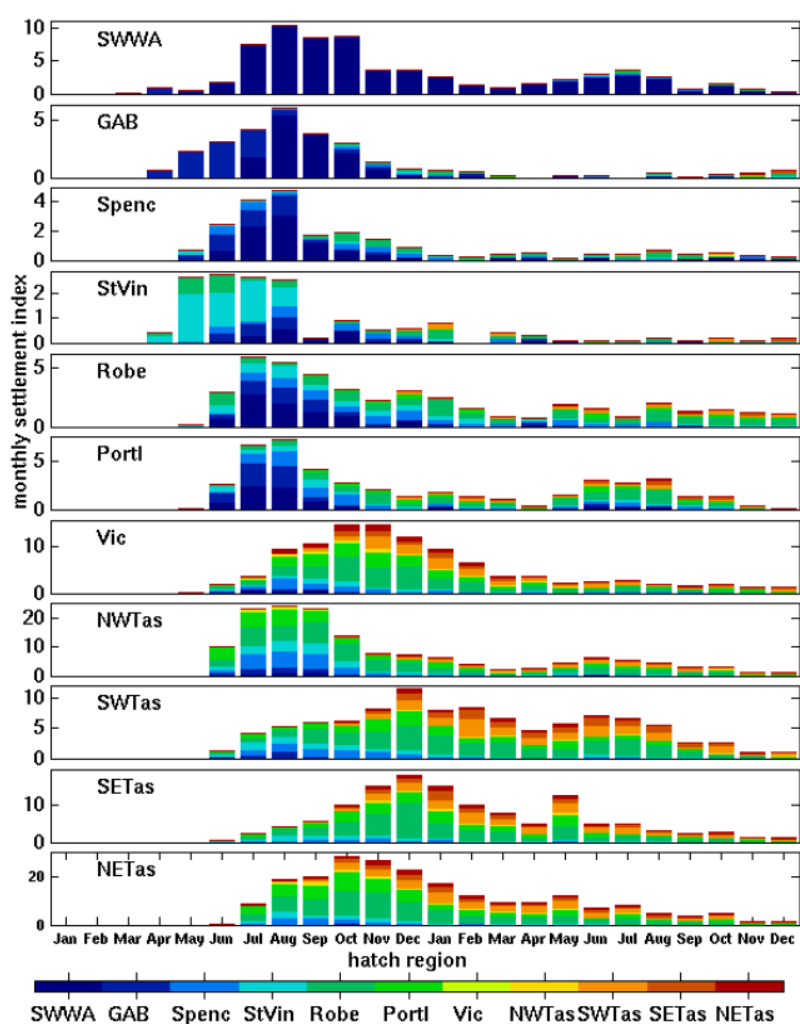


Figure 15 from Bruce et al. (2007): Source-sink dynamics from a larval transport model for southern rock lobster. Monthly indices of settling larvae are given for each region, colours indicate the origin of the larvae. © Fisheries Research and Development Corporation, reproduced under a creative commons license

Broadscale studies of southern rock lobster genetics indicate that there is a high level of connectivity between populations across the whole species' range in Australia and New Zealand (Linnane et al. 2015 and references therein). This level of connectivity is likely to be due to the combination of a long pelagic larval phase and oceanographic drivers. This is supported by larval transport modelling done

by Bruce et al (2007) who show that larvae quickly disperse from release sites and travel alongshore and into offshore waters where they may become entrained in shelf edge flows, cyclonic and anticyclonic eddies. Even so, there is a reasonable amount of regional retention of larvae, especially in the Great Australian Bight. In south-eastern SA there is a greater chance of larvae being moved out of the region causing greater levels of broad-scale connectivity with Tasmania and eastern Victoria. Bruce et al. (2007) provide detailed results of larval retention and external recruitment (i.e. source-sink dynamics; Figure 15) for each region within SA (split into nominally: northern SA, GAB, Spencer region, Vincent region, southern SA and Robe). These data could be extremely useful in looking at detailed connectivity between specific SA Marine Parks.

There is a reasonable amount of information on adult western king prawn movement, with inferred connectivity between northern and southern Spencer Gulf and eastwards along the coast of western SA from Ceduna to Coffin Bay, potentially passing through parts of Nuyts Archipelago, West Coast Bays and Investigator Marine Parks (movement information is reviewed in Beckman et al. 2014; Noell et al. 2017; Figure 16). Spatial patterns of larval settlement for western king prawn in Spencer Gulf have recently been modelled by McLeay et al (2016). Their results indicate source-sink dynamics, highlight key areas for supply and settlement of recruits into the Spencer Gulf prawn population and illustrate the importance of including larval swimming behaviour in such models (Figure 17). The main settlement sites were in mangrove areas along the western and north-eastern coast of Spencer Gulf, which coincide with the locations of the Upper Spencer Gulf, Franklin Harbour and Sir Joseph Banks Group Marine Parks (McLeay et al. 2016; Figure 17).

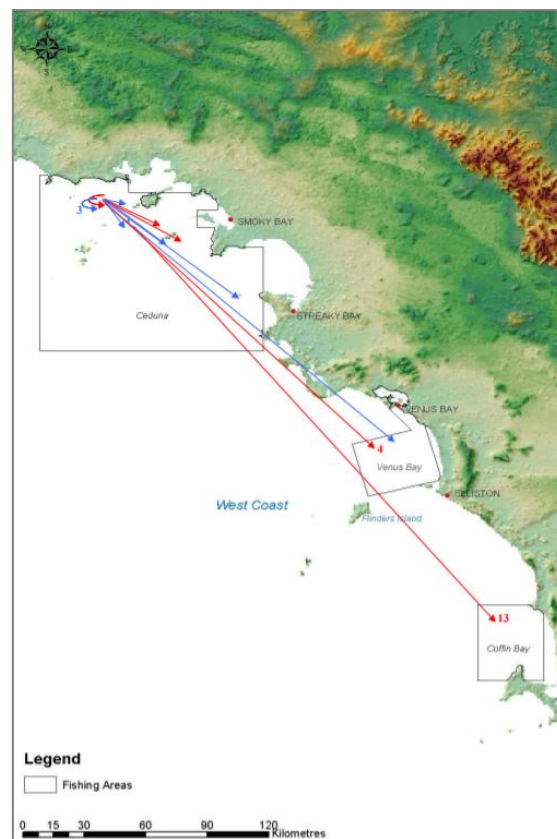


Figure 16 from Beckman et al. (2014): Map indicating prawn movements from tag-recapture data. Tagged prawns were deployed in Ceduna in 2002 (red) and 2003 (blue) and recaptures were made in Venus and Coffin Bays. Numbers indicate more than one recapture in an area. Looped arrows show local recaptures (provided only for Ceduna). © South Australian Research and Development Institute, reproduced with permission.

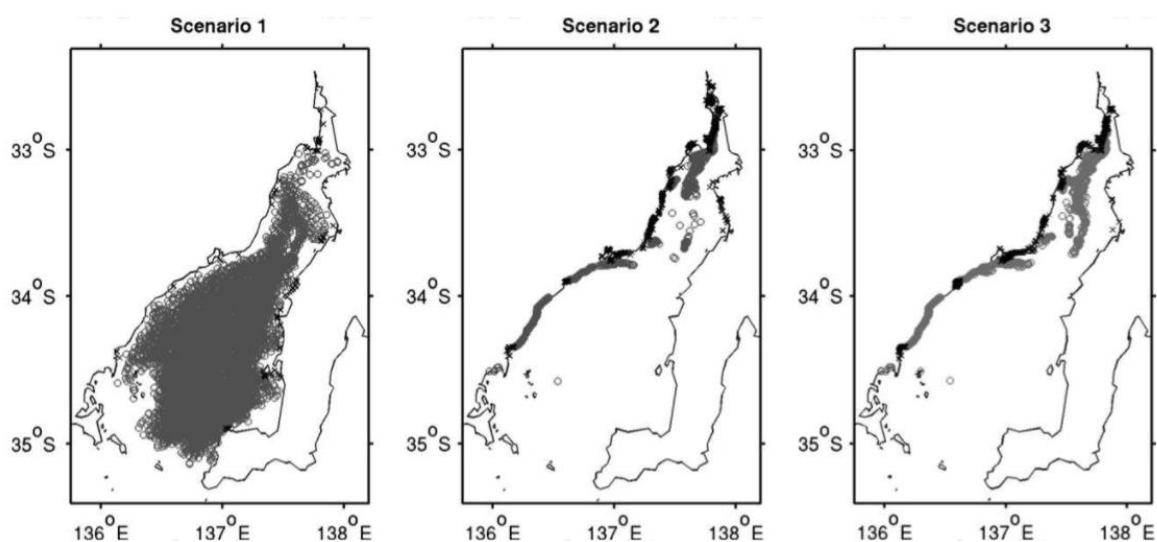


Figure 17 from McLeay et al. (2016): Final distribution of settled (black) and non-settled (grey) larvae simulated under each of three scenarios in a biophysical model. All models included tidal and atmospheric forcing. Scenario 1 did not include larval swimming behaviour. The difference between scenarios 2 and 3 was the average water temperature at the time of spawning, which were set at 16.9 °C and 19.9 °C respectively (and impacted larval duration). © 2014 John Wiley and Sons Ltd. Reproduced with permission.

Distribution of habitats:

The majority of the area of SAs marine park network is unmapped (Bryars et al. 2017a), meaning that there is a lack of information about the locations and extents of the different marine habitats contained within the parks. It is particularly important to have adequate spatial data and summary data for key habitat-forming species such as seagrasses, saltmarshes, macroalgae and mangroves, which are known to play important roles in supporting the larval and juvenile life stages of many of SAs coastal fish and invertebrate species. There are better data for some habitat types than for others – for example intertidal habitats (mangrove, saltmarsh and intertidal seagrasses) tend to be mapped better than subtidal habitats (DEWNR 2015b; DEWNR 2015a), with deeper subtidal areas particularly lacking in adequate mapping. However, the majority of the 83 sanctuary zones have been mapped to some extent (DEWNR 2017).

4. Summary, knowledge gaps and recommendations

4.1. Summary of the existing literature

We have reviewed and summarised the data and existing studies that are relevant to connectivity within the South Australian marine parks network. The SA Marine Park Network was designed to protect biodiversity; however, the vast majority of the current literature on connectivity focuses at the species level. The most comprehensive information is generally available for species that support commercial fisheries, such as Australian sardine (Izzo et al. 2017), greenlip abalone (Miller et al. 2014), King George whiting (Jenkins et al. 2016) and snapper (Fowler et al. 2017). There are very few studies that have attempted to look at multiple species ($n = 2$) or that have integrated complementary approaches to enable a more robust understanding of connectivity over various spatial and temporal scales ($n = 16$).

A major limitation to the design of any marine park network is that it is unlikely to achieve its objectives for all species. This is because different species have different movement patterns, population structure and life histories. That being said, it seems intuitive that area-based protection measures, such as marine parks, will be of most benefit to relatively site-attached species such as the western blue groper (Bryars et al. 2012), harlequin fish (Bryars et al. 2016), leafy sea dragon (Stiller et al. 2017) or greenlip abalone (2014); and that they will have limited effectiveness for wide-ranging or migratory pelagic species such as the shortfin mako shark (Rogers et al. 2015a; Rogers et al. 2015b), southern right whale (Mackay et al. 2015a) or southern bluefin tuna (Proctor et al. 1995). However, even the site-attached species mentioned above have pelagic larval phases, the dispersal of which we know very little, if anything about. Therefore, if their populations are not self-sustaining, but rather are connected through larval dispersal with dependence on external recruitment, then the marine parks may not provide as much protection to their populations as anticipated – particularly if important source populations are in unprotected areas. This highlights the primary limitation that applies to any marine protected area or network, which is that they are unlikely to be able to protect all life stages of marine species, which tend to have either a pelagic larval phase and/or some separation of juvenile and adult life histories and habitats (Crowder et al. 2000; Walters 2000; Palumbi 2004; Olds et al. 2016).

The fact that very few of the reviewed studies were undertaken specifically to address the question of connectivity between SA marine parks makes it difficult to generalise or predict connectivity for the network on the basis of existing knowledge. There is clearly no ‘one-size-fits-all’ relationship between

life-history and connectivity. However, it is probably unrealistic to attempt to generate sufficient, connectivity-specific research on *all* SA marine species with which to answer the connectivity (and adequacy) question. So, we have attempted to summarise and tabulate the reviewed data in a couple of ways. This will hopefully be useful, at least as a starting point, for synthesising the available information on connectivity across all species (for which there are data) and the limitations of the network with regard to these species; as well as highlighting knowledge gaps (Table 2).

We have classified all species into groups related to their dispersal, movement and life-history characteristics, as well as qualifying the type of population structure reported for each species (if any) into broad categories. Note that these classifications are *examples* of ways to potentially synthesise connectivity information across species, and the specific thresholds of dispersal or classes of population structuring that we have used may need to be reviewed and revised, depending on the context of the question being asked.

The life history ‘types’ we have used to group the organisms are:

- Pelagic 1: Mobile adult with pelagic larvae/propagules (n = 10)
- Pelagic 2: Site-attached (< 2 km range) adult with pelagic larvae/propagules (n = 6)
- Pelagic 3: Mobile adult with fully developed young (n = 17)
- Benthic 1: Adults move over substrate with pelagic larvae/propagules (n = 7)
- Benthic 2: Adults rooted to substrate with pelagic larval phase (n = 7)

The population structure classes that we have used (inferred from the available information) are:

- Not reported/cannot be ascertained from the data available (n = 16)
- No structure (i.e. high levels of connectivity within SA waters) (n = 12)
- Isolation by distance (i.e. connectivity is greatest between neighbouring populations and decreases with distance) (n = 7)
- East-west/north-south differentiation (i.e. connectivity is systematically related to longitude or latitude) (n = 8)
- Geographic structure (i.e. some structuring, but the pattern did not fit the above classes or there was not enough data provided to categorise it) (n = 4)

Larval/propagule dispersal was classified broadly into ‘+’ and ‘-’ groups, which were defined using a dispersal threshold of 1 km (if the larvae were capable of dispersal distances greater than this they were given ‘+’ and less than this were given a ‘-’). This threshold was somewhat arbitrary and it may

be more informative and biologically relevant to determine the dispersal categories based on whether propagules disperse beyond their local population (however the data required to classify this are not available for most species in this review), or further than the smallest distance between marine parks containing relevant habitat types. In particular for ‘Pelagic 3’ type organisms (mobile adults with live young) this propagule dispersal categorisation is tricky. For example, many species of shark give birth to live young that are immediately fully independent and capable of moving > 1km, however their populations may still show structuring with clear differentiation of habitat use between adults and juveniles (e.g. dusky shark: Rogers et al. 2013; Huveneers et al. 2014).

Out of the 47 species that we found data on, 30 have adult movement distances of > 10 km and 35 have larvae/propagules that are capable of dispersing or moving distances greater than 1 km. None of the species that have adult movement distances of < 10 km (i.e. that may have the potential to be protected within a single marine park) were in the ‘– ‘ group for larval dispersal. This sheds light on the potential limitations of the SA marine parks in terms of their ability to encompass a species’ entire life history within a single protected area. It also highlights the importance of gaining a good understanding of species’ movement behaviour, space use, dispersal patterns and demographic connectivity, in order to be able to assess how well protected they are by the marine parks network as a whole.

Table 2: Summary of each species' 'adult & juvenile/post-settlement' and 'propagule/larval' movement/dispersal ranges, along with classification into an 'organism type' and 'population structure' group (see definitions on previous page), based on the data available to date. If a species is not included in the table, we did not find any literature on it in relation to connectivity, movement or population structure in SA waters. Propagule/larval dispersal was grouped into two classes using a threshold of 1 km dispersal distance (see details on previous page). Grey shading indicates that no quantitative data specific to dispersal/movement were available for a specific life stage. The * indicates that in cases where organisms are clonal (e.g. seagrasses), then adult dispersal ranges are commonly 100 m – 1 km, and may even be > 1 km. In addition, the * indicates that rafting flora (e.g. red algae) may lead to dispersal increasing to > 100 km. The version of this table in the Excel file associated with this document contains notes in each cell that explain the groupings and give citations for each species' classifications (see the file called 'Connectivity_database_v1.', sheet name 'Matrix').

Species	Adult & juvenile/post settlement movement range	Propagule/larval dispersal range '+' > 1km; '-' < 1km	Organism type	Population structure in SA
Wireweed (<i>Amphibolis antarctica</i>)	cms - 1 m*	-	Benthic 2	Geographic structure
Australian anchovy (<i>Engraulis australis</i>)	> 100 km	+	Pelagic 1	Not reported
Australian Sardine (<i>Sardinops sagax</i>)	> 100 km	+	Pelagic 1	East-west
Australian sea lion (<i>Neophoca cinerea</i>)	> 100 km	-	Pelagic 3	Isolation by distance
Bigeye thresher (<i>Alopias superciliosus</i>)	> 100 km	+	Pelagic 3	Not reported
Black bream (<i>Acanthopagrus butcheri</i>)	> 100 km	+	Pelagic 1	No structure
Black nerite (<i>Nerita atramentosa</i>)	1 m - 100 m	+	Benthic 1	Isolation by distance
Blacklip abalone (<i>Haliotis rubra</i>)	1 m - 100 m	+	Benthic 1	Geographic structure
Blue shark (<i>Prionace glauca</i>)	> 100 km	+	Pelagic 3	Not reported
Blue swimmer crab (<i>Portunus pelagicus</i> , <i>P. armatus</i>)	10 - 100 km	+	Pelagic 1	Geographic structure
Bluespot goby (<i>Pseudogobius olorum</i>)	10 - 100 km		Pelagic 2	Not reported
Bronze whaler sharks (<i>Carcharhinus brachyurus</i>)	> 100 km	+	Pelagic 3	No structure
Bottlenose dolphin (<i>Tursiops sp</i>)	> 100 km	-	Pelagic 3	East-west
Common galaxias (<i>Galaxias maculatus</i>)	10 - 100 km	+	Pelagic 2	Not reported
Common thresher shark (<i>Alopias vulpinus</i>)	> 100 km	+	Pelagic 3	Not reported
Crested tern (<i>Sterna bergii</i>)	> 100 km	-	Pelagic 3	Not reported

Species	Adult & juvenile/post settlement movement range	Propagule/larval dispersal range '+' > 1km; '-' < 1km	Organism type	Population structure in SA
Dusky shark (<i>Carcharhinus obscurus</i>)	> 100 km	+	Pelagic 3	No structure
False limpet (<i>Siphonaria diemenensis</i>)	1 m - 100 m	+	Benthic 1	Isolation by distance
Giant Australian cuttlefish (<i>Sepia apama</i>)	> 100 km	+	Pelagic 1	North-south
Greenlip abalone (<i>Haliotis laevigata</i>)	1 m - 100 m	+	Benthic 1	Isolation by distance
Harlequin fish (<i>Othos dentex</i>)	100 m - 1 km	+	Pelagic 2	Not reported
Garweed (<i>Heterozostera spp.</i>)	cms - 1 m*	+	Benthic 2	Not reported
Kelp (<i>Ecklonia radiata</i>)	100 m - 1 km	+	Benthic 2	Isolation by distance
King George Whiting (<i>Sillaginodes punctata</i>)	> 100 km	+	Pelagic 1	No structure
Leafy seadragon (<i>Phycodurus eques</i>)	100 m - 1 km	+	Pelagic 2	East-west
Little penguin (<i>Eudyptula minor</i>)	10 - 100 km	-	Pelagic 3	Isolation by distance
Long-nosed fur seal (<i>Arctocephalus forsteri</i>)	> 100 km	-	Pelagic 3	Not reported
Maori octopus (<i>Octopus maorum</i>)	1 - 10 km	+	Benthic 2	No structure
Mulloway (<i>Argyrosomus japonicus</i>)	> 100 km	+	Pelagic 1	East-west
Tapeweed (<i>Posidonia australis</i>)	cms - 1 m*	+	Benthic 2	East-west
Pygmy blue whales (<i>Balaenoptera musculus</i>) - subspecies (<i>B. m. brevicauda</i>).	> 100 km	-	Pelagic 3	No structure
Red algae (<i>Capreolia implexa</i>)	cms - 1 m*	+	Benthic 2	Not reported
School shark (<i>Galeorhinus galeus</i>)	> 100 km	+	Pelagic 3	No structure
Sea urchin (<i>Heliocidaris erythrogramma</i>)	1 m - 100 m	+	Benthic 1	East-west
Short-beaked common dolphin (<i>Delphinus delphis</i>)	> 100 km	-	Pelagic 3	No structure
Shortfin Mako, (<i>Isurus oxyrinchus</i>)	> 100 km	+	Pelagic 3	No structure
Short-tailed Shearwater (<i>Puffinus tenuirostris</i>)	> 100 km	-	Pelagic 3	Not reported
Snapper (<i>Chrysophrys auratus/Pagrus auratus</i>)	> 100 km	+	Pelagic 1	East-west
Southern blue devil (<i>Paraplesiops meleagris</i>)	1 m - 100 m		Pelagic 2	Not reported
Southern bluefin tuna (<i>Thunnus maccoyii</i>)	> 100 km	+	Pelagic 1	No structure
Southern garfish (<i>Hyporhamphus melanochir</i>)	10 - 100 km	+	Pelagic 1	Geographic structure

Species	Adult & juvenile/post settlement movement range	Propagule/larval dispersal range '+' > 1km; '-' < 1km	Organism type	Population structure in SA
Southern right whale (<i>Eubalaena australis</i>)	> 100 km	+	Pelagic 3	Not reported
Southern rock lobster (<i>Jasus edwardsii</i>)	10 - 100 km	+	Benthic 1	No structure
Western blue groper (<i>Achoerodus gouldii</i>)	100 m - 1 km	+	Pelagic 2	Not reported
Western king prawn (<i>Penaeus (Melicertus) latisulcatus</i>)	10 - 100 km	+	Benthic 1	Not reported
White shark (<i>Carcharhinus carcharias</i>)	> 100 km	+	Pelagic 3	No structure
Garweed (<i>Zostera muelleri</i>)	cms - 1 m*	+	Benthic 2	Isolation by distance

4.2. Key knowledge gaps

It is worth noting that the majority of relevant research is species-specific, whereas the marine parks design principles were based around protecting biodiversity more broadly, not specific species. However, species (and their connectivity) form the building blocks of biological communities and biodiversity, as well as directly providing key habitats (such as mangrove, macroalgae and seagrass). Our review can be used to inform a very broad assessment of the likelihood that the parks will, or will not, provide adequate protection to a species, depending on the amount of information available on its movement and population structure. However, there are few, if any, species where there are adequate data to answer the connectivity question thoroughly and quantitatively across their full spatial range and life cycle. This is a significant barrier to systematically assessing (using existing data) whether the marine parks program objectives regarding conserving biodiversity and maintaining ecological processes, and assumptions on adequacy, are being met. There are several key knowledge gaps that we have identified when reviewing the relevant literature, which are outlined below.

Distribution of habitats:

With comprehensive data that can be used to generate complete habitat maps, it will be possible to initially generate summary statistics of the distances within and between zones/parks containing specific habitat types, which may be informative when considering the connectivity of these habitats, and their accessibility to the species that utilise them. Without this basic information on the extents, coverage and locations of habitats within in SA marine parks and zones (as well as more broadly across the State's waters), it will be difficult to fully address the question of connectivity. This should be considered a high-risk knowledge gap, because many of the more detailed assessments of connectivity for specific species will rely on having information about the distribution of their preferred habitats.

There is also a paucity of data on both the population structure and ecological connectivity of habitat-forming species such as seagrasses, mangrove and macroalgae; although see Ticli (2015) who provides detailed information on the population structure and connectivity of *Zostera muelleri* and Coleman et al. (2009) who produced similar outputs for the kelp *Ecklonia radiata*.

Biophysical models:

There are few studies that have made use of available physical oceanographic data (for example the Southern Australian Regional Ocean Model grid developed by SARDI and similar products for Gulf St Vincent developed by SA Water) to either characterise the physical environments available

throughout the marine parks network (e.g. Harris et al. 2008) or to develop coupled biophysical models of connectivity. These types of models could be used to both investigate larval transport (for an SA example, see McLeay et al. 2016) and/or help to understand the drivers of mobile species movement within the network (non-SA examples include Scales et al. 2014; Braun et al. 2015).

Multidisciplinary approaches:

Each type of external tag, bio-marker, genetic approach and modelling framework have their own pros and cons and are effective over different spatial and temporal scales (for a review of tags see Gillanders (2009) and for a review of genetic approaches see Hellberg et al. (2002)). Multidisciplinary studies that combine multiple methods provide a better overall assessment of species' population structure and connectivity (Baguette et al. 2013; Dubois et al. 2016).

Whilst tracking of individuals (using both natural and external tags) indicates movement behaviour, this does not necessarily relate directly to demographic connectivity. The same is true for modelling approaches, which incorporate physical characteristics of the environment and can also include individual behaviour. Although these two methods both provide key information about movement of individuals, they cannot assess whether individuals settled successfully in the area they arrived into, or whether they survived to reproduce. On the other hand, genetic approaches (particularly using SNPs and microsatellites, which have better temporal resolution than mitochondrial or chloroplast DNA) can give an indication of the outcome of movements and dispersal between marine parks (i.e. gene transfer). However, genetic approaches do not provide insight into the mechanism of this recruitment, factors affecting its variability in time and space, or its demographic significance (e.g. the relative contributions of immigration and self-recruitment to population persistence) (Lowe et al. 2010).

In reviewing the SA literature, we have found that there are often multiple, disparate studies on a species, each employing their own approach to answering questions regarding connectivity and population structure. This ad-hoc approach means that key bits of information must be drawn out of each study and it can be difficult to integrate these in a way that is easy to interpret and provides useful outputs for management and conservation purposes. However, there are some species for which a multidisciplinary approach has been successfully used, resulting in a weight of evidence analysis, where the outcomes of the different methods are used in a holistic way to determine population structure and connectivity (e.g. Australian sardine - Izzo et al., 2017; western king prawn - McLeay et al., 2016; black nerite - Teske et al, 2015 & 2016). Despite these few studies, the overall lack of multidisciplinary, multi-life stage and/or multi-species studies is a critical knowledge gap.

Scale mismatch:

Generally, the scale of existing studies is broad and there is a mismatch between the temporal and spatial scales of data required for assessing marine parks connectivity and the scale used in existing studies. This is primarily due to previous studies not being undertaken for the purpose of assessing connectivity in the marine parks network. Many of the existing studies focus on the scale required for fisheries management at the State level and how populations in SA may be linked to those in other regions of Australia.

4.3. Recommendations for future research

Based on our thorough review of the available literature and the identified critical knowledge gaps above, we recommend that future studies be integrated across different methodologies and scales, such that they can provide a robust assessment of connectivity throughout the SA marine parks network (Krueck et al. 2017). For future studies to assess connectivity at appropriate scales (Figure 18), they will need to be highly spatially and temporally resolved, but conducted over wide areas (i.e. they must be able to identify the utility of individual zones/parks, even for well-connected and wide-ranging species; Williamson et al. 2016). The organism type groupings that we have defined in section 4.1 (on the basis of common life-history characteristics) may be used as surrogates or ‘exemplar’ life history types in future work, as it is unrealistic to aim for thorough assessment of the connectivity of all species individually across the network.

Future research will need to use methods that can assess not only the time individuals spend within the boundaries of marine parks (e.g. biomarker and tagging data), or the likelihood of connectivity between parks at relevant time scales (e.g. biophysical models); but can also test the realised outcomes of those movements using genetic tools (Pinsky et al. 2017). These genetic assessments can provide key information about whether individuals survive, settle and go on to reproduce successfully in the population that they arrive in. D’Aloia et al. (2015) recently implemented just such a comprehensive and integrated analysis (albeit at a relatively small spatial scale). They quantified the probability of larval exchange throughout a coral reef system in Belize based on modelled dispersal kernels validated using field data and genetic parentage analysis. Similar assessments combining otolith marking, dispersal modelling and genetic parentage analyses have been used to track larval dispersal, assess scales of population connectivity and quantify source and sink dynamics across marine reserves in the Great Barrier Reef (Williamson et al. 2016) and Kimbe Island (Papua New Guinea; Salles et al. 2016).

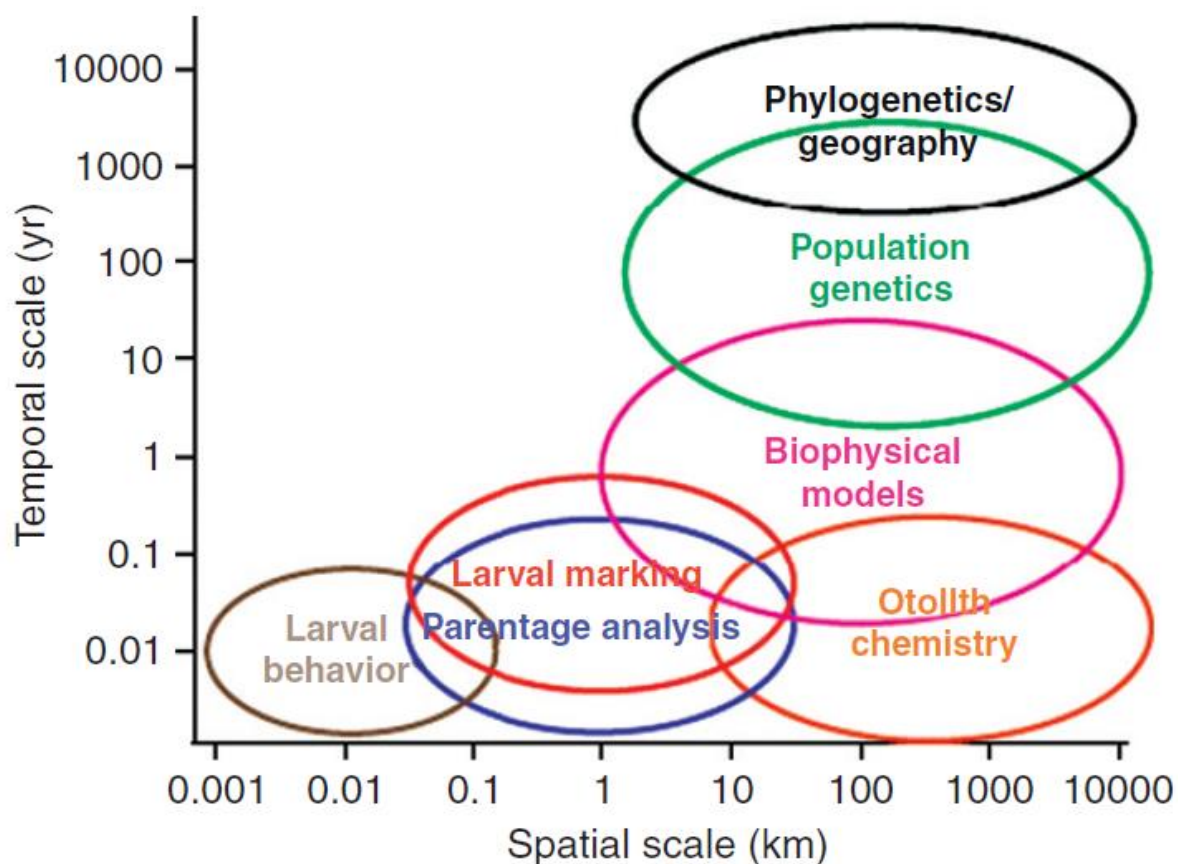


Figure 18 from Jones et al. (2009): Schematic of the spatial and temporal scales over which different techniques can provide information on larval retention and dispersal for coral reef organisms with pelagic larvae. © Springer-Verlag 2009. Reproduced with permission.

Below we make some specific recommendations for future work based on the identified knowledge and data gaps, as well as recommendation from the recent literature.

Habitat mapping:

The marine parks program has objectives related to maintaining and enhancing marine biodiversity into the future and therefore must include and protect high-quality habitats within park boundaries and within appropriate zone types. It is critical that habitats required for foraging, reproduction, nursery areas etc. are available within the network as these will support species whilst inside the parks (regardless of whether they then remain within parks or move to unprotected areas outside) (Magris et al. 2014). Therefore, spatially accurate information is required on the distribution of habitats throughout SA waters (both inside and outside the marine parks network), with supplementary data on habitat quality or condition where possible. These data are required, not only for assessing the

representativeness and comprehensiveness of the network, but also for the assessment of connectivity of key habitats, for example larval nurseries in seagrass areas with offshore reefs that support adult populations (Olds et al. 2012; Carr et al. 2017). Such base habitat maps are a requirement for the integrated modelling recommendations that we make below. The incorporation of spatial habitat data can refine models of dispersal, such that they provide more realistic outputs (i.e. quantification of larval dispersal resulting in arrival at areas of suitable habitat for settlement) (Huijbers et al. 2013).

The Marine Parks team has an ongoing mapping program (since 2012), which in 2017 had at least some coverage of benthic mapping within 80 of the 83 Sanctuary Zones. However, habitat mapping data are expensive to collect and it is unrealistic to expect that large proportions of the State's waters could be mapped within the timeframe of the first marine parks effectiveness assessment (i.e. by 2022). However, value could be added to existing DEWNR spatial habitat data sets (DEWNR 2015b; DEWNR 2015a) by combining these with other potential data sources such as EPA's habitat condition assessment data (Gaylard, unpublished data) and the Spencer Gulf Ecosystem and Development Initiative habitat map of Spencer Gulf (Jones et al., in review). Additional geospatial data sets (multibeam bathymetry and backscatter) may be held by industry (e.g. shipping, oil, gas) and defence.

Oceanographic connectivity models and larval transport models:

These models use physical oceanographic data on flow, temperature, salinity etc. and particle movement to generate predictions of larval transport and connectivity. Dubois et al. (2016) carried out a large-scale analysis of connectivity across the entire Mediterranean Sea by modelling a Lagrangian flow network to simulate larval transport under various scenarios of seasonality and pelagic larval duration (imitating a variety of different species' larval behaviour). The outcome was a suite of spatially explicit modelled connectivity metrics across their study area, providing information on source sink dynamics (Dubois et al. 2016). A similar approach was taken by Andrello et al. (2017) for a global scale analysis of larval supply to marine reserves and by Kool & Nichol (2015) to quantify connection among marine reserves in northern and western Australia (Figure 19).

Generally, broad scale oceanographically forced larval dispersal models have drawbacks in that they are necessary simplifications of reality and may not account for active movement of larvae and/or the suitability of habitat at the arrival location (Andrello et al. 2017). Put simply, they assess levels of connectivity between locations that are based purely on the arrival of passively transported individuals (Thomas et al. 2014; Figure 20). These models therefore tell us little about the survival of individuals after arrival, or their ability to reproduce and contribute to demographic connectivity.

However, the models can be improved by the inclusion of data on habitat distribution (Magris et al. 2016) and larval movement (McLeay et al. 2016) and can be validated and refined using genetic analyses or movement data from natural/external tagging (Coleman et al. 2009; Coleman et al. 2017).

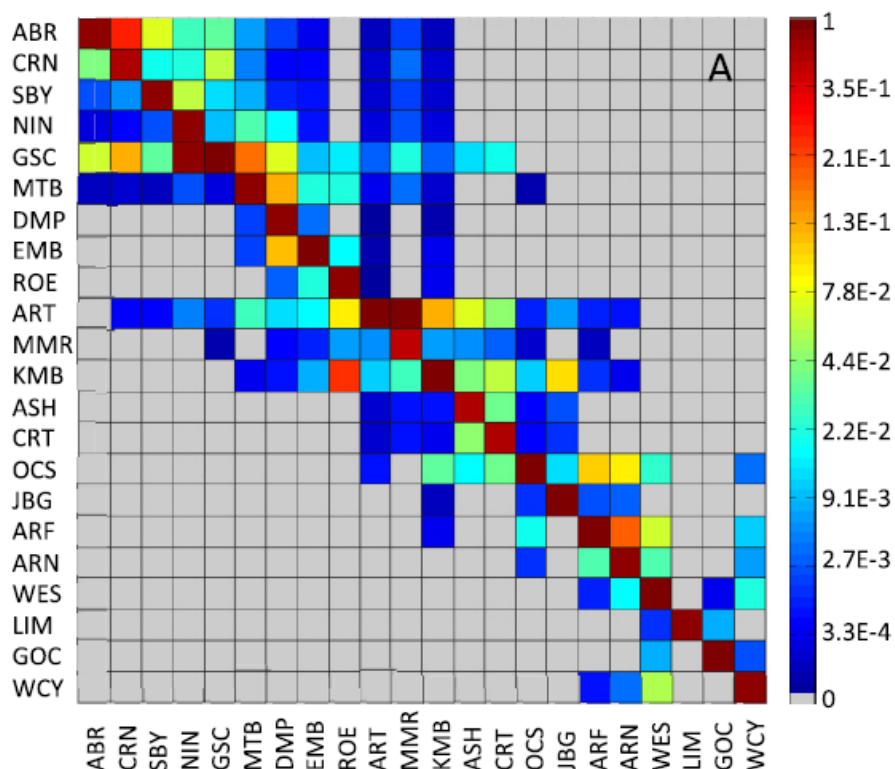


Figure 19 from Kool & Nichol (2015): Matrix representation of connection strengths among north and northwest Commonwealth Marine Reserves (CMRs) expressed as probabilities of being connected (i.e. red is strongly connected, green is moderately connected and blue is weakly connected). CMRs are indicated as follows: ABR: Abrolhos, SBY: Shark Bay, CRN: Carnarvon Canyon, NIN: Ningaloo Reef, GSC: Gascoyne Canyon, MTB: Montebello, DMP: Dampier, EMB: Eighty Mile Beach, ROE: Roebuck, ART: Argo-Rowley Terrace, KMB: Kimberley, ASH: Ashmore Reef, OCS: Oceanic Shoals, JBG: Joseph Bonaparte Gulf, ARF: Arafura, ARN: Arnhem, WES: Wessel, LIM: Limmen, GOC: Gulf of Carpentaria, WCY: West Cape York. © 2014 Elsevier Ltd, reproduced with permission.

It is clearly not possible to carry out larval transport modelling separately for all species that use the marine parks network. However, it would be possible to generalise across multiple species by incorporating several realistic and broadly representative dispersal strategies (using groupings like those in Table 2, ‘organism type’; see Jonsson et al. 2016). This approach would generate predictions of larval dispersal and connectivity relevant to many different species. Such generalised connectivity models can be of great value, as they provide a baseline of bio-physical connectivity which can then be coupled with biological data (see below) and/or used for scenario testing. For example, such models can be used to investigate the effects of seasonality of flow and temperature regimes on larval dispersal (Roughan et al. 2011; McLeay et al. 2016), or the effect of spatial and temporal changes in spawning on larval dispersal and connectivity.

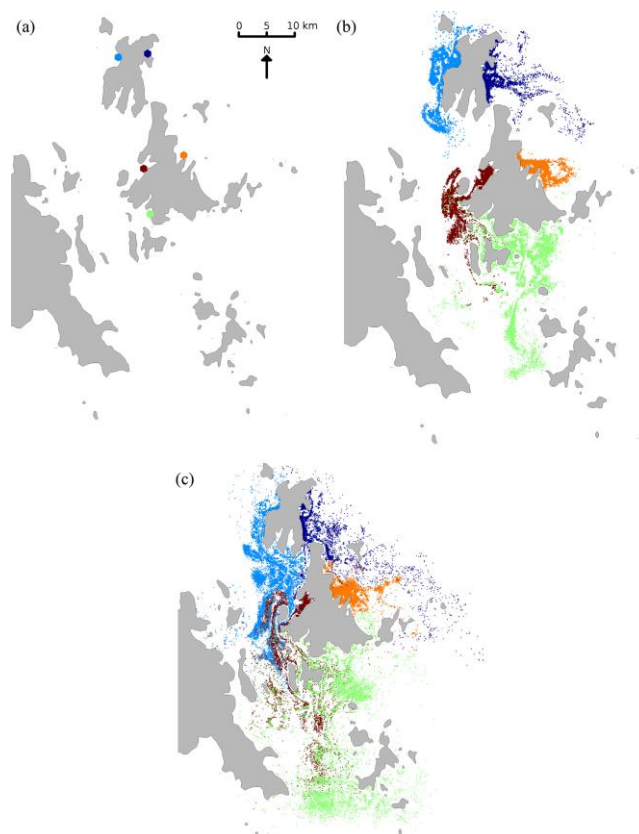


Figure 20 from Thomas et al. (2014): Images showing the dispersal of particles released at five chosen sites around the Whitsunday Islands over a week. Particles are colour-coded by release site. Mortality and settling were ignored. (a) Initial particle positions. (b) Positions after 3.5 days. (c) Positions after 7 days. © 2014 Elsevier Ltd, reproduced with permission.

Coupled bio-physical models:

This recommendation builds on the oceanographic/larval transport types of connectivity models outlined above and overcomes some of their drawbacks through the inclusion of biologically relevant data on movement patterns (adult and larval), habitat requirements and population dynamics based on key life history parameters (such as vital rates, population growth rates, fecundity and dispersal behaviour). Inclusion of such biological data into connectivity analyses have been demonstrated to impact on the effectiveness of marine protected area planning (Claudet et al. 2010) and the realism of models of population connectivity (Burgess et al. 2014; Tremblay et al. 2015). Coupling biological and physical models can therefore result in comprehensive spatial assessments of population dynamics, sources and sinks for dispersal and overall seascape connectivity (Fordham et al. 2013).

The biological data required for this type of integrated analysis could come from a variety of sources including tag-recapture (survival rates and movement), tracking data (individual movements and dispersal), fisheries data (age-growth, distribution, habitat associations and population structure) and

otolith/statolith/vertebral chemistry (growth rates, age structuring, dispersal and movement patterns).

Undertaking a bio-physical modelling analysis of connectivity for the SA Marine Parks Network would need to draw on existing oceanographic models for SA (see McLeay et al. 2016 and discussion above for oceanographic connectivity models). Coupled (bio-physical) models of spatial population dynamics are complex and it is not realistic that they be generated for all species. The priority species for these analyses would need to be identified by DEWNR (and would be extremely dependent on the availability of relevant life-history data). Suggestions of possible priority species are: habitat forming species that support communities of other organisms, such as seagrasses; iconic species or species of conservation concern such as western blue groper; species of importance to recreational fishers, such as blue crab.

It is likely that some of DEWNR's marine parks monitoring data on species occupancy and assemblages (both within and outside the park boundaries), as well as existing data sets regarding species movement, habitat preferences and age structuring, could contribute to the biological data sets required for this type of comprehensive modelling analysis. However, depending on the species selected, additional data may also be required (see below).

Sample data: genetic, bio-marker and tagging approaches:

Although large scale theoretical and coupled models (such as those discussed above) have the potential to provide critical information on connectivity across the entire marine parks network, their parameterisation and validation relies heavily on field sample data for key information on species distribution, life-history, population structure, movement and genetic connectivity. Therefore, it is crucial that such datasets continue to be collected, preferably in a systematic way throughout the marine parks network.

The key information provided by genetic data, which cannot be gleaned from other data sources is whether movements of migrants from one population or marine park to another result in successful recruitment into the recipient population. Genetic samples of key species from across the network would be required to carry out a systematic assessment of genetic relatedness, population structuring and thus connectivity. To make the best use of time and resources, samples could be collected as part of the existing marine parks monitoring work (with additional ad-hoc collection based on opportunity).

It should be remembered that the genetic analysis method used will dictate the utility of the results to the marine parks connectivity question, with SNPs, molecular methods and parentage analyses being able to provide data at the most appropriate scales (Figure 18). In addition, simple assessments of genetic differentiation and/or gene flow using genetic markers, won't necessarily be able to identify the mechanisms responsible for maintaining genetic connectivity between populations, nor its demographic significance. Genetic markers can't tell us about where individuals spent time before they entered the sampled population, or whether they may previously (or subsequently) be resident within other populations/marine parks.

On the other hand, analysing the elemental composition of calcified structures, such as fish otoliths, cephalopod statoliths and elasmobranch vertebrae can provide data on both movement patterns and population structure (Doubleday et al. 2009; Izzo et al. 2012), as can external tracking and telemetry devices. Therefore, it is critical to couple genetic approaches with tracking methods (whether using bio-markers or external tagging devices), as each of these approaches are representative of varying temporal and spatial scales (Gillanders 2009). Integration of genetic analyses, bio-markers and individual tracking data with larger-scale oceanographic modelling or population dynamics models would provide robust and validated predictions of connectivity using multiple methods.

Making use of existing data

The recommendations above will all require acquisition of new data and comprehensive analyses using modern and sometimes complex methods. Whilst these types of assessments represent the most integrated approach to understanding and quantifying connectivity across the marine parks network at appropriate spatial and temporal scales, we appreciate that our recommendations also need to be realistic in terms of time scales and costs. Therefore, we have also made some recommendations below for meta-analyses using existing data sets. It must be noted that these recommendations, whilst having cost and time benefits, are not ideal for a comprehensive assessment of connectivity across the SA marine parks network.

There are a reasonable amount of data on the movement of marine species in SA waters reported in the literature (whether through natural/external tags, tag-recaptures/fisheries survey data or modelling of larval transport). It is also likely that there are additional unpublished datasets being held by SA research groups. However, few of the papers or reports that we found were focussed on the marine parks, so it would be valuable to undertake a meta-analysis of all these existing spatial datasets, which would achieve a multi-species summary of occupancy across the marine parks network.

Figure 21 shows the results of a recent global meta-analysis using external tracking data for 60 different species of seabird (Lascelles et al. 2016). A meta-analysis of this type for SA could quantify the number of species spending time inside different parks/zones, and whether they were recorded moving between parks/zones. Although this analysis would not provide detailed information on demographic or genetic connectivity, it would be a good way to integrate existing data sets into a useful output for the marine parks program based purely on space-use. The utility of this exercise would depend on how many of these datasets were made available for inclusion in such a meta-analysis.

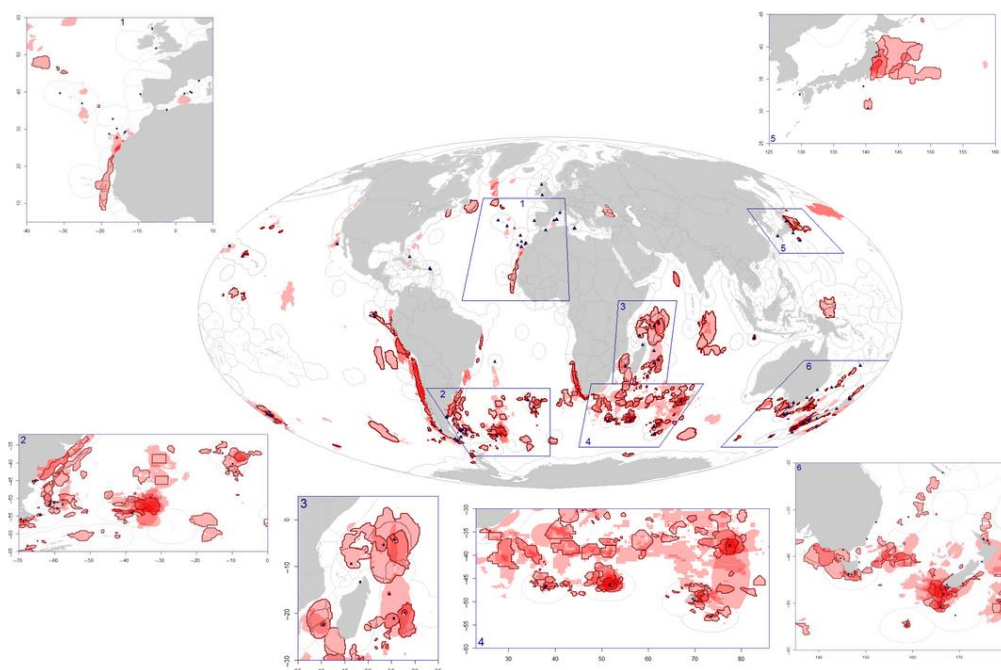


Figure 21 from Lascelles et al. (2016): Polygons resulting from the analysis of all seabird tracking data for 60 species. Polygons are aggregated to show areas of overlap (darker areas), with insets providing further detail on those with greatest convergence. © 2016 John Wiley & Sons Ltd, reproduced with permission.

A further meta-analysis could be carried out on the data available on the habitat use of SA's marine species, their maximum movement distances and propagule dispersal characteristics (see Table 2 and the associated Excel worksheet). If these data were combined with spatial information on the habitat types within the marine parks (where available) it may be possible to generate a relatively quick and very simplistic assessment of the *potential* connectivity of various species throughout the network. Undertaking this type of analysis would be cost-effective, in that little additional data would be required. However, it would involve making a lot of assumptions about the distribution of each species and the outcomes would need to be caveated by the fact that they could not provide information on

realised connectivity (i.e. demographic or genetic connectivity), but would be based purely on *potential* connectivity.

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