

Assessing space use and abundance of marine fishes to evaluate the conservation benefit of South Australia's Marine Parks Network

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Photo: Andrew Fox / Rodney Fox Sharks Expeditions

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4. Acknowledgements

This study was funded by the South Australian Department for Environment and Water. The data was sourced from the Ocean Tracking Network project (<http://oceantrackingnetwork.org>) and from Australia's Integrated Marine Observing System (IMOS) – IMOS is enabled by the National Collaborative Research Infrastructure Strategy (NCRIS). We thank scientists for uploading receiver detections on the IMOS acoustic tracking database, enabling us to access detections beyond our specific projects.

All applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed and all animal handling complied with the animal ethics standards from the following Flinders University Animal Ethics Committee or SA Wildlife Ethics Committee approvals: 35-2008-M4 (bluethroat wrasse, western blue groper, and harlequin fish), AEB1698 (silver trevally), E467-18 (yellowtail kingfish), E485-19/AEB1517 (southern eagle ray), E360 (bronze whaler and dusky shark), and E398 and E464-17 (white shark).

Fish were captured and tagged under the following research permit: Primary Industries and Resources South Australia (PIRSA) Ministerial Exemption No. 9902196 (western blue groper) and 9902693 (white shark), National Parks research permit Q26612 (trevally), E26769 (yellowtail kingfish)

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5. Executive Summary

Area-based management is of central importance to global marine biodiversity conservation efforts. Networks of no-take Marine Protected Areas (hereafter referred to as MPAs) are an essential component of these conservation efforts that are implemented worldwide to conserve natural biogeochemical processes, habitats, and species, and to ensure continued socio-economic benefits. In South Australia (SA), a network of 19 marine parks was implemented in 2012, covering 44% of state waters, with about 6% of that being equivalent to no-take MPAs (5% Sanctuary Zones, and 1% Restricted Access Zones). The aim of the SA marine park network is to protect and conserve the state's marine biological diversity and marine habitats, and support ecologically sustainable development.

Here, we use an individual-based modelling approach to investigate the effectiveness of no-take MPA sizes (defined as the 83 Sanctuary Zones only, and not the Restricted Access Zones) represented within the SA marine parks network in protecting ten taxonomically- and ecologically-diverse fish and elasmobranch species across their lifetime. We further investigate the effectiveness of what larger MPAs could achieve for decision makers to consider when potentially expanding existing or implementing new MPAs in the future. The selection of species analysed included small and large reef-associated fishes (bluethroat wrasse, harlequin fish, and western blue groper), benthic-pelagic and pelagic fishes (silver trevally, snapper, and yellowtail kingfish), a medium to large ray (southern eagle ray) and medium to large, coastal-pelagic sharks (bronze whaler, dusky shark, and white shark). Our individual-based model was parameterised using the movements of 406 acoustically tagged individuals and 859 BRUVS deployments from South Australian waters. Modelling outcomes were used to calculate four metrics of conservation effectiveness for a given MPA size: 1) time spent in MPA, 2) annual fishing mortality offset, and two alternative metrics of lifetime fishing mortality, representing 3) survival to maximum age, and 4) survival to age-at-maturity.

We found that substantial protection could be achieved using small (<5 km wide) MPAs for those species with limited scales of short-term movement. For example, for four out of the 10 study species (harlequin fish, bluethroat wrasse, silver trevally, western blue groper), annual fishing mortality could be reduced from 20% to less than 5%. However, as expected, this level of fishing mortality reduction could not be achieved for our most mobile species (bronze whaler, dusky shark), even if MPAs were 100 km wide. White sharks represented a notable exception, given that it is a large mobile species which would not traditionally be considered to benefit from MPAs, but which shows extended residency at foraging locations (e.g., at seal colonies), which makes them more likely to benefit from MPAs than expected.

The magnitude of lifetime fishing mortality was dependent on the combination of a species longevity (or age-at-maturity as an alternative) and the amount of time it was predicted to spend within MPA boundaries. For example, although bluethroat wrasse had slightly higher longevity than yellowtail kingfish (23 vs. 12 years, respectively), the MPA size required to reduce lifetime fishing mortality to only 20% could be achieved by a 5 km wide MPA for bluethroat wrasse vs. ~25 km wide MPA for yellowtail kingfish. However, most fishes do not

live to their maximum age due to natural mortality, resulting in a truncated age structure. Thus, specifying the value of MPAs in protecting species to first reproduction (i.e. age-at-maturity) is a useful consideration for future conservation planning and appropriate estimation of MPA effectiveness in supporting population recovery. The relative increase in protection to reproduction provided by MPAs varied between species depending on the difference between longevity and age-at-maturity. For example, in MPAs that are 10 km wide, lifetime fishing mortality of snapper decreased from 75% to 40% when based on longevity (35 years) vs. age-at-maturity (6 years). In contrast, accounting for age-at-maturity did not affect lifetime fishing mortality estimates of long-lived and highly mobile species (e.g. bronze whaler, dusky shark), as these species are highly exposed to fishing mortality for long periods of time regardless of whether lifetime mortality is estimated based on longevity or age-at-maturity. For such species, MPAs have an overall low capacity to contribute to population replenishment and species persistence, unless their width extends across vast areas (>100 km).

Based on the median maximum width of South Australia's no-take MPAs (7.8 km), the current South Australian MPA network might be suitable to protect reef-associated species with limited short-term movements, and species with medium short-term movements combined with comparatively early maturation. Larger no-take MPAs are likely to be required to ensure notable protection of species that are highly mobile and long-lived with a comparatively high age-at-maturity. Spatial conservation planning in South Australia can use the results provided in this study to determine suitable size of existing and future no-take MPAs, including multiple species of conservation and management concern which might require either very large no-take MPAs and/or additional management across much of their range, e.g. both whaler sharks. Our study also shows that conservation benefits can be achieved in several ways, e.g. by increasing the size of small MPAs (e.g. to 10 km wide), or by further increasing the size of fewer comparatively large MPAs. Clearly, the former can be expected to benefit more species, but the latter might be required to ensure conservation gains for species with more substantial short-term movements and late maturation. Additionally, targeting areas where species have extended periods of residency could also provide refuge and conservation benefit beyond expectations (as shown here for white sharks).

Future research should explicitly address the potential benefit of MPA networks by calculating our baseline metric of conservation effectiveness (time spent in MPAs) based on more comprehensive acoustic tracking data suitable for simulation modelling in spatially realistic two-dimensional space.

6. Introduction

Area-based management is of central importance to global marine biodiversity conservation efforts, including the expansion of existing networks of no-take Marine Protected Areas (hereafter referred to as MPAs) (Agardy 1994; Blyth-Skyrme *et al.* 2006; Angulo-Valdés and Hatcher 2010). By preventing damaging activities, such as habitat destruction (Haddad *et al.* 2015), over-exploitation (Jackson *et al.* 2001), and certain types of pollution (Islam and Tanaka 2004), MPAs can help conserve natural biogeochemical processes, habitats, and species composition. MPAs can also provide important socio-economic benefits, such as increased tourism and employment, increased capacity for scientific research of natural systems, and a stronger public connection to nature (Balmford *et al.* 2002; West *et al.* 2006; Apps *et al.* 2016). Thus, well-designed and effective MPAs have become a fundamental component of holistic and precautionary marine management.

The goals and design of MPA networks are context-dependent. Nonetheless, effective conservation-oriented MPAs share a consistent set of characteristics, including strong enforcement, minimum size, and age (Edgar *et al.* 2014). In South Australia, the marine park network was established based on several key biophysical principles, with associated documentation highlighting that effective MPAs must be *comprehensive* (Biophysical Design Principle 2; cover a full range of habitats and species), *adequate* (Biophysical Design Principle 3; be an appropriate size so as to provide sufficient protection for a given species), and must also support *connectivity and linkages* within the environment (Biophysical Design Principle 5; provide for the sharing of plants, species, and materials between sites). MPAs designed using these core principles are assumed to be more likely to provide broad and lasting protection for its plants, animals, and ecosystems (Agardy *et al.* 2011; Claudet 2011). However, adequacy can be difficult to achieve for highly mobile species, such as sharks, marine mammals, or tunas (McLaren *et al.* 2015; Jones *et al.* 2018). This is because the extent of these species' movements is usually much larger than the size of MPAs. In consequence, mobile species might often spend a substantial amount of their time outside of MPA boundaries where they are exposed to potentially damaging human activities (Claudet 2011; Grüss *et al.* 2011; McLaren *et al.* 2015). As the majority of MPAs are small (< 10 km diameter; UNEP-WCMC 2019) and rarely encompass all key habitats of resident species (Chin *et al.* 2022), individuals will often undertake short- or long-term movements that extend across MPA boundaries. In consequence, population abundance and biomass tends to decrease gradually from the centre of MPAs across their boundaries and into fished areas (Ohayon *et al.* 2021). Although rarely quantified, this "edge effect" is likely to be substantial (often resulting in a 50% loss of the estimated recovery potential) unless MPAs are rigorously enforced and large enough to encompass the movements of resident species (Krueck 2021).

The recently introduced "MPA Guide" proposes an intuitive concept for MPA classification that recognises a potential for positive outcomes through MPAs that are mostly only "partially protected" (Grorud-Colvert *et al.* 2021). Indeed, MPAs can have positive

conservation gains while balancing sustainable uses even when they do not fully protect a species home range, when only limited enforcement is possible, or when fishing effort is low regardless of regulations (Letessier *et al.* 2019; Cashion *et al.* 2020). For example, MPAs can still benefit mobile species even when they are smaller than the species' home range provided the MPAs are adequately designed and located, e.g. at aggregation areas or focusing on important life history stages (Hooker *et al.* 2011; Chin *et al.* 2022). Expectations on the likely conservation gains of MPAs appear to move from the full protection of resident individuals (Krueck *et al.* 2018) to a reduction in mortality risks (Dwyer *et al.* 2020). The latter could be achieved even for mobile and migratory species, but the extent of likely reductions in mortality risks to be expected for MPAs of various sizes has not yet been rigorously tested (but see Krueck *et al.* 2018; Dwyer *et al.* 2020).

In South Australia (SA), a network of 19 marine parks was implemented in 2012, covering 44% of state waters, with about 6% of that being equivalent to no-take MPAs (5% Sanctuary Zones, and 1% Restricted Access Zones). The aim of the SA marine park network is to protect and conserve the state's marine biological diversity and marine habitats, and support ecologically sustainable development. Here, we use an individual-based modelling approach to investigate the effectiveness of no-take MPA sizes (defined as the 83 Sanctuary Zones only, and not the Restricted Access Zones) represented within the SA marine parks network in protecting ten taxonomically- and ecologically-diverse fish and elasmobranch species across their lifetime.

We combined acoustic tracking and baited camera datasets to provide a unique understanding of how intra- and interspecific variations in animal movements and local estimates of abundance affect MPA sizes expected to achieve alternative levels of protection in South Australian species. We further investigate the effectiveness of what larger MPAs could achieve for decision makers to consider when potentially expanding existing or implementing new MPAs in the future. Species were selected based on data availability, to encompass a diversity of movement patterns, life history characteristics, exposure to fishing mortality, and conservation status. The selection of species analysed included small and large reef-associated fishes (bluethroat wrasse, harlequin fish, and western blue groper), benthic-pelagic and pelagic fishes (silver trevally, snapper, and yellowtail kingfish), a medium to large ray (southern eagle ray) and medium to large, coastal-pelagic sharks (bronze whaler, dusky shark, and white shark). Our individual-based model was parameterised using the movements of 406 acoustically tagged individuals and 859 BRUVS deployments from South Australian waters. Modelling outcomes were used to calculate four metrics of conservation effectiveness for a given MPA size: 1) time spent in MPA, 2) annual fishing mortality offset, and two alternative metrics of lifetime fishing mortality, representing 3) survival to maximum age, and 4) survival to age-at-maturity.

7. Methods

7.1 Movement data

We analysed movement data from a range of studies that had tagged fish and sharks along the southern coast of Australia via passive acoustic telemetry. Acoustic telemetry has become a standard tool for marine biologists to quantify fish and shark residency and movement (Hussey *et al.* 2015). A uniquely ID-coded transmitter is attached or implanted in the animal and its high frequency acoustic transmission detected by an array of acoustic receivers deployed throughout the animal predicted range. Receivers record the occurrence of tagged animals when within its detection range (~ 500 m; Huveneers *et al.* 2016). Six fish, three shark, and one ray species (Table 1) were tagged with a coded acoustic transmitter (V9, V13, or V16; innovasea.com). Animals were either caught and internally- or externally-tagged while free-swimming using standard tagging methods (e.g. Drew *et al.* 2019; Niella and Huveneers 2021).

Animal movements were detected via the acoustic receiver network of the Australian Integrated Marine Observing System's (IMOS, imos.org.au) Animal Tracking Facility (Hoener *et al.* 2018). The IMOS Animal Tracking Facility is Australia's national-scale acoustic telemetry network and combined core IMOS Animal Tracking Facility infrastructure and receiver arrays maintained by independent researchers. To date, acoustic receivers (VR2W, VR2Tx, VR3, and VR2AR; innovasea.com) have been deployed at over 1,000 locations in continental shelf areas around the country (Hoener *et al.* 2018; animaltracking.aodn.org.au). Further details about the tagged animals and primary receiver arrays used to monitor movements are provided in Drew *et al.* (2019), Fowler *et al.* (2017), Bryars *et al.* (2011), Bryars *et al.* (2012), Bryars and Rogers (2016), Clarke *et al.* (2022), Niella and Huveneers (2021), Huveneers *et al.* (2021b), and Davey *et al.* (in press).

7.2 Abundance data

Standardised metrics of shark and fish abundance were collected using baited remote underwater video stations (BRUVS). This technique is a popular method to quantify fish assemblages and abundance (Whitmarsh *et al.* 2017; Langlois *et al.* 2020) and has been used successfully for a wide variety of studies including the assessment of the efficacy of marine protected areas, effects of anthropogenic impacts, or spatial variation in fish assemblages (Kelaher *et al.* 2014; Whitmarsh *et al.* 2014; Whitmarsh *et al.* 2018; Clarke *et al.* 2019; Whitmarsh *et al.* 2019). BRUVS were set up with high-definition video cameras (e.g. GoPro, gopro.com) on steel frames, baited with 500 g of minced sardines (*Sardinops sagax*) and deployed for 60 min during daylight hours. At each site, four to 12 replicate BRUVS were deployed to capture variability in the relative abundance estimates across the study sites. Simultaneous deployments of BRUVS within a site were spaced with a minimum of ~350 m apart to minimise the potential of bait plume overlapping between replicates (Heagney *et*

al. 2007; Santana-Garcon *et al.* 2014). We analysed videos using the specialised SeaGIS EventMeasure software (version 5.72, SeaGIS Pty Ltd, Bacchus Marsh, VIC, Australia; seagis.com.au/event.html). For each replicate, we counted the maximum number of individual fish (for each species) observed in a single frame throughout the deployment duration (MaxN) as a measure of relative abundance (Whitmarsh *et al.* 2017; Langlois *et al.* 2020). MaxN is a conservative estimate of abundance, particularly where large fish numbers are present or there is a large turnover of individuals during deployment (Ellis and DeMartini 1995; Willis 2001). Greater detail on methods can be found in Whitmarsh *et al.* (2019). Data from baited cameras were obtained through GlobalArchive (globalarchive.org), a centralised repository that allows open access and private sharing of fish image annotation data from BRUVS or similar imagery-based sampling techniques. GlobalArchive was used to compile a comprehensive BRUVS dataset, including 19,939 deployments, observations of over 1.1 million individual fishes (sum of MaxN) and more than 1,450 species, which was compiled as part of a nationwide Australian BRUVS workshop (Harvey *et al.* 2021).

7.3 Dispersal distance metrics and movement profiles

Acoustic detections for the six fish species and four elasmobranch species were quality controlled following the methods outlined by Hoenner *et al.* (2018) using the remora package in R ([imos-animaltracking.github.io/remora](https://github.com/imos-animaltracking/remora)). For each week of detection, we calculated the maximum distance between any acoustic receiver that a tagged animal was observed (Fig. 1). A weekly maximum observed movement distance was chosen over a daily or monthly interval to capture the extent of the animal's home range, while still providing enough data to generate a dispersal location kernel for a large cohort of individuals (Dwyer *et al.* 2020).

For each tagged individual, we calculated a dispersal location kernel by sampling all measured maximum weekly movement distances undertaken during the tracking period. From this dispersal location kernel, we generated a movement profile by taking a mirror image of the kernel that assumed each weekly movement represented excursions from a central core area (i.e., the animal's home range centroid). Thus, the furthest distance that a tagged individual travelled in a given week is found at the foot of the movement profile, and the sum of all values for a given individual is 1 (Fig. 2). This approach assumes that each weekly distance represents excursions around a centre of activity and that the likelihood of encountering an individual is greatest at the centre of this movement profile (i.e. the home range centroid). From a conservation perspective, this assumption implies that MPAs need to be situated close to the centre of activity to ensure that individuals are effectively protected. In other words, if an MPA covered only 20% of the edge of the movement spectrum of an individual, this did not mean that the likelihood of fishing mortality was 20% lower as assumed under a uniform approach (e.g. Krueck *et al.* 2018). As the movement profile for each tagged individual relied on replicate dispersal events, only those tags with > 7 days of detection data and at least 2 weekly replicates were included in our analysis.

Histograms of individual movement distances of all species except bronze whaler and bluetthroat wrasse revealed a strongly right-skewed distribution (Fig. 1), suggesting that the scale of short-term movements of most individuals was lower than suggested by the average across individuals. Individual movement profiles provided another perspective on this observation by translating the contrast between averaged and individual scales of movement into relative probabilities of space use (Fig. 2). Importantly, quantifying and incorporating individual movements in this way allowed for capturing variability of space use not just between but also within individuals.

Table 1. Summary of tagged species including biological information, number tagged (*n*), period monitored, movement information, MaxN, and references providing more details about the movement study for each species.

common name	scientific name	longevity (T_{max})	age-at-maturity (T_{mat})	T_{mat}/T_{max} (percentage)	<i>n</i>	size range	weekly distance estimates (N)	maximum distance (mean \pm standard deviation)	MaxN _{max}	MaxN _{sum}	reference
bluethroat wrasse	<i>Notolabrus tetricus</i>	23	6	55%	5	225-345	153	1.1 + 0.6	24	1042	Bryars <i>et al.</i> (2011)
harlequin fish	<i>Othos dentex</i>	42	6	14%	10	330-620	559	1 + 0.6	2	20	Bryars and Rogers (2016)
silver trevally	<i>Pseudocaranx georgianus</i>	45	6	13%	15	515-655	784	1.2 + 2.4	150	2746	J. Dennis unpublished data
snapper	<i>Chrysophrys auratus</i>	35	6	17%	27	320-970 FL	683	6.2 + 7.2	81	1144	Fowler <i>et al.</i> (2012)
western blue groper	<i>Achoerodus gouldii</i>	70	17	24%	15	690-1120	750	1.7+ 0.8	5	129	Bryars <i>et al.</i> (2012)
yellowtail kingfish	<i>Seriola lalandi</i>	12	5	42%	19	80-151	449	6.5 + 11.7	60	70	Clarke <i>et al.</i> (2022)
southern eagle ray	<i>Myliobatis tenuicaudatus</i>	25	8	32%	39	695-1600	1168	10 + 7.4	5	137	Davey <i>et al.</i> (in press)
bronze whaler	<i>Carcharhinus brachyurus</i>	30	20	67%	105	74-275	3879	100.5 + 143.4	1	6	Drew <i>et al.</i> (2019)
dusky whaler	<i>Carcharhinus obscurus</i>	40	20	50%	85	104-358	1462	134.7 + 102.3	0	0	Huveneers <i>et al.</i> (2021)
white shark	<i>Carcharodon carcharias</i>	70	25	36%	86	1800-4500	776	12.7 + 27.5	1	6	Niella and Huveneers (2022)

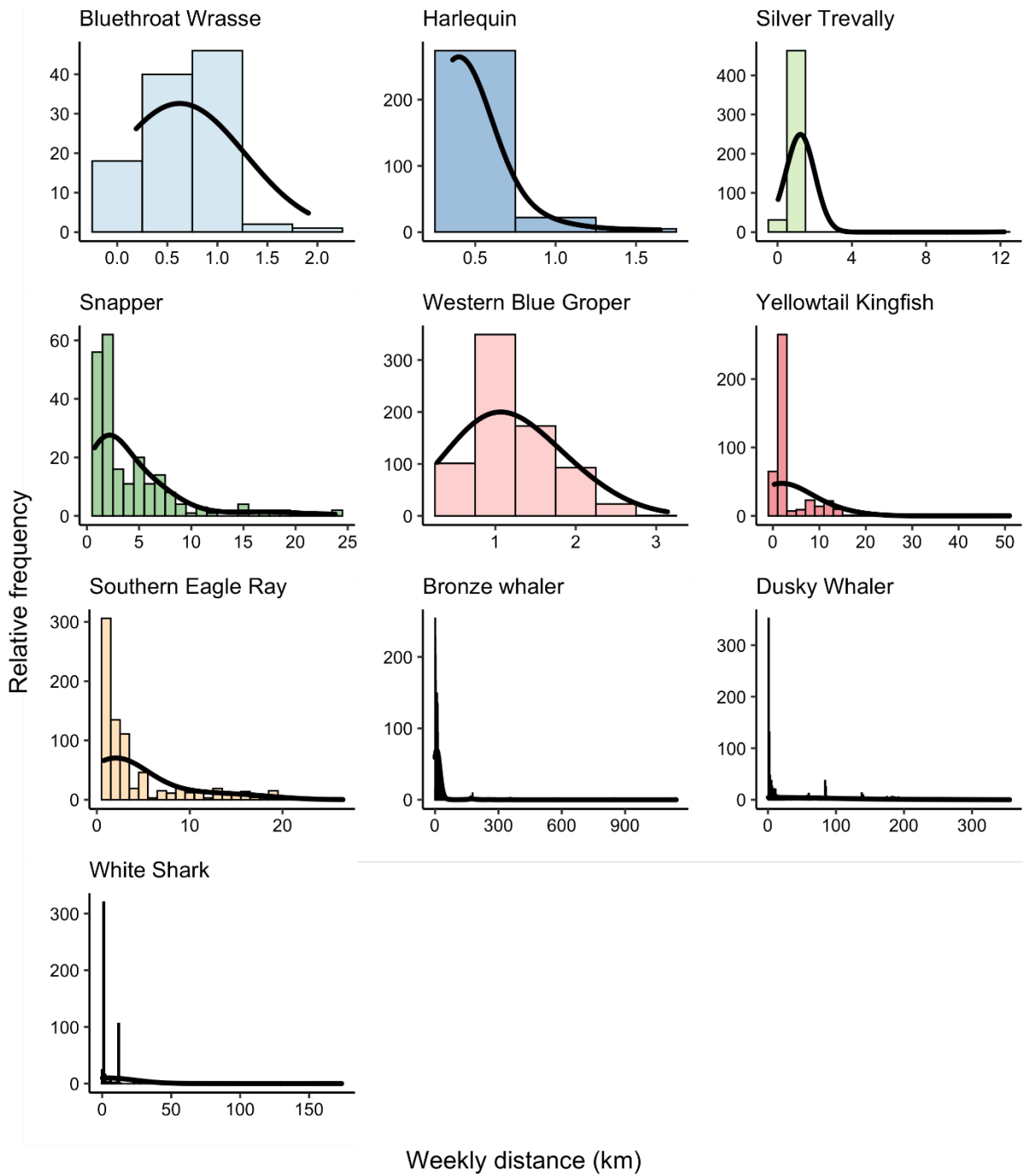


Figure 1. Histogram of weekly dispersal distances of tagged fish and sharks with the fitted dispersal distance kernel. The fitted kernel (solid line) represents the probability density function of the distribution of weekly distances travelled by all tagged individuals of each species.

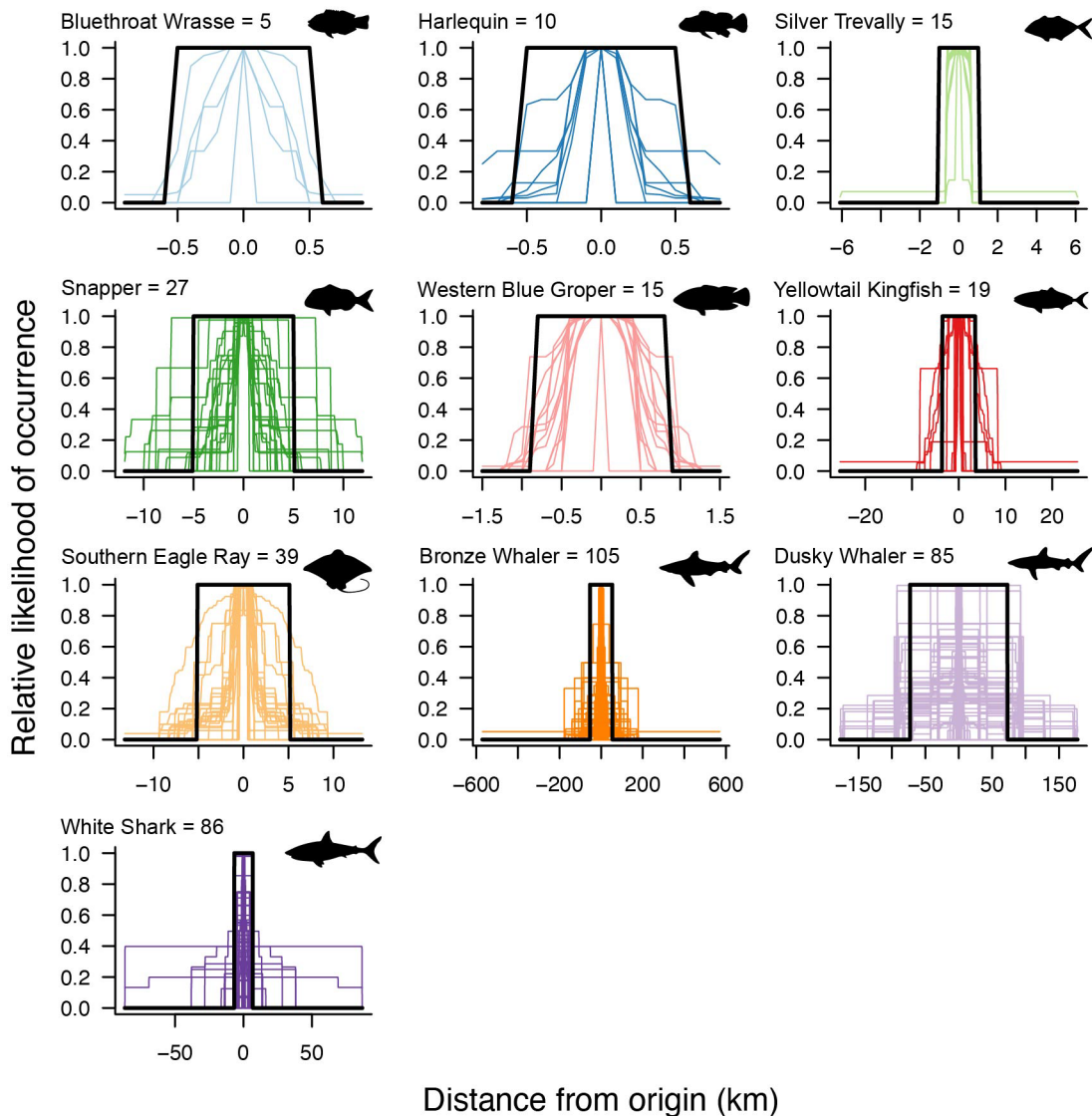


Figure 2. Species-specific movement spectra showing individual movement profiles generated from the acoustic tracking data. Each panel represents a different species, with coloured lines representing individual fish and all associated measurements of its maximum weekly movement distance around an assumed centre of activity at 0 km. Thick black lines are species averages for maximum weekly observed movements. The y-axis represents the relative likelihood of occurrence of individuals along their movement spectrum (normalised to values of 1 at the centre of activity).

7.4 Simulation modelling

To quantify the potential conservation effectiveness of MPAs, we captured empirical data on relative abundance and individual movements in a simple simulation model adapted from previous studies (Krueck *et al.* 2018; Dwyer *et al.* 2020). In brief, our simulation model performed hypothetical fish/shark surveys along an idealised coastline covered by MPAs of various plausible sizes. During each simulation, individual fish were counted and distributed in space as expected according to BRUVS-based field measurements and empirically measured movement profiles calculated for all study species. In each simulation scenario, we then assessed how many individual fish or sharks overlapped with a hypothetical MPA boundary of a set size (0.5–100 km) and how much time individuals spend within vs. outside

of this boundary. In combination with alternative assumptions about fishing mortality risks outside of MPAs, this information allowed us to calculate mortality rates over the assumed life of resident individuals.

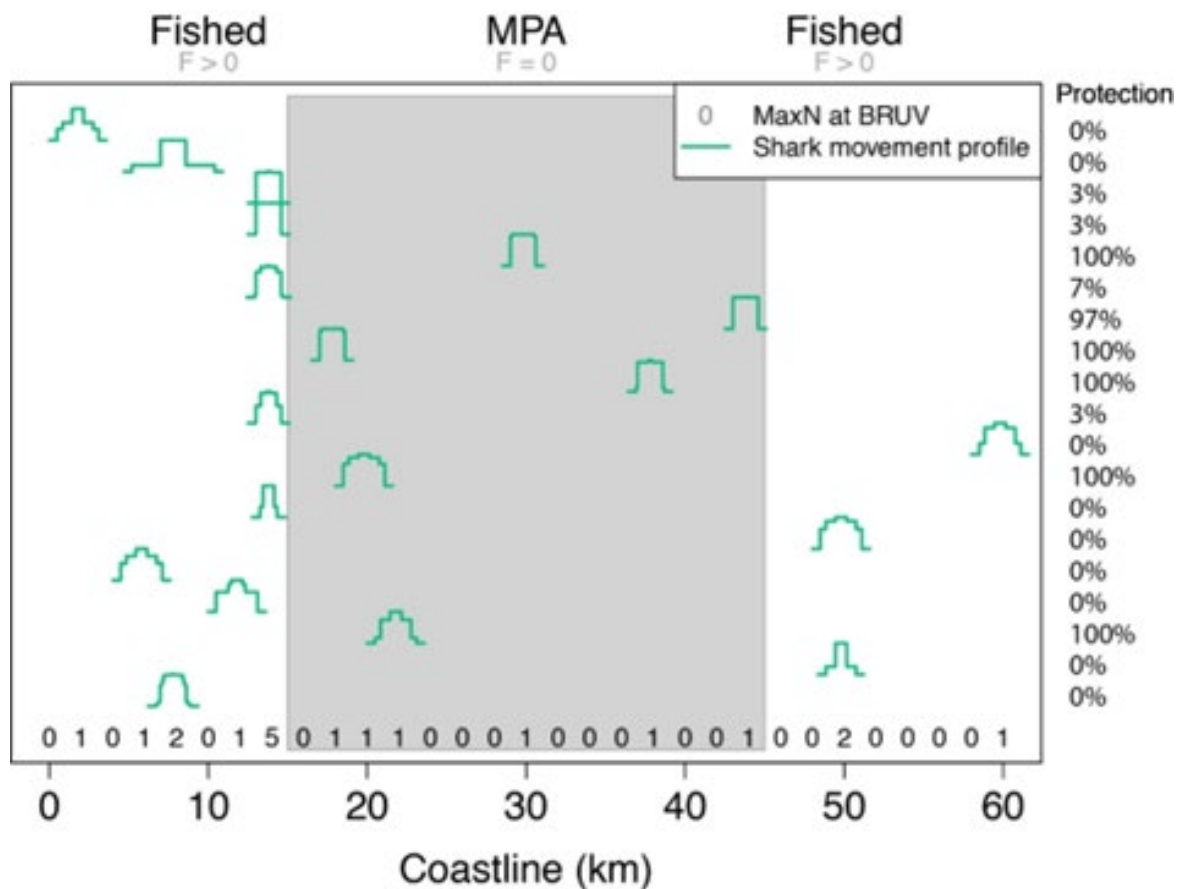


Figure 3. Illustration of the modelling procedure. The one-dimensional individual-based modelling environments show the location of hypothetical BRUVS used to sample individual sharks and fishes and calculate the percentage of their movements falling within MPA boundaries (a 30 km MPA in this example). The number of individuals present at each BRUVS (number above the x-axis) and their individual scale of movements represent random samples from empirical data. The base of individual movement profiles represents the overall maximum weekly movement distance an individual shark or fish undertook during the tracking period (copied with permission from Dwyer et al, 2021).

Individual-based simulation modelling was conducted in one-dimensional space, implicitly representing an idealised coastline and assuming that animals are equally likely to move in both directions along this coastline (Fig. 3). For each scenario, modelling environments were created by firstly determining the length of the coastline such that simulations could be expected to capture all individuals that could potentially overlap with the specified MPA. In the next step, we assigned hypothetical BRUVS sampling locations along the coastline according to the assumed BRUVS plume catchment area. The assumed plume catchment area dictated overall BRUVS coverage and thus total numbers of individuals represented in the model, because each BRUVS was located in the centre of its plume catchment area and the next BRUVS was situated at a distance representing the catchment area diagonal or

length. The number of individual fish attracted to a BRUVS was sampled at random according to empirical measurements, thus commonly including no individuals at all. The actual activity space of simulated individuals in the modelling environment was determined according to their randomly sampled movement probability profile. That is, BRUVS locations represented one particular location along the activity space of sampled individuals that was most likely (but not necessarily) close to the centre of their home range. Once all individuals had been sampled, located in the modelling environment and their activity space defined, the data was then used to calculate multiple alternative metrics of conservation gains expected from MPAs of various plausible sizes. This procedure was then replicated 1000 times for each modelling scenario to minimise stochastic variability.

7.5 Metrics to assess conservation benefits

Four related metrics of MPA conservation benefit were calculated from the simulation modelling outcomes.

1) Time spent in MPAs

The primary MPA performance metric was represented by the mean proportion of an individual's activity space (equivalent to time spent) within MPA boundaries. Values close to 1 for this metric mean that the size of the MPA is sufficiently large to protect most individuals according to the measured scale of individual movements.

2) Annual fishing mortality offset

The offset in fishing mortality represents the expected contribution of MPAs to the overall survival probability of individuals per year. Thus, calculating mortality offsets provides an important connection between metrics of use for conservation planning and sustainable fisheries management.

3) Lifetime fishing mortality (to longevity)

Lifetime fishing mortality is an alternative offset that integrates the above metrics while considering differences in species life history. This metric represents the number of individuals surviving to maximum age relative to the total number of individuals found to experience any potential protection from the MPA. Averaged across 1000 replicate simulations, this metric quantifies the potential contribution of MPAs to the lifetime survival of resident individuals. Importantly, in contrast to the annual fishing mortality offset, the lifetime fishing mortality metric considers the survival of all individuals regardless of how much time they spend in MPAs.

4) Lifetime fishing mortality (up to age-at-maturity)

Our last metric acknowledges that most individuals cannot be expected to survive to a species-assumed maximum age, even where fisheries management is highly effective. To capture the potential contribution of MPAs to individual survival up to the arguably most

important life stage for population replenishment (i.e. maturity or reproduction) we calculate a final metric of relative individual survival that replaces the assumed maximum age with the assumed age-at-maturity. Assumed maximum age and age-at-maturity for each species was obtained following a literature search (Table 1).

In addition, we contextualised our findings in relation to South Australia's 83 no-take MPAs (i.e. Sanctuary Zones). For this analysis, we used Australian protected areas listed in the Collaborative Australian Protected Areas Database (CAPAD) 2020, which included spatial information on Australia's protected area network current to 30 June 2020 (www.environment.gov.au/fed/catalog/search/resource/details.page?uuid=%7BBAF4EE98E-7F09-4172-B95E-067AB8FA10FC%7D). The database was filtered for any IUCN Category II protected area located in South Australian waters. We also removed the protected area polygon positioned in the Great Australian Bight due to its large size. We estimated the maximum width of each protected area by extracting the maximum distance between vertices within a designated Cat II protected area. We measured the minimum distance between each protected area by extracting the minimum distance between vertices between neighbouring designated Cat II protected area. Both these analyses were performed using the `sfc` package in R (Pebesma 2018). Based on these measurements, we present the estimated mean and median maximum width of Cat II protected area, and mean and median maximum minimum distance to the nearest protected area. We presented interactive plots to assess the current conservation benefits of South Australia's no-take MPAs network and enable comparisons with potential future changes to the network (e.g. potential changes still under government review).

7.6 Interactive plots

To assist with the interpretation of the model outputs, the results of our model were published as an interactive R markdown report document generated in RStudio https://rpubs.com/DwyKruHuv/FinalReport_DEW.

8. Results and discussion

Summary of data included in the analysis

We combined data from 406 individuals detected in South Australia between 20 January 2009 and 01 October 2021 (Table 1). The species included in our study were taxonomically and ecologically diverse, and included small and large reef-associated fishes (bluethroat wrasse, harlequin fish, and western blue groper), benthic-pelagic and pelagic fishes (silver trevally, snapper, and yellowtail kingfish), medium to large ray (southern eagle ray) and medium to large, coastal-pelagic sharks (bronze whaler, dusky shark, and white shark). Life history characteristics also varied across the species included and within taxa groups. For example, age-at-maturity and longevity of fishes ranged from 6–17 years and 11–70 years, respectively, whereas age-at-maturity and longevity of elasmobranchs ranged from 8–25 years and 25–70 years, respectively (Table 1). The spatial extent of where tag detections were obtained also varied within and between species, showcasing the behavioural diversity of species included in our study. For example, some species were only detected by 1–2 receivers (e.g. bluethroat wrasse), whereas others were detected by 42 receivers up to 2,300 km from each other (e.g. white shark).

Abundance data was collated from 859 BRUVS deployments throughout South Australia and was also variable between species. No dusky sharks were observed by BRUVS, possibly due to misidentification with bronze whaler sharks. Instead, we used an idealised abundance (1 individual at each BRUV) for this species in the simulation models. The other two species of pelagic sharks (bronze whaler and white shark) had a maximum MaxN of 1 and sum of MaxN across all BRUVS of 6, indicating the low number of these species recorded by BRUVS. In contrast, fishes were more abundant with trevally being the most abundant species, revealing a maximum MaxN of 150 and a sum of MaxN of 2,746 (Table 1).

1) Time spent in MPAs

Results indicated that substantial protection could be achieved relatively easily for some species. For example, four species were estimated to spend >50% of their individual activity within MPA boundaries even if MPAs were only 2 km wide (Fig. 4). This included both small and large reef-associated species (i.e. harlequin fish, blue throat wrasse, and western blue groper) as well as benthic-pelagic species (i.e. trevally). In contrast, the most mobile species could only be expected to spend >40% of their activity within MPA boundaries when the MPA was greater than 60 km in width (i.e. dusky whaler, bronze whaler). Interestingly, MPAs were more effective for white sharks than the other two shark species despite their known capacity for large scale movements. Our model predicted ~50% protection of white sharks' activity space could be achieved with an MPA width of only 10 km, which was a result similar to outcomes for southern eagle ray and snapper.

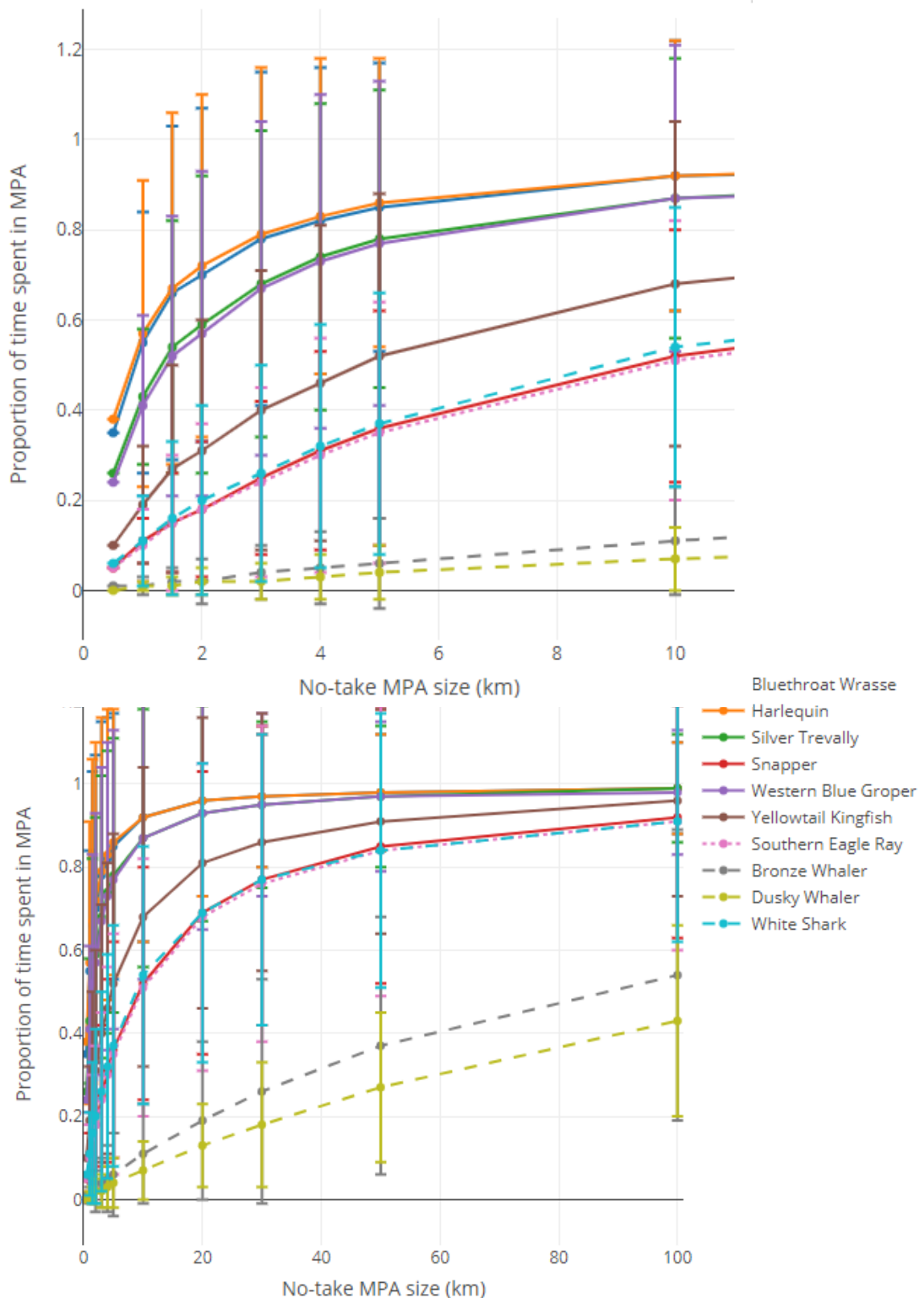


Figure 4. Level of protection (mean \pm standard deviation) provided by an MPA of increasing size, showing the proportion of an individual's movement profile that falls within simulated MPA boundaries. Top panel shows increase proportion of time spent in MPA for MPAs up to 10 km; bottom panel extends x-axis to 100 km. See https://rpubs.com/DwyKruHuv/FinalReport_DEW for interactive plots.

2) Annual fishing mortality offsets

Translating these findings into explicit estimates of associated offsets in background fishing mortality gives conservation planners and fisheries managers a clear rationale for decisions on locally-suitable MPA sizes. For example, if managers aimed at reducing fishing mortality for resident species from 20% to 5%, our simulations suggest that this target could be achieved for 4/10 species if MPAs were approximately 5 km wide, 5/10 species if MPAs were approximately 20 km wide, and 8/10 species if MPAs were approximately 30 km wide. For bronze whalers and dusky sharks, this level of mortality reduction could not be expected even if MPAs were 100 km wide. Accordingly, conservation measures other than MPAs would need to be actioned to safeguard such species. Estimates of mortality offsets provide conservation planners with a clear baseline for informed decisions on MPA designs that will most effectively support the persistence of local species relative to the level of threat these species are likely to be exposed to in fished areas.

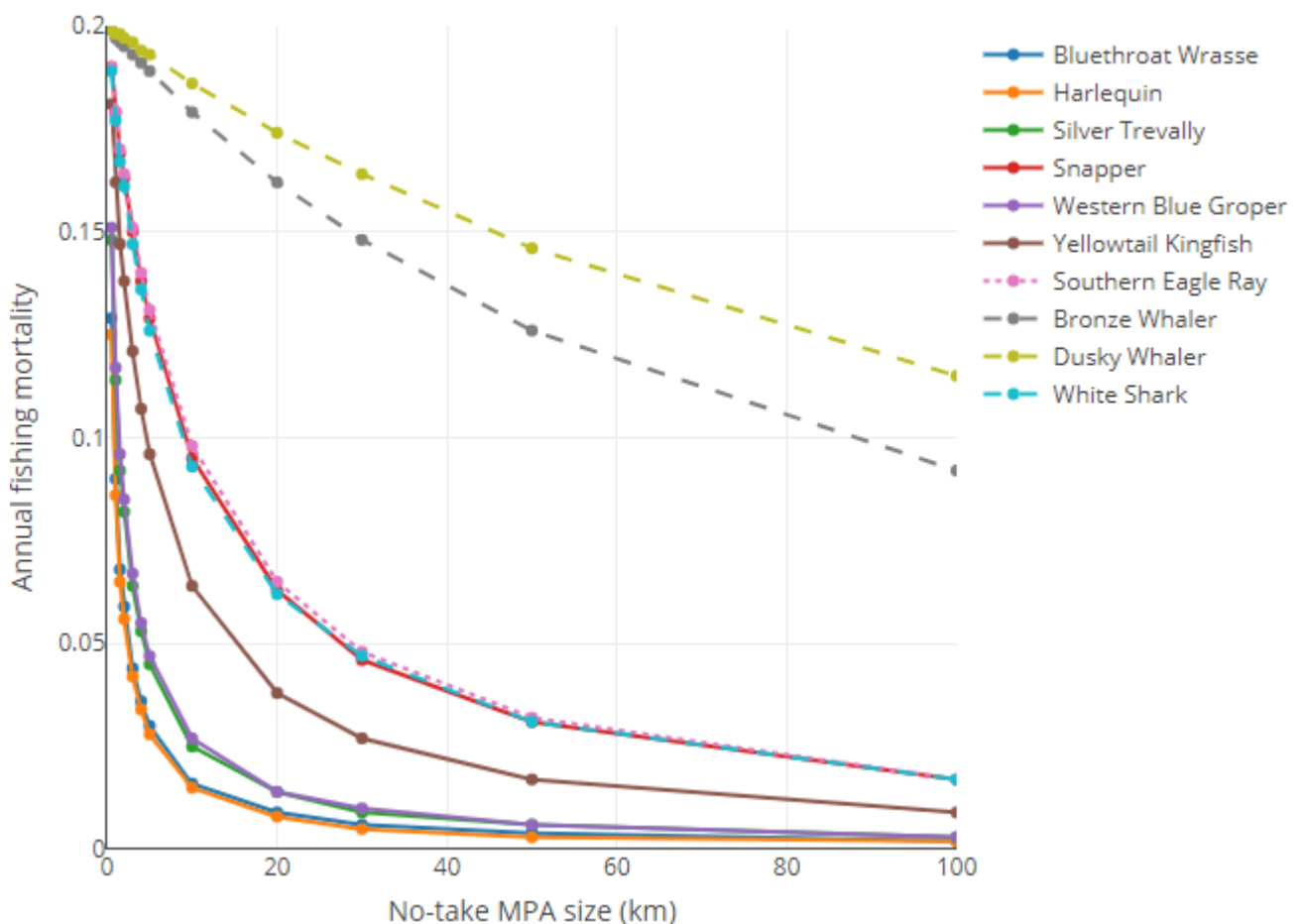


Figure 5. Offset in annual fishing mortality with increasing MPA size assuming a background fishing mortality risk of 0.2 (20% per year). See https://rpubs.com/DwyKruHuv/FinalReport_DEW for interactive plots and trends at fishing mortality from 0.05 to 0.5.

3) Lifetime fishing mortality (to longevity)

Lifetime fishing mortality was dependent on the combination of species longevity and amount of time spent within MPAs. For example, dusky sharks and bronze whalers are long-lived sharks (i.e. 40 and 30 years, respectively) and require large MPAs to encompass their weekly movements. This combination resulted in these sharks being exposed to fishing mortality for many years, with MPAs having a limited capacity to reduce fishing mortality over an individual's expected lifetime (Figure 6). As a result, lifetime fishing mortality for these two species was high (70–90%) even when MPAs were assumed to be 100 km wide. In contrast, for relatively shorter-lived species such as bluethroat wrasse (maximum age = 23 years), lifetime fishing mortality was low even at small MPA sizes and decreased rapidly with increases in MPA width. This positive response to MPAs was due to lower exposure to fishing-related mortality over the animal's shorter lifespan and also because of the small-scale movements of this species that provided for a large proportion of its activity space to be covered by MPAs even if these were small.

Comparing lifetime fishing mortality between species with contrasting traits illustrated the interplay between species longevity and the amount of time they could be expected to spend in MPAs of variable sizes. For example, although bluethroat wrasse had slightly higher longevity than yellowtail kingfish (23 vs. 12 years, respectively), the MPA size required to reduce lifetime fishing mortality to only 20% could be achieved by a 5 km wide MPA for bluethroat wrasse vs. ~25 km wide MPA for yellowtail kingfish. This finding was explained by the larger-scale movements of yellowtail kingfish compared to bluethroat wrasse and the associated lower amount of time this species was estimated to spend within MPA boundaries (e.g. 52% vs. 85% of time spent in a 5 km wide MPA, respectively; see Fig. 3). Conversely, while bluethroat wrasse and harlequin fish were estimated to spend a similar amount of time in MPAs and were therefore similarly vulnerable in terms of their annual fishing mortality risk (Fig. 3), lifetime fishing mortality of harlequin fish was greater than for bluethroat wrasse due to its longer life span (42 vs. 23 years; Fig. 6 for $F = 0.05$ and 0.1).

When comparing white shark, southern eagle ray, and snapper movements, all three species were expected to spend a comparable amount of time in MPAs (Fig. 3), but given the white sharks higher estimated longevity (70 years compared to 25 and 35 years for southern eagle ray and snapper, respectively), its predicted lifetime fishing mortality was higher. The reason why estimated lifetime fishing mortality was not more divergent among species with substantial different lifespans is that even just 5 years of exposure to a high background fishing mortality risk of, for example 20%, is likely to result in the mortality of most resident individuals unless they spend a significant proportion of their activity within MPA boundaries.

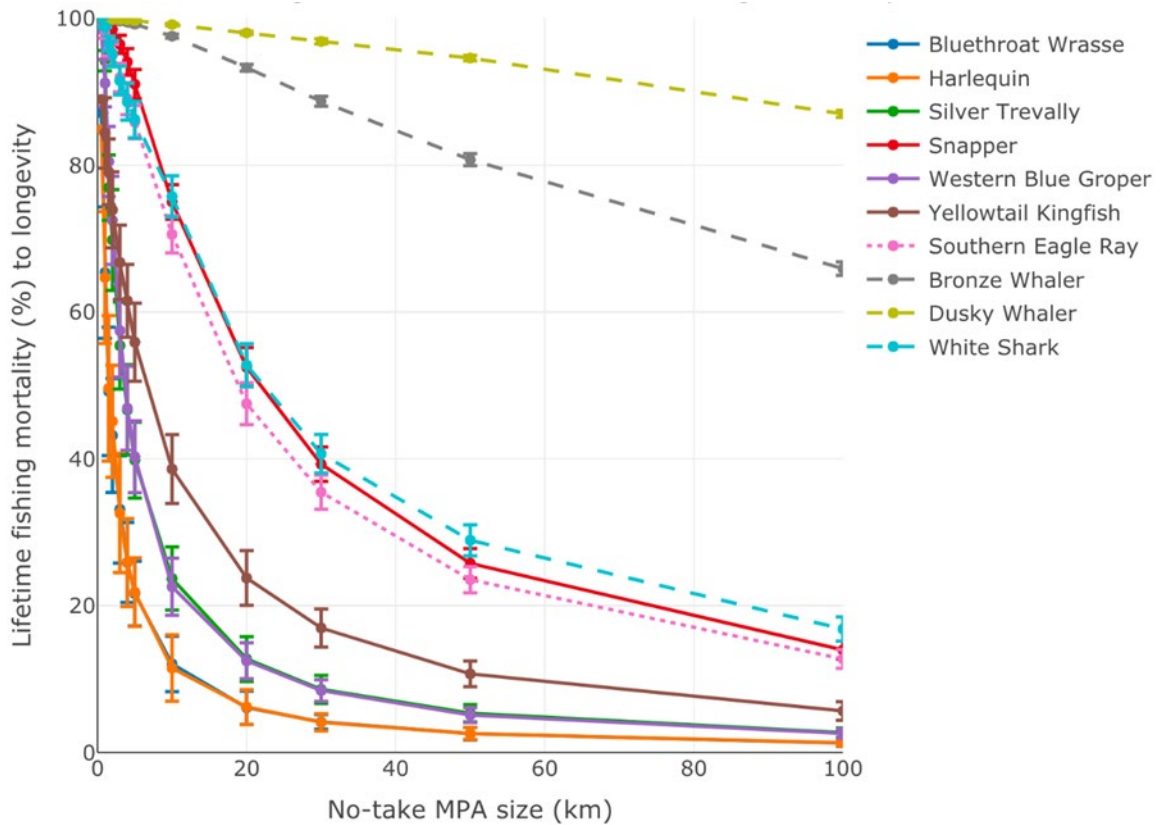


Figure 6. Fishing mortality to longevity (mean \pm standard deviation) with increasing MPA size and for a fishing mortality (F) of 0.2. See https://rpubs.com/DwyKruHuv/FinalReport_DEW for interactive plots and trends at fishing mortality from 0.05 to 0.5.

4) Lifetime fishing mortality (up to age-at-maturity)

Modelling outcomes revealed substantial variation in the estimated conservation benefits of MPAs across our ten study species. As expected, the two most sedentary species (bluethroat wrasse and harlequin fish), with short-term movement distances of approximately 1 km, were effectively protected in relatively small MPAs. Under a 20% annual fishing mortality risk in surrounding areas, a reduction of lifetime fishing mortality to age-at-maturity of at least 50% required MPA widths of approximately 0.5–1 km for these two comparatively site-attached species (Fig. 7). For more wide-ranging and/or longer-lived species, including western blue groper, silver trevally, and yellowtail kingfish, the same level of protection was achieved when protected areas were 2–3 km wide. Snapper and southern eagle ray revealed short-term movement distances that did not allow for effectively protecting resident individuals to reproductive age unless MPAs were at least \sim 10 km wide. In the case of bronze whaler and dusky shark, even MPAs which extended over 100 km could not provide for effective protection given the two species' short-term movement distances of an average of 107 km and 146 km, respectively (Fig. 7).

Most fishes do not live to their maximum age due to premature natural mortality (e.g. due to predation) or anthropogenic impacts (e.g. due to fishing mortality), resulting in a

truncated age structure, especially for commercially-targeted species. Calculating and valuing protection to age-at-maturity is, therefore, a suitable objective for MPA design which highlights that fishes can be protected to reach spawning age and thereby contribute to population replenishment even though they might not be protected over their entire lifetime. However, even though age-at-maturity was lower than longevity for all species, the relative increase in protection varied between species depending on the actual number of years required to reach maturity and the assumed fishing mortality risk. Intuitively, species characterised by a low age-at-maturity and a substantial difference between the assumed age-at-maturity and longevity benefited the most. For example, lifetime fishing mortality of snapper in MPAs of 10 km decreased from 75% to 40% when based on longevity (35 years) vs. age-at-maturity (6 years) (Fig. 7). Similarly, the large difference between age-at-maturity and longevity of silver trevally (45 vs. 6 years) resulted in a reduction of lifetime fishing mortality with a 10 km MPA from 24% to 11%, respectively (Fig. 7). In contrast, and as expected, accounting for age-at-maturity did not notably affect lifetime fishing mortality estimates of long-lived species that were unlikely to spend much time in MPAs (e.g. dusky shark and bronze whaler), as these species are highly exposed to fishing mortality for long periods of time regardless of whether lifetime mortality is estimated based on longevity or age-at-maturity. For such species, MPAs have an overall low capacity to contribute to population replenishment and persistence, unless their width extends across vast areas (>100 km) (Fig. 7).

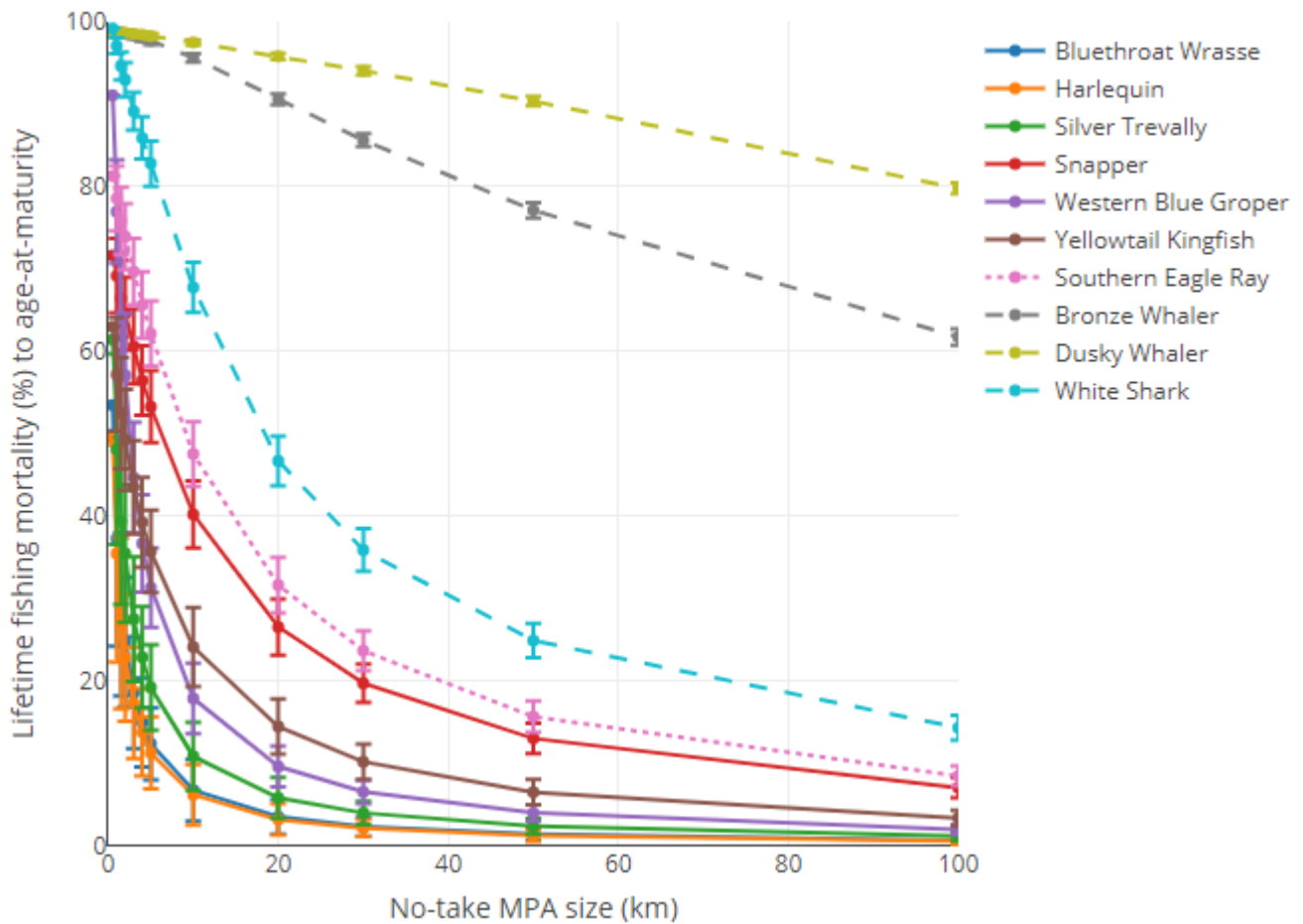


Figure 7. Fishing mortality until reproductive age (i.e. age-at-maturity) (mean \pm standard deviation) with increasing MPA size and for a fishing mortality (F) of 0.2. See https://rpubs.com/DwyKruHuv/FinalReport_DEW for interactive plots and trends at fishing mortality from 0.05 to 0.5.

5) Relevance to South Australia's Marine Park Network

Based on the median maximum width of South Australian no-take MPAs (7.8 km; https://rpubs.com/DwyKruHuv/Draft2_1), the current South Australian MPA network might be suitable to protect reef-associated species with limited short-term movements, and species with intermediate short-term movements that also have early maturation. Larger no-take MPAs would be required to significantly protect species which mature late and/or show more substantial short-term movements. Whether the current South Australian MPA network ensures suitable protection depends on the anticipated reduction in fishing mortality for species of conservation and management concern (Fig. 5–7). Our findings and interactive plots provide multiple alternative metrics for managers to assess these conservation benefits of MPAs relative to their current sizes or potential future changes to the network. For example, if fishing mortality was 20% without MPAs, a 10 km no-take MPA would reduce lifetime fishing mortality to 6–7% for resident harlequin fish and bluetthroat wrasse, 10.9% for resident silver trevally, 17.9% for resident western blue groper, 24.2% for resident yellowtail kingfish, 40.3% for resident snapper, 47.6% for resident southern eagle ray, 67.8% for resident white shark, and ~95% for resident bronze whaler and dusky shark.

Reducing MPA size to a median of 5 km would lead to only three of the 10 studied species to have a lifetime fishing mortality to age-at-maturity less than 20%, i.e. harlequin fish, bluethroat wrasse, and silver trevally. Even the western blue groper which shows limited weekly short-term movements, and can therefore be expected to spend a substantial proportion of time in 5 km wide MPAs (67%; Fig. 3), would still experience 31.8% lifetime fishing mortality in such MPAs because of its late age-at-maturity, which leads to an exposure of many individuals to a cumulatively high fishing mortality risk outside of the MPA over many years. In contrast, expanding MPA size to a median of 20 km can be expected to double the number of species experiencing <30% fishing mortality until reproduction, including western blue groper, yellowtail kingfish, and snapper with values of 9.7%, 14.5%, and 26.6%, respectively. However, the largest decrease in lifetime fishing mortality was predicted to be achieved when MPA width increased from 1 to 10 km (regardless of whether it was estimated based on longevity or reproductive age). For example, extending MPA width from 1 to 10 km was found to decrease western blue groper and silver trevally lifetime fishing mortality from 77.0% to 17.9%, and from 48.2% to 10.9%, respectively. Therefore, spatial conservation planning in South Australia would benefit from considering whether increased benefits are better obtained by increasing the size of small MPAs (e.g. to 10 km wide) vs further increasing comparatively large MPAs. Clearly, the former can be expected to benefit more species, but the latter might be required to ensure conservation gains for species with more substantial short-term movements and late maturation which would remain at an otherwise high risk of depletion. Additionally, targeting areas where species have extended periods of residency and predictable site fidelity can also provide refuge and conservation benefit (as seen with white sharks).

6) Benefits of modelling approach and metrics used

The effectiveness of MPAs for species conservation is generally assessed using relative differences in fish abundance regardless of the movement pattern or home range size of resident species (Albano *et al.* 2021; Haberstroh *et al.* 2022). However, this practice is risky given the critical relevance of knowledge on species residency times within MPA boundaries to estimate associated conservation impact. Our method incorporates movement information by accounting not only for inter-specific but also for intra-specific variability in movement, which was not previously possible (but see Dwyer *et al.* 2020). Intraspecific variability in movement behaviours is common and can result from a variety of ecological processes. For example, individuals can vary in the movement behaviours and space use due to physiological differences, e.g., the timing of migrations, occurrence and residency patterns of grey nurse sharks (*Carcharias taurus*) differs between sexes and maturity (Bansemer and Bennett 2011). Intra-individual differences in movement behaviours can also occur, where individuals change their movement patterns according to abiotic factors (e.g. dynamic oceanographic features), physiological condition, and resource availability (Tyler and Rose 1994; Humphries *et al.* 2010; Humphries *et al.* 2016), e.g. while relocating to a different foraging patch, between different habitats, or between foraging vs. breeding seasons. The use of acoustic tracking data captured in individual-based models enables us to

account for these kinds of inter and intra-specific variation as well as other sources of variations in movement patterns even when the mechanistic drivers of variability are not fully understood.

Accounting for variability of individual movements resulted in an additional 10–50% of all individuals protected over their lifetime. The lower end of this spectrum was represented by species that could not be effectively protected because they were highly mobile and long-lived (e.g. both whaler sharks). The upper end of this spectrum was represented by all other species whenever the fishing mortality risk was so high that few individuals survived without protection in MPAs that were sufficient to cover the scale of their core area of short-term space use. The largest increase in lifetime survival was observed in species with small movement (e.g. harlequin fish, silver trevally, western blue groper). Accounting for variability also increased MPA benefits in mobile species (e.g. dusky shark, bronze whaler), but increased protection was smaller and took longer to increase as MPA size needs to be substantial to cover the movements of a large proportion of individuals from these species.

One of the species which most benefited from accounting for movement distribution, the white shark, is a large mobile species which would not traditionally be considered to benefit from MPAs due to its large-scale movements and migrations (McAuley *et al.* 2017; Bradford *et al.* 2020). However, their temporary residency at foraging locations (e.g. at seal colonies; Bruce *et al.* 2006; Bruce and Bradford 2013) makes them more likely to benefit from MPAs than expected. This observation was only possible by using individual movement profiles for individual-based modelling which accounted for the comparatively limited weekly movements of white sharks when residing at seal colonies.

Further considering that survival to reproduction (i.e. age-at-maturity) might be a more feasible conservation goal than lifetime survival, our results show that MPA contribution to protecting fish increased when assessing survival to reproductive age rather than maximum age. Assuming the otherwise same fishing mortality risk outside of MPAs (20%), even on average just 2 km wide MPAs were found to protect between 43% and 77% of all individuals of teleost fishes until they were theoretically able to reproduce and thus contribute to population replenishment. Trends under the assumption of both lower and higher fishing mortality risks adjacent to MPAs remained principally similar. However, the interplay between fishing pressure, individual movements, longevity, and age-at-maturity resulted in dynamic variations of predicted conservation benefits. When the fishing mortality risk outside of MPAs was assumed to be low (5%), for example, species with a shorter lifespan were more effectively protected in small MPAs than those experiencing a cumulatively still high risk of mortality over their more extensive lifetime (Fig. 6). In contrast, survival to reproduction was more feasible for all species, considering that the age-at-maturity is always lower than a species' maximum age, and that interspecific differences in the age-at-maturity are thus less pronounced (Fig. 7). Even most individuals of the two migratory whaler species could theoretically be protected until reproduction, but MPAs would have to be very large (100 km wide). For all other species, protection to the age-at-maturity could be achieved much earlier (0.5–10 km wide MPAs). When the fishing mortality risk outside of MPAs was assumed to be excessive (50–100%), trends were almost identical to those

observed under the above described 20% mortality risk scenario. The key difference was that changes in MPA sizes required to achieve protection over a species' lifetime vs. its age-at-maturity were minimal.

9) Limitations

Our approach provides robust estimates of short-term movement through the use of a single technology (acoustic telemetry). However, there are inherent limitations in using data derived from acoustic telemetry to estimate movement. First, acoustic telemetry is not suited to tracking movements of all aquatic species (Hussey *et al.* 2015; Harcourt *et al.* 2019), and so our approach is limited to coastal species that frequent areas where receivers can be placed. Second, acoustic receivers can have variable detection ranges, influenced by a variety of factors including transmitter power output, biofouling, ambient noise, and environmental conditions (Heupel *et al.* 2008; Kessel *et al.* 2014; Huveneers *et al.* 2016; Huveneers *et al.* 2017). As such it is possible that deployed receivers can miss detections of animals even when in the vicinity of deployed receivers. Finally, small arrays and small distances between receivers potentially lead to underestimating movement for some species that move over larger distances into areas where receivers are not present. We limited such biases by using a large number of receivers deployed at >1,000 locations across Australia through the IMOS continental acoustic telemetry network. This network has been successfully used to measure intra- and inter-specific functional movement behaviours (Brodie *et al.* 2018), stock structure of commercially-important marine species (Lédée *et al.* 2021), as well as impacts of changes in human activity on animal populations during global disruptions such as the COVID-19 pandemic (Huveneers *et al.* 2021a). Similar large-scale acoustic networks have also been used to estimate small- and large-scale movement (Brodie *et al.* 2018), highlighting the suitability of our method.

Further limitations arise from the challenge to measure alternative types of movements, such as short-term movements at different locations that are visited for alternative ecological reasons, e.g. breeding vs. foraging, and how animals migrate between such locations. Hence, our individual-based model is currently restricted to representing short-term movements as bidirectional diffusion across a home range. Clearly, this simplified representation of movements potentially risks mixing up data points that actually represent long-term migrations or relocations of the home range, and are then implicitly merged into a combined overall estimate of the home range. However, such occurrences should be rare given that we focused on weekly scales of movement. While longer time periods (e.g. monthly) should clearly be considered in future studies, data availability limited the number of monthly movement estimates to an extent that it would have greatly reduced our power to reliably estimate MPA conservation effectiveness.

9. Summary and recommendations

We used a novel individual-based model incorporating intra and inter variability of individual movements to assess the conservation benefit of no-take MPAs in the context of South Australia's Marine Park Network. Our findings show that small MPAs (i.e. 2 km wide) can be sufficient to protect species with limited short-term movements (i.e. four out of ten study species spend more than 50% of the time in such sized MPAs). Our new approach also shows that species with large-scale migrations might benefit from MPAs more than previously assumed due to their temporary residency and limited short-term movements at particular sites, thus enabling MPAs to reduce fishing mortality during extended residency periods at such sites. Furthermore, the consideration of survival to reproduction as a realistic and useful conservation objective shows that MPA contributions to fish population recovery and persistence could be greater than widely assumed. However, MPAs larger than currently existing in South Australia are required to provide substantial protection to large and highly mobile species.

Our findings and interactive plots (https://rpubs.com/DwyKruHuv/FinalReport_DEW) will allow managers to consider the best investment in spatial conservation planning by enabling managers to assess explicit predictions of conservation benefits associated with various plausible MPA sizes in South Australia's Marine Parks Network, and in direct relation to the ecology and life history characteristics of a diverse range of species captured in this study.

Further research would fundamentally benefit from tagging many more individuals per species and by tracking their movements based on an increasingly comprehensive network of acoustic receiver arrays, which should ultimately allow for measuring both short- and longer-term movements of a variety of ecologically-diverse species. The South Australian marine parks network provides a useful case study for future expansion. Outcomes from our study indicate that the size and spacing of MPAs could be planned such that most species experience protection in multiple MPAs. Explicit consideration of this conservation impact of the MPA network (rather than of individual MPAs) will require modification of the simulation modelling approach into spatially realistic 2D space, which can represent empirically-grounded movements of individual fish across explicit patches of habitat.

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