



Increased connectivity and depth improve the effectiveness of marine reserves

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► To cite this version:

Jordan Goetze, Shaun Wilson, Ben Radford, Rebecca Fisher, Tim Langlois, et al.. Increased connectivity and depth improve the effectiveness of marine reserves. *Global Change Biology*, 2021, 27 (15), pp.3432-3447. 10.1111/gcb.15635 . hal-03277253

HAL Id: hal-03277253

<https://hal.science/hal-03277253>

Submitted on 2 Jul 2021

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1 **Increased connectivity and depth improve the effectiveness of marine reserves**

2
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46 **Keywords:** Marine protected areas, sanctuaries, fully protected areas, meta-analysis,
47 marine conservation, marine reserve effectiveness, marine reserve design

48
49 **Abstract (200 words)**

50
51 Marine reserves are a key tool for the conservation of marine biodiversity, yet only ~2.5% of
52 the world's oceans are protected. The integration of marine reserves into connected networks
53 representing all habitats has been encouraged by international agreements, yet the benefits
54 of this design has not been tested empirically. Australia has one of the largest systems of
55 marine reserves, providing a rare opportunity to assess how connectivity influences
56 conservation success. An Australia-wide dataset was collected using baited remote
57 underwater video systems deployed across a depth range from 0–100 m to assess the
58 effectiveness of marine reserves for protecting teleosts subject to commercial and recreational
59 fishing. A meta-analytical comparison of 73 fished species within 91 marine reserves found
60 that, on average, marine reserves had 28% greater abundance and 53% greater biomass of
61 fished species compared to adjacent areas open to fishing. However, benefits of protection
62 were not observed across all reserves (heterogeneity), so full subsets generalised additive
63 modelling was used to consider factors that influence marine reserve effectiveness, including
64 distance-based and ecological metrics of connectivity among reserves. Our results suggest
65 that increased connectivity and depth improve the aforementioned marine reserve benefits
66 and that these factors should be considered to optimise such benefits over time. We provide
67 important guidance on factors to consider when implementing marine reserves for the purpose
68 of increasing the abundance and size of fished species, given the expected increase in
69 coverage globally. We show that marine reserves that are fully protected (no-take) and
70 designed to optimize connectivity, size and depth range can provide an effective conservation
71 strategy for fished species in temperate and tropical waters within an overarching marine
72 biodiversity conservation framework.

73
74 **Introduction**
75
76 Marine reserves exist across the world's oceans with the broad objective of contributing to the
77 conservation of marine biodiversity through the exclusion of extractive activities such as
78 fishing. Some of the most tangible measures of ecological changes within marine reserves are
79 increased abundance, size, and biomass of fished species (Lester et al. 2009), which make
80 up an important component of marine biodiversity. The protection of large-bodied individuals,
81 with higher fecundity may result in significant larval supply (Marshall et al. 2019) or spillover
82 of adult fish (Di Lorenzo et al. 2016, 2020), hence providing benefits to adjacent fished areas.
83 However, while the parties to the convention on biological diversity agreed to protect 10% of
84 their coastal and marine waters by 2020, only 2.5% of the global ocean is presently within fully
85 protected marine reserves (Sala et al. 2018), with striking differences across sea basins
86 (Claudet et al. 2020).

87

88 Previous meta-analyses over continental to global scales have demonstrated that the
89 conservation benefits of marine reserves depend on the taxa considered and increase with
90 reserve size, age, level of protection, enforcement and management effectiveness (Mosquera
91 et al. 2000; Claudet et al. 2008, 2010; Gill et al. 2017; Lester et al. 2009; Edgar et al. 2014;
92 Bergseth et al. 2015; Zupan et al. 2018; Di Lorenzo et al. 2020). While empirical evidence is
93 limited (Grorud-Colvert et al. 2014, Harrison et al. 2020), theory suggests that the ability of
94 marine reserves to improve ecosystem resilience and benefit ecosystem services, such as
95 fisheries, will depend on the extent to which reserves are connected (Botsford et al. 2009;
96 Ballantine 2014). Some studies recognise connectivity (i.e., demographic links among
97 assemblages via the dispersal of individuals as adults, juveniles, and larvae) as a key
98 component in the design of marine reserve networks (Álvarez- Romero et al. 2018; Tittensor
99 et al. 2019), while others suggest it is less important (Costello & Connor 2019). An empirical
100 assessment of connectivity between reserves, at appropriately large spatial scales, is
101 therefore required. Similarly, the extent of fishing adjacent to marine reserves combined with
102 distal social drivers can have a strong effect on local fish assemblages and should be
103 considered in any large-scale assessment of marine reserves. For example, Cinner et al.
104 (2018), found that fish biomass within marine reserves, declines with increasing human
105 impacts outside of reserves, and areas with moderate human impacts show the greatest
106 differences in fish biomass.

107
108 The influence of social, ecological and design factors on marine reserve effectiveness has
109 also differed among studies. For example, Halpern (2003) found that reserve size did not
110 influence fish abundance within reserves, yet subsequent empirical studies and meta-
111 analyses found that large reserves were more effective in promoting biomass and abundance
112 (Claudet et al. 2008; Edgar et al. 2014; Malcolm et al. 2016). Differences among studies may
113 be due to data being sourced from different social and ecological systems such that the range
114 of marine reserve sizes differs among studies, or over-representation of significant results in
115 the published literature compared to null results (Graham et al. 2011). In addition, meta-
116 analyses often pool data collected using different methods, yet this may not always be
117 appropriate (Cresswell et al. 2019). Species-level measures of fish size and abundance can
118 vary considerably among methods (Murphy & Jenkins 2010) and as such may influence the
119 ability to detect spatial differences in fishes (Goetze et al. 2015).

120
121 One way to avoid the confounding effects of different methodologies in meta-analyses is to
122 only consider data collected by a single technique. Baited remote underwater video systems
123 (BRUVs) are now commonly used for monitoring and research, providing non-extractive,
124 spatially extensive data for the assessment of the relative abundance of fishes and, when
125 stereo systems are used, length and biomass. This method is especially adept at detecting
126 mobile predatory species (Watson et al. 2005; Goetze et al. 2015; Harvey et al. 2018), many
127 of which are targeted by fishers. Moreover, BRUVs have repeatedly recorded the direct effects
128 of fishing on the abundance, biomass and/or size of targeted species (Malcolm et al. 2007;
129 Goetze et al. 2011; Langlois et al. 2012) and are more likely to detect differences in fish
130 abundance between marine reserves and fished areas than underwater visual census (UVC)
131 due to bait increasing the proportion of predatory species surveyed (Willis & Babcock 2000;
132 Goetze et al. 2015). BRUVs are, however, limited to relative estimates of abundance/biomass
133 due to variation in the bait plume (which prevents the calculation of a definitive sampling area;
134 Harvey et al. 2007) and have a limited ability to survey cryptic species (Watson et al. 2005).
135 There is also the potential for changes to fish behaviour when they approach baited cameras,

136 which can influence abundance estimates (Dunlop et al. 2015), although this is most
137 problematic in downward facing BRUVs which have a limited field of view (Cundy et al. 2017;
138 Coghlan et al. 2017). Conversely, most broad-scale assessments of marine reserve have used
139 UVC to survey reef fishes, which limits these studies to shallow waters (e.g. a mean depth of
140 7.5 m in Edgar et al. 2018). Like BRUVs, UVC is also subject to biases. For example, divers
141 can cause behavioural responses of fish, which in some locations has exaggerated the
142 effectiveness of marine reserves (Lindfield et al. 2014a; Januchowski-Hartley et al. 2015; Gray
143 et al. 2016). Importantly, BRUVs are a remote technique, removing the biases associated with
144 divers and enabling assessments of marine reserves over a much greater depth range
145 (Whitmarsh et al. 2017), and are being used extensively to study fisheries targeted
146 communities globally (MacNeil et al., 2020).

147
148 In Australia, BRUVs have been used extensively over a range of depths and habitats to answer
149 a broad range of ecological questions, including those related to marine reserves (Harvey et
150 al. 2021). Both state and federal governments have aimed to establish a comprehensive,
151 adequate and representative system of marine reserves (Kenchington 2016), providing a
152 unique opportunity to assess a broad range of marine reserves. Here, we make use of a
153 national-scale BRUVs dataset to empirically assess a snapshot of the effect that Australian
154 marine reserves have had on the abundance and biomass of fishes over a broad depth-range.
155 We use meta-analyses to investigate how relative measures of fish abundance and biomass
156 vary among these reserves. Uniquely, our analysis considers the influence of depth over
157 ranges previously not considered (0–100m) in similar studies (Edgar et al. 2018), as well as
158 the role of ecological and distance-based connectivity of marine reserves. The inclusion of
159 these factors, with others known to affect the abundance or biomass of fish within marine
160 reserves, enables a comprehensive assessment of which are most important when designing
161 marine reserve networks.

162

163 **Methods**

164

165 *Selection criteria and data evaluation*

166

167 Australia has one of the largest systems of marine reserves, with more than 400 reserves
168 (CAPAD 2018), covering an area close to 1 million km² (mpatlas.org 2020). However, most
169 bioregions across Australia still have less than 10% of their waters within marine reserves
170 (Roberts et al. 2018). The size range of marine reserves in Australia is also extensive, ranging
171 from <0.1 to >100,000 km² (Department of Agriculture, Water and the Environment 2020). We
172 utilised a national dataset compiled in GlobalArchive (<https://globalarchive.org/>) consisting of
173 both single camera and stereo-BRUVs deployments, covering the Australian continental shelf,
174 across six states and five marine regions. Survey data were collected and analysed using
175 standard operating procedures for BRUVs (Langlois et al. 2020). Bait type (pilchards), the
176 method of recording abundance (MaxN; calculated as the maximum number of individuals of
177 a given species present in a single video frame; [Priede et al. 1994](#)) and taxonomic resolution
178 (species level where possible), were consistent across 19,260 BRUVs replicates, deployed
179 between 2004 and 2017. MaxN is a conservative estimate of relative abundance that has
180 become the standard metric for BRUVs given it avoids double counting (Langlois et al. 2020)
181 and tracks absolute abundance well for predatory species which are often observed in lower
182 abundance (MacNeil et al. 2020). There were differences across studies in the quantity of bait,
183 cameras used, single vs stereo systems and separation distance (discussed in detail in Harvey

184 et al. 2021), however, these factors did not vary for each marine reserve/control pair and log-
185 ratio effect sizes were used to account for between study variation (described below).

186
187 The following criteria were used to select data that were suitable for assessing the effectiveness of marine reserves; (1) BRUVs collected data on demersal fishes with at least two replicates inside and two replicates outside of a zone designated as a sanctuary, marine national park, conservation park/area or no-take following Australian nomenclature used in different state and commonwealth waters (herein referred to as marine reserves). While this includes some partially protected areas that allow fishing within a proportion of their boundaries (e.g. fishing from shore or trolling for pelagic species), all were designated as no-take for demersal fishing from a boat and the extent of fishing regulations were taken into account as a covariate (see regulation classification below); (2) sampled during daylight hours at depths less than 100 m, (3) relative abundance data (MaxN) was available for fished species and (4) only the most recent inside/outside assessment was used if temporal sampling had occurred, unless a dataset had greater replication and was completed less than two years earlier. In this case the study with greater replication was used. (5) Paired inside/outside assessments were only taken from the same field campaign (so were completed at the same time of year).

202
203 To ensure the appropriate controls were assigned for each marine reserve, the spatial layout of data was overlayed on satellite imagery with reserve boundaries and the closest sites across similar broad-scale geography (e.g., exposure/distance from shore) either side of each reserve were assigned as controls. This was done in consultation with the researchers that had originally designed each study and three studies were deemed to have inadequately sampled the marine reserve (e.g. had <4 replicate BRUVs deployed in marine reserves > 100 km²) so were removed from the analysis (Supp. I). A total of 91 individual marine reserves were included after selection criteria and data evaluation, representing ~25% of marine reserves across Australia (CAPAD 2018; Supp I).

212
213 *Response variables*

214
215 Species were classified as 'fished' if they were retained as food fish by either recreational or commercial fishers in Australia using the expert knowledge of fisheries managers across each state (listed in Supp. II). Non-targeted species (classified as all remaining species) were also examined to provide a control for fished species. Relative abundance data were available for all 91 marine reserves, however, length data were only collected in studies using stereo-BRUVs, hence relative biomass data were available for 69 marine reserves.

221
222 *Meta-analysis*

223
224 The average abundance and biomass (based on MaxN) was calculated per replicate inside and outside of each marine reserve. Effect sizes were modelled as log-ratios to quantify differences in the average abundance and biomass (of both fished and non-target species) inside relative to outside for each marine reserve. In cases where fish were absent either inside or outside the reserve (i.e. zero values), one individual fish and the average (mean) weight of an individual fish was added to one replicate (inside and outside the reserve) to allow calculation of the log ratio for abundance and biomass, following Thiault et al. (2019). Effect sizes were calculated as follows:

232

$$E_{m,i} = \ln\left(\frac{\bar{X}_{m,P,i}}{\bar{X}_{m,F,i}}\right)$$

233

234

235 where $E_{m,i}$ is the log response ratio for each marine reserve i based on the metric m
236 (abundance or biomass) and $\bar{X}_{m,P,i}$ and $\bar{X}_{m,F,i}$ are the mean of each metric m in protected (P)
237 and fished (F) areas, respectively.

238

239 Variance of the effect sizes were calculated as:

240

$$V_{E_{m,i}} = \sum_{P,F} \sigma_i^2 / (n_i * \bar{X}_i^2)$$

241

242 where $v_{Em,i}$ is the variance associated with the effect size $E_{m,i}$, σ_i is the standard deviations
243 associated with the mean, and n_i is the number of replicates and \bar{X}_i the means for the protected
244 (P) and fished areas (F).

245

246 We then used a mixed-effects weighted meta-analysis where weights of each individual effect
247 size incorporate these variances as follows:

248

$$w_{m,i} = \frac{1}{V_{E_{m,i}} + v_{m,a}}$$

249

250

251 where $w_{m,i}$ is the weight associated to each effect $E_{m,i}$, $v_{Em,i}$ is the within study variance for each
252 marine reserve i using the metric m and $v_{m,a}$ is the among-study variance across marine
253 reserves for each metric. The among-study variance was obtained using the generalised
254 equation reported in Hedges & Pigott (2004). Confidence intervals for group and overall effect
255 sizes were derived from a Student's t statistic. The among study variance were calculated
256 using the restricted maximum likelihood estimator with the metafor package (Viechtbauer
257 2010) in the statistical program R (R Core Team, 2017). Log-ratio effect sizes were converted
258 back to percentage differences in text to assist with the interpretation of magnitudes.

259

260 *Habitat analysis*

261

262 To ensure studies had sampled comparable habitat and depths inside compared to outside of
263 each marine reserve, information on the mean relief, depth, and percentage composition of
264 biotic reef was collected following the procedures outlined in (Langlois et al. 2020). Paired t-
265 tests compared the means for each of these factors inside/outside of each marine reserve.
266 For assessments with a significant difference in habitat or depth inside compared to outside
267 the reserve ($P < 0.05$), outlying replicates were removed until no significant differences were
268 found ($P > 0.05$). As a result, the habitat sampled was balanced inside vs outside and these
269 variables were not considered as covariates when modelling.

270

271 *Factors influencing marine reserve protection*

272
273 For each marine reserve, we collated information on the size (total area in km²) and age based
274 on the time between active enforcement of the reserve regulations and sampling (CAPAD
275 2020). Depth was calculated as the average depth of BRUVs deployed within the marine
276 reserve. The influence of fishing pressure was assessed using a modification of the human
277 gravity metric (Cinner et al. 2018). Gravity was calculated as the sum of the human population
278 within a 200 km radius of each marine reserve (using the LandScan 2011 human population
279 grid) divided by the distance (km) from the marine reserve to the nearest town centre. Distance
280 to boat ramp was calculated as the average distance (km) from the marine reserve to the
281 nearest boat ramp. To determine the protection level and level of exploitation in each marine
282 reserve and fished site, respectively, we used the regulation-based classification system for
283 marine protected areas of Horta e Costa et al. (2016). This system gives a score from one to
284 eight based on the number and potential impact of different fishing gears, other human
285 activities (e.g. aquaculture) and accessibility (e.g. no anchoring) on fishes and their
286 environment. We used the difference in zone classification scores between each marine
287 reserve and its corresponding control/fished areas as a measure of the level of protection
288 afforded by each marine reserve (herein referred to as the regulation difference). Note we
289 assume that the classification scores represent a linear relationship with the impact of
290 restrictions, given this could not be calculated. Compliance was categorised into three levels
291 by local park authorities or researchers with substantial experience working in the area: high
292 (infrequent breaches of management rules), moderate (occasional breaches of management
293 rules) and low (frequent breaches of management rules).

294

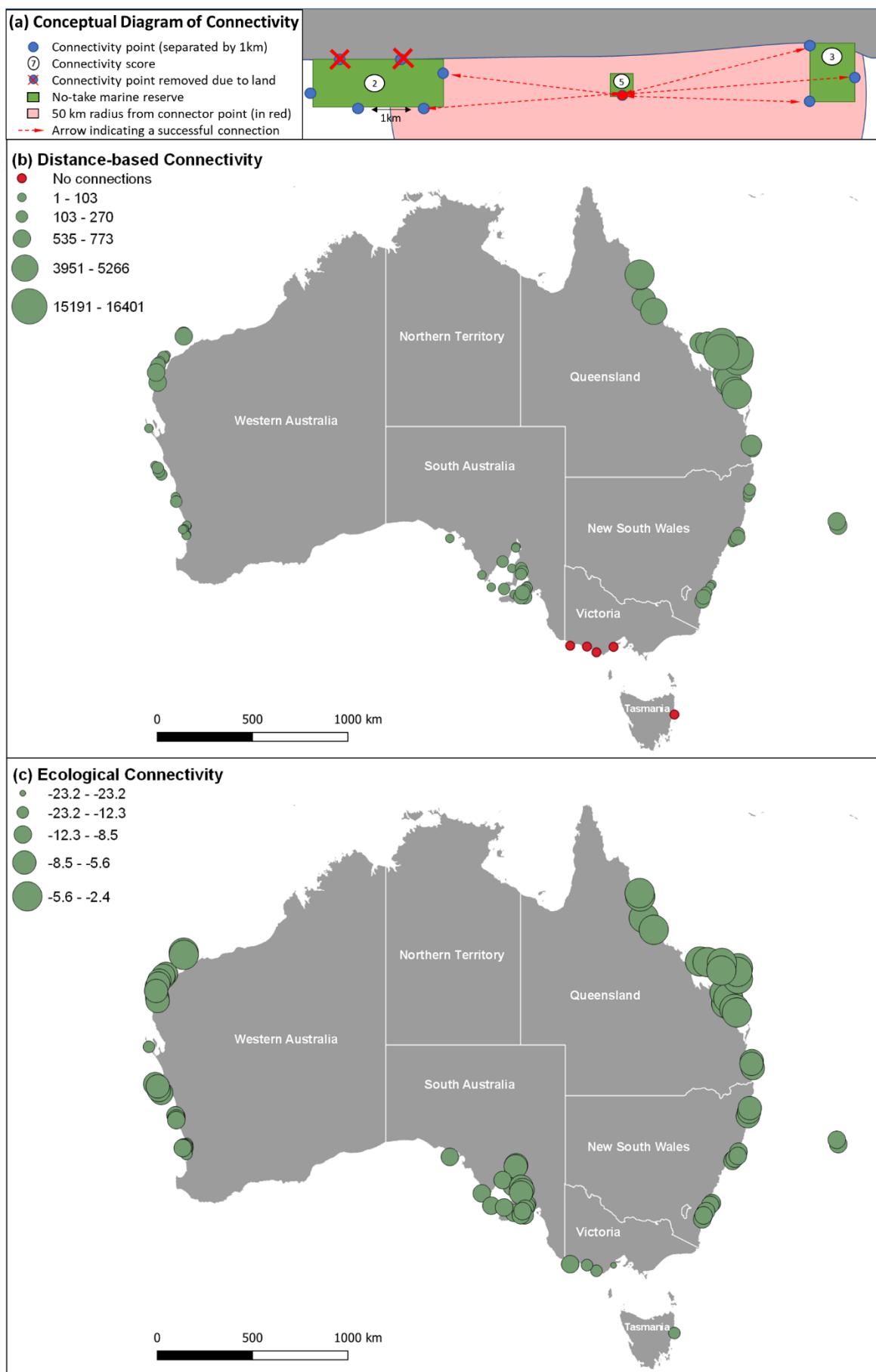
295 *Connectivity*

296
297 To explore the influence of 'demographically significant' connectivity based on a biophysical
298 model of larval fish dispersal (Tremblay et al. 2012), we summarised the total relative in-flow for
299 each marine reserve location, from a recent study quantifying the ecological connectivity
300 among Australia's MPA system (Roberts et al. 2020). In-flow is a relative measure of
301 connectivity representing the amount of incoming larvae into a destination site and does not
302 include local retention (Young et al. 2020). Only protected patches were used to calculate
303 connectivity, where an upstream connection was considered protected, if it contained a
304 protected area (see Roberts et al. 2020 for details). This analysis was based on the ecological
305 connectivity of wrasses (Labridae) as they are relatively well represented in our fished species
306 list (9 species; Supp. II), while other species presented in Roberts et al. (2020) were not
307 included in our analysis. However, the top models did not change when large-bodied, long-
308 range dispersers were considered (Trevally), and ecological connectivity was absent from top
309 models when small-bodied, non-targeted Damselfish were considered (Supp III).

310

311 A distance-based connectivity metric was also calculated by summing the number of spatial
312 connections a marine reserve has to all other marine reserves within a 50 km radius. A 50 km
313 radius was chosen to empirically test if there are conservation benefits based on the
314 recommendation made by Almany et al. (2009), to ensure that between reserve distance is
315 ≤50 km. This distance provides a conservative estimate of a distance-based connectivity that
316 ensures zones are demographically connected for most fish species (Almany et al 2009). For
317 each marine reserve, potential connection points were spaced 1 km along the boundary, using
318 a random starting position. Points that fell on a boundary attached to land were removed so

319 that distance-based connectivity was only assessed using boundary points connected by sea.
320 The distance-based connectivity of each marine reserve was calculated by summing the
321 number of points that connected to other points belonging to neighbouring marine reserve
322 within a 50 km Euclidean distance radius (or vector). Vectors that intercepted land (e.g. a
323 headland) were excluded from analysis. Analysis was completed using the “EucDistance”
324 function arcpy python library in ESRI ArcPro version 2.4, with planar coordinates within marine
325 reserve boundary points (GDA94 Geoscience Australia Lambert projection; EPSG:3112).
326 Figure 1a shows a conceptual diagram of how distance-based connectivity was calculated
327 and Fig. 1b shows the distance-based connectivity scores for the 91 marine reserves sampled.
328 We also calculated distance-based connectivity for all marine reserves within the 2018
329 Collaborative Australian Protected Area Database (CAPAD 2020), to highlight gaps in the use
330 of marine reserves across Australia (Supp. IV). Distance-based connectivity of marine
331 reserves was highest on the Great Barrier Reef, as there is a high density of marine reserves
332 compared to other locations around Australia (Figure 1b). Clusters of relatively high distance-
333 based connectivity were also observed in the Ningaloo Marine Park, Western Australia, the
334 Encounter Marine Park (Adelaide/Kangaroo Island) in South Australia and Moreton Bay
335 Marine Park in Queensland. No distance-based connectivity was observed between marine
336 reserves in Victoria or Tasmania. There were also two significant gaps in use of marine
337 reserves, one in the Northern Territory and northern Queensland (to the start of the Great
338 Barrier Reef Marine Park) and the other across the southern coast from south-west Western
339 Australia to South Australia, including the Great Australian Bight (Supp IV).
340



342 Figure 1: (a) A conceptual diagram showing how distance-based connectivity was calculated
343 for a small marine reserve in between two large reserves with land boundaries. (b) the resulting
344 map of distance-based connectivity marine reserves and (c) the ecological connectivity (based
345 on wrasses) for the sampled marine reserves across Australia using Jenks natural breaks. R
346 = 0.815 between distance based and ecological connectivity.

347

348 The two measures of connectivity were termed; ecological connectivity (which was based on
349 realistic oceanography, biology, and habitat characteristics) and distance-based connectivity
350 (which incorporated the spatial distance-based connectivity of zones based on an estimate of
351 a suitable distance for demographic connectivity of fishes; Almany et al. 2009). Ecological
352 connectivity was calculated independent of local larval retention and therefore the size of the
353 focal marine reserve, while the distance-based metric was dependent on the size of the focal
354 marine reserve.

355

356 *Models*

357

358 The influence of marine reserve characteristics (size, age, compliance, ecological and
359 distance-based connectivity, depth, gravity, distance to boat ramp and regulation difference)
360 and location covariates (marine region and state) on abundance and biomass effect sizes
361 were investigated using weighted generalised additive mixed models (GAMMs; Lin & Zhang
362 1999). The distribution of continuous predictors (depth, age, size, connectivity, and gravity)
363 was examined and transformed appropriately to ensure they were evenly distributed across
364 their range. We examined the possibility of any spatial correlation in the data based on latitude
365 and longitude using a variogram, which showed no evidence of spatial autocorrelation and
366 therefore no spatial correlation structure was used in the models (Supp. V). Any effects of
367 State or Marine Region were included as potential fixed effects in models rather than random
368 effects, as they were highly correlated with several continuous predictors (Supp. VI). A
369 weighted full subsets method was used to fit models of all possible combinations up to a
370 maximum of three variables (Fisher et al. 2018). To avoid multicollinearity issues, predictor
371 variables with Pearson correlations (or an equivalent approximation) greater than 0.33 were
372 not included in the same model (Supp. VI). The correlation cut-off value was increased from
373 the recommended value of 0.28 (based on Graham 2003), to allow simultaneous inclusion of
374 the covariates size and age which are known to influence marine reserve effectiveness
375 (Claudet et al. 2008; Edgar et al. 2014). This represents only a marginal increase to a very
376 conservative cut-off and is unlikely to cause issues with bias in parameter estimates. In all
377 models the smoothing parameter was limited to a simple spline, allowing only monotonic
378 relationships ($k = 3$). Model selection was based on Akaike's Information Criterion for small
379 sample sizes (AICc; Akaike 1998) and AICc weights (ω AICc; Burnham & Anderson 2007).
380 Models with AICc values that differ by less than two units show weak evidence for favouring
381 one over the other (Raftery 1995; Burnham & Anderson 2004). The best models were
382 therefore the ones within two AICc units of the lowest AICc values. The ω AICc, which
383 represent probabilities or weights of evidence for each model, were used to facilitate
384 interpretation of the best models. Relative support for each predictor variable was obtained by
385 calculating the summed ω AIC across all subsets of models containing that variable to obtain
386 its relative importance which were plotted in R. Importance plots and P-values derived with
387 the GAM model summaries (Wood et al. 2012) were used to assess whether a significant
388 relationship with effect sizes and covariates existed, which were subsequently plotted in R.
389 Effect sizes were modelled with a Gaussian distribution using `gam()` in the `mgcv` package in

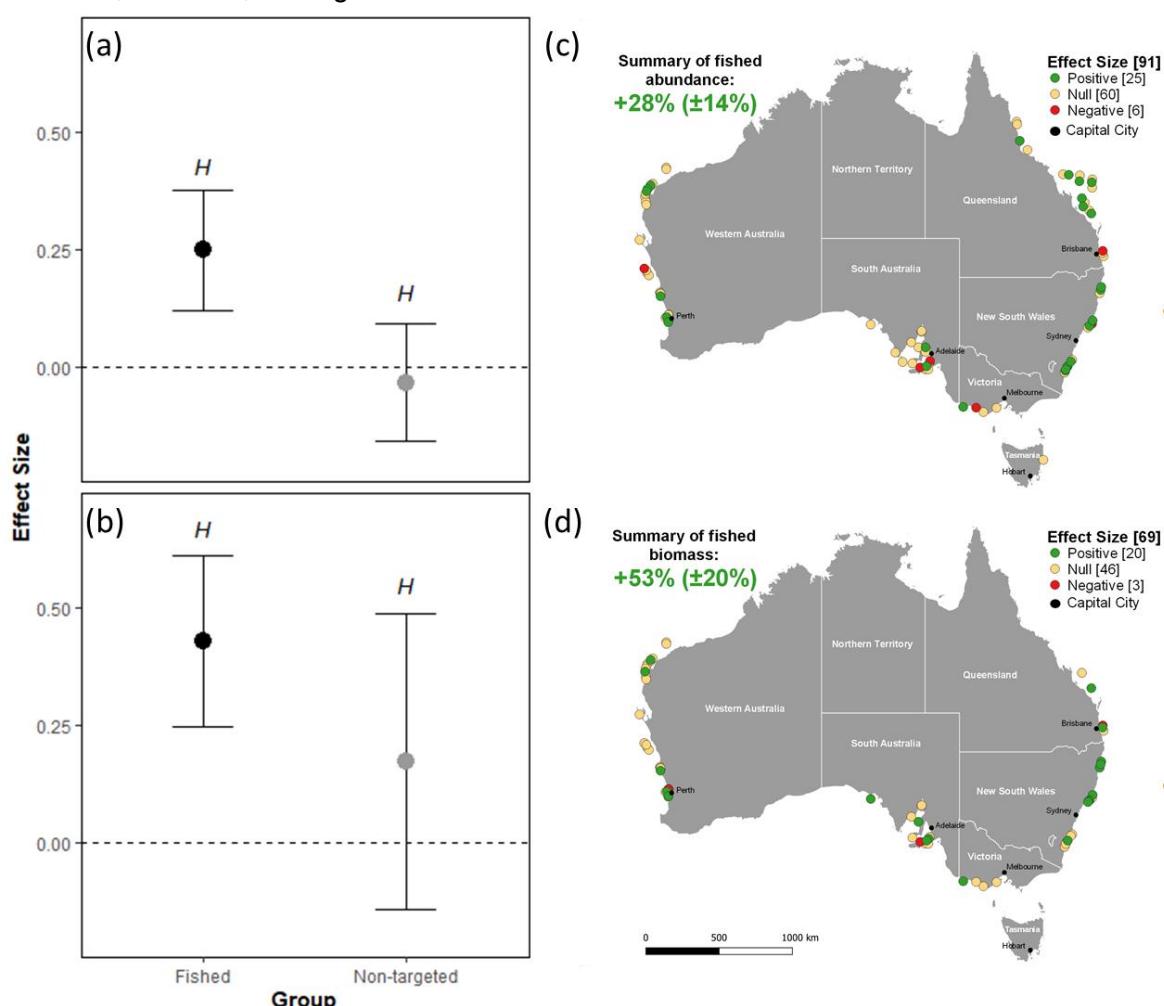
390 R (Wood 2011). The R language for statistical computing (R Core Team 2018) was used for
391 all data manipulation (dplyr, Wickham et al. 2018) and graphing (ggplot2, Wickham 2009).

392

393 Results

394

395 On average, Australian marine reserves had a 28% greater abundance and 53% greater
396 biomass of fished species compared to areas open to fishing (Fig. 2a & b). There were no
397 effects of protection on the abundance or biomass of non-targeted species. There was
398 heterogeneity across effect sizes, suggesting considerable variation in the effectiveness of
399 marine reserves across Australia. For the abundance of fished species across the 91 reserves
400 studied, we observed 60 null (66%), 25 positive (27.5%) and six negative (6.5%) effect sizes
401 (Fig. 2c). Positive and negative effect sizes for abundance were detected in all states, except
402 for Tasmania (where only one marine reserve was sampled). For biomass of fished species
403 across the 69 reserves studied, we observed 46 null (66.5%), 20 positive (29%) and three
404 negative (4.5%) effect sizes (Fig. 2d). Positive effect sizes for biomass also occurred across
405 all states, however, no negative effect sizes were observed in NSW or Victoria.

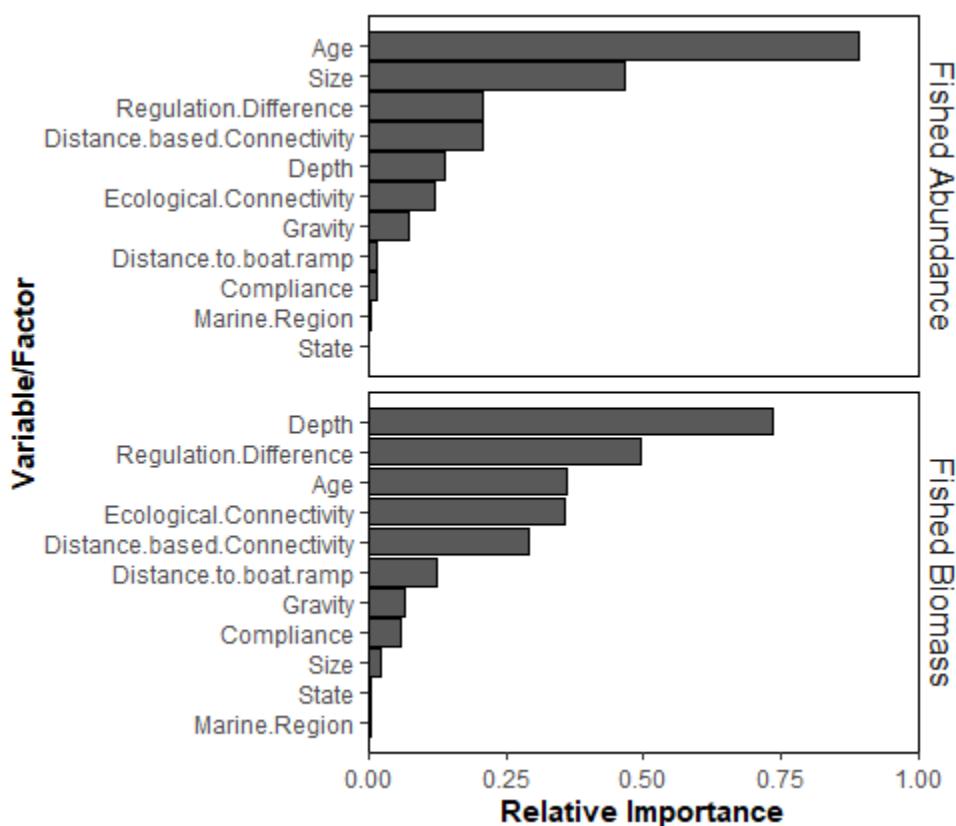


406

407 Figure 2. The log ratio effect sizes of (a) abundance and (b) biomass of fished and non-
408 targeted species inside/outside of marine reserves across Australia. Black dots represent
409 significant results where the 95% confidence interval does not overlap zero. The superscript
410 H indicates that significant heterogeneity ($H < 0.05$) was associated with the effect size. Effect
411 sizes are converted back to percentages and the spatial extent shown for (c) abundance and

412 (d) biomass of fished species only; green points represent a marine reserve with a significantly
413 greater abundance or biomass of fished species; yellow a marine reserve where confidence
414 levels overlapped zero and red where a significantly lower abundance was observed within
415 marine reserve boundaries compared to nearby fished sites.

416
417 The five most important variables for explaining variation in marine reserve effectiveness for
418 fished abundance were age, size, regulation difference, distance-based connectivity, and
419 depth (Fig. 3). The five most important variables for explaining variation in marine reserve
420 effectiveness for fished biomass were depth, regulation difference, age, ecological
421 connectivity and distance-based connectivity.
422

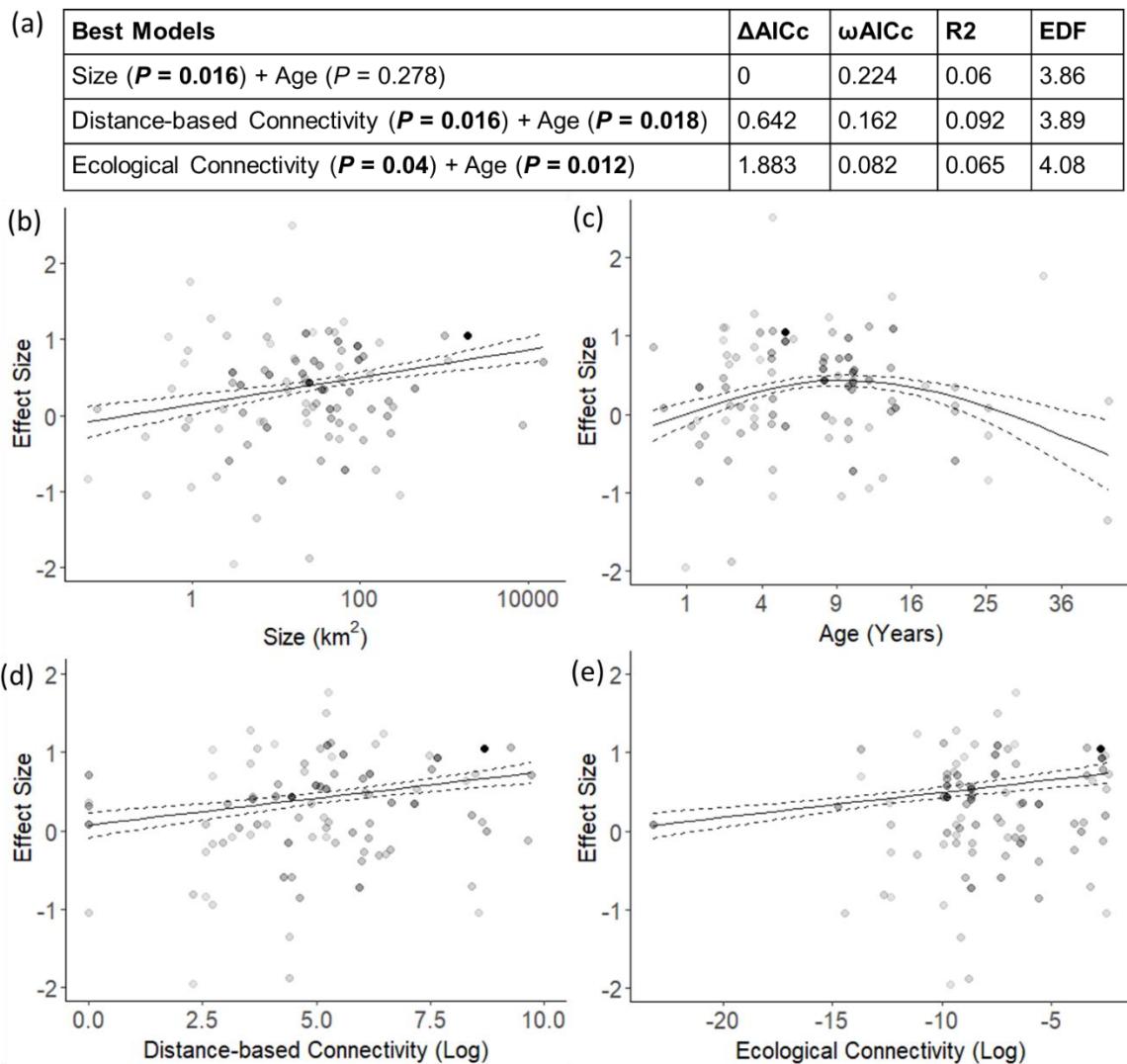


423
424 Figure 3. Importance scores for each explanatory variable in predicting the effectiveness of
425 marine reserves to protect the abundance and biomass of fished species.
426
427

428 All variables were considered in the full subset modelling and while the variance explained by
429 top models was low (Fig 4a, Fig 5a), suggesting factors not considered here and natural
430 variation are contributing to unexplained variance, they explained a greater proportion of the
431 variance than the null model for both abundance ($\Delta\text{AICc} = 9.9$, $\omega\text{AICc} = 0.001$) and biomass
432 ($\Delta\text{AICc} = 6.7$, $\omega\text{AICc} = 0.004$). For fished abundance there were three competing top models,
433 with size in the first model, distance-based connectivity and age in the second and ecological
434 connectivity and age in the third model having a significant relationship with effect size ($P <$
435 0.05 ; Fig 4a). Abundance of fished species within marine reserves compared to fished areas
436 (effect size) increased with increasing marine reserve size, distance-based connectivity and
437 ecological connectivity (Fig 4b,d & e). Effect size also increased with the age of marine
438 reserves up to approximately 10 years, and then remained relatively stable (Fig 4c). The small

439 number of marine reserves greater than 25 years old, provided little confidence in the
 440 interpretation of a decrease in effectiveness in older reserves.

441
 442
 443

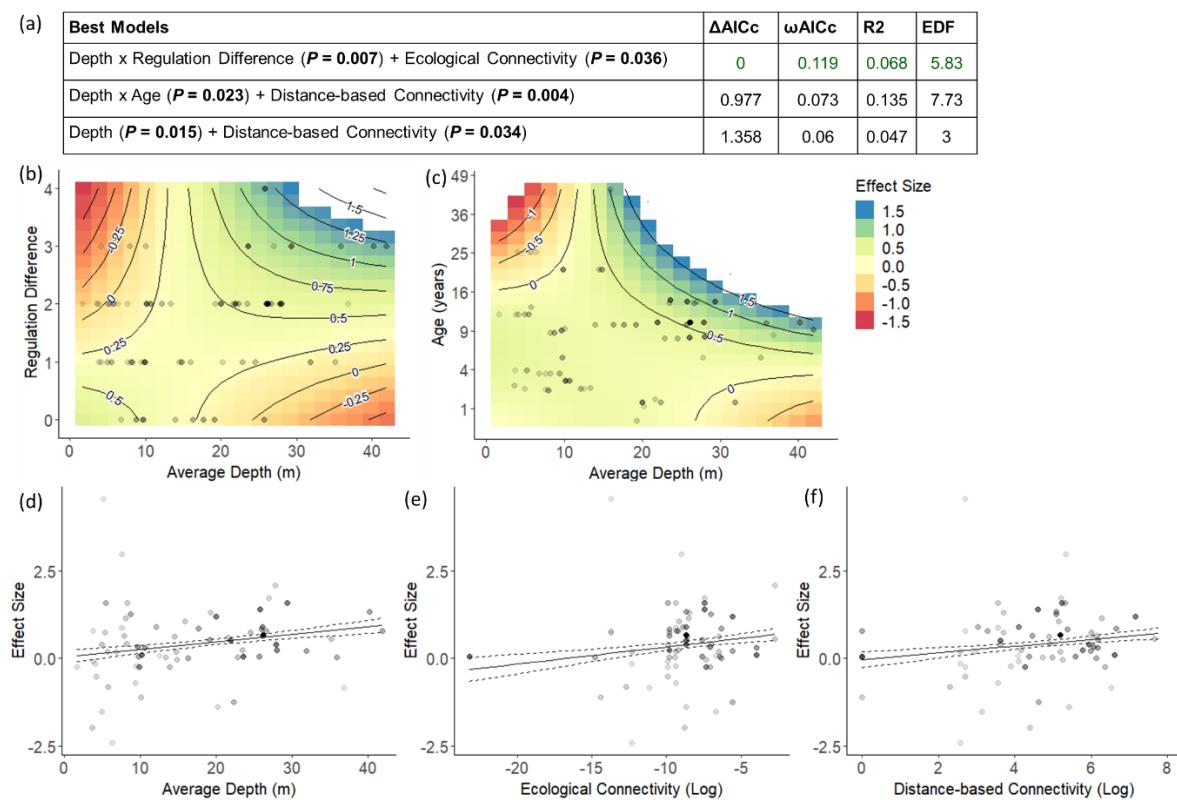


444
 445 **Figure 4.** (a) Top models for explaining the effectiveness of marine reserves to increase the
 446 abundance of fished species. Difference between lowest reported corrected Akaike
 447 Information Criterion (ΔAICc), AIC weights (ωAICc), variance explained (R^2) and effective
 448 degrees of freedom (EDF) are reported for model comparison. The resulting relationships
 449 between (b) marine reserve size, (c) age of marine reserve in years, (d) distance-based
 450 connectivity and (e) ecological connectivity, with log-ratio effect sizes for fished abundance
 451 are shown. Darker dots represent effect sizes with a greater weighting based on the inverse
 452 of variance. Solid lines are fitted GAM curves, with dashed lines indicating standard error
 453 confidence bands.

454

455 For fished biomass there were three competing top models with all covariates having a
 456 significant impact on effect sizes ($P < 0.05$; Fig 5a). While the effect size for fished biomass
 457 increased with depth and greater variation in the effectiveness of marine reserves within
 458 shallow waters (<15m) was observed (Fig 5d), this factor interacted with regulation difference

459 and age in other top models. The interaction between regulation difference and depth,
 460 suggests that marine reserves needed to incorporate deeper waters and be fully protected
 461 (which results in a high regulation difference), to provide significant benefits for fished biomass
 462 (Fig. 5b). An interaction between age and depth, suggests that marine reserves which
 463 incorporated deeper waters (>15m), showed increased effect sizes as age increased, with
 464 most positive effect sizes occurring in older, deeper marine reserves (Fig 5c). Effect size also
 465 increased with increasing ecological and distance-based connectivity, indicating the fished
 466 biomass within marine reserves compared to fished areas was greater for reserves with
 467 greater connectivity to other reserves (Fig. 5e,f).



468 **Figure 5.** a) Top models for explaining the effectiveness of marine reserves to increase
 469 biomass of fished species. Difference between lowest reported corrected Akaike Information
 470 Criterion (ΔAICc), AIC weights (ωAICc), variance explained (R2) and effective degrees of
 471 freedom (EDF) are reported for model comparison. Relationship of log-ratio effect sizes for
 472 fished biomass with (b) the interaction between depth and regulation difference (c) depth and
 473 age (d) marine reserve depth, (e) ecological connectivity and (f) distance-based connectivity.
 474 The contours in plots (b) and (c) represent the predicted effect sizes based on the interactions.
 475 In plots (d-f) the solid line is a fitted GAM curve and dashed line a standard error confidence
 476 band. For all plots darker dots represent effect sizes with a greater weighting based on the
 477 inverse of variance.

479

480 Discussion

481

482 Our broad-scale assessment of 91 marine reserves across Australia shows that both
 483 abundance and biomass of fished species is on average greater in marine reserves than in
 484 adjacent areas open to fishing. However, these benefits were not observed across all marine
 485 reserves, were greater in fully protected (no-take) reserves and increased with size, age,
 486 connectivity, and the average depth of marine reserves. Although the positive relationship with

age and benefits from full protection are well established (Claudet et al. 2008; Edgar et al. 2014), we demonstrate that these relationships can be complex with substantial influence from other emergent factors. We provide the first empirical evidence that both connectivity among marine reserves and the depths they cover influence the effects of their protection. Conceptually, marine reserves that are well connected with each other are thought to improve resilience to disturbance and ongoing stressors as the dispersal of eggs, larvae and adult fishes between boundaries is more likely and could contribute to maintaining populations (Leis 2003; Almany et al. 2009; Álvarez- Romero et al. 2018). The Great Barrier Reef and Ningaloo Marine Parks are two examples where marine reserves have been implemented as interconnected networks, with evidence of small networks in the former, generating a connectivity portfolio that can potentially replenish exploited fish stocks (Harrison et al. 2020).

We found that increased ecological and distance-based connectivity among Australian marine reserves is associated with a higher abundance and biomass of fished species within their boundaries. It is possible that the positive relationships of abundance and biomass with connectivity are partly driven by increased capability to manage marine reserves that are closer together (e.g. increased enforcement and compliance due to public awareness; Edgar et al. (2018)). However, compliance did not explain a significant proportion of the variance across marine reserves and both ecological and distance-based connectivity metrics had a positive influence on effect size, suggesting that both ecological and marine reserve design factors are contributing to this result. While both metrics of connectivity were complementary with a relatively high correlation (Supp V), the distance-based connectivity metric suggests that a maximum separation distance of 50km between marine reserves (Almany et al. 2009) will provide increased conservation benefits for fishes. There is increasing evidence to suggest that simple distance-based measures of connectivity can provide a useful tool for conservation and marine reserve planning at local scales (D'Aloia et al., 2015; Abesamis et al., 2017), and the metric presented here may provide a useful tool for countries/jurisdictions with limited in-situ larval and oceanographic information, that is needed for modelling ecological connectivity.

By utilising a nationwide BRUVs dataset, we were able to elicit complicated interactions with marine reserve effectiveness and depth, demonstrating the ability of this method to examine marine reserves over depth ranges to at least 40m, and with the potential to explore broader depth ranges as data becomes available. We found differences in biomass between marine reserves and fished areas across depths, suggesting it is important to incorporate a broad depth range within marine reserve boundaries where possible. This contrasts with other studies that found a greater response to protection in shallower depths compared to deeper areas, attributed to the stronger fishing pressure in shallow water and depth refugia (Claudet et al. 2011; Goetze et al. 2011; Lindfield et al. 2014b). This is likely due to the increased occurrence of larger fished species at greater depths. Interestingly, the relationship between marine reserve effect on fish biomass over time (age) was influenced by depth. Consequently, when deeper areas are not incorporated within marine reserve boundaries, benefits for the biomass of fished species may be reduced, even for very old reserves. This might be explained by the relatively large depth range of many commonly fished species in Australia (e.g. pink snapper from 1–200 m; Paulin 1990), as well as ontogenetic shifts, whereby larger individuals move into greater depths as they get larger and older, partly driven by the tendency for harvest of larger individuals to first occur in shallow, more accessible waters (Frank et al. 2018). These results may suggest a depth refuge effect in some marine reserves, where species most vulnerable to fishing are uncommon in shallower waters, and do not participate in the response

535 to protection in this depth range (<20 m). The effect of depth refugia may be even greater in
536 areas where the absence of fishing technologies (sonar, electric reels) inhibits fishing
537 efficiency in deeper waters. There was also a high proportion of marine reserves with lower
538 levels of protection in shallow waters (e.g. shore fishing in some marine reserves in Western
539 Australia). This may be contributing to the interaction between the regulation difference and
540 depth, where marine reserves that were fully protected and greater than 20 m deep resulted
541 in the greatest differences in fished biomass. As mentioned above many exploited species
542 exhibit broad depth ranges across and along the continental shelf around Australia. Indeed,
543 most of the commercial harvest and some recreational capture of many of these species, lie
544 outside of the depth ranges of the marine reserves considered herein. As such, the marine
545 reserves considered here may not contribute directly to the conservation benefits (i.e.
546 increased abundance and biomass) of many exploited species. Nevertheless, marine
547 reserves that exhibit a broad depth range are more likely to have increased levels of biomass
548 and abundance that benefit the conservation of marine biodiversity. Moreover, high levels of
549 biomass and abundance of species targeted by fishers (artisanal, commercial and
550 recreational) in marine reserves offer a range of non-extractive benefits and related business
551 opportunities such as tourism and diving.

552

553 While the benefits of marine reserves to fished species were consistent with other broad-scale
554 syntheses of marine reserves (Molloy et al. 2009; Lester et al. 2009; Edgar et al. 2014), the
555 magnitude of our results (28% > abundance and 53% > biomass) were generally lower than
556 global assessments (Molloy et al. 2009; Lester et al. 2009). This may be explained by the
557 broader range of fished species that were considered here, which are subject to varying levels
558 of fishing pressure and/or the broader depth range that was examined. However,
559 overestimation of marine reserve effectiveness has been observed when using diver-based
560 methodologies in areas where spearfishing is common (Lindfield et al. 2014a; Januchowski-
561 Hartley et al. 2015; Gray et al. 2016). Australia is also considered above the global average
562 for effective fisheries management (Mora et al. 2009), and the gravity of human impacts are
563 generally low (Cinner et al. 2018), resulting in lower rates of exploitation in areas open to
564 fishing. Indeed, effective fisheries management across Australia contributes to robust
565 populations of some predators (e.g. reef sharks; MacNeil et al. 2020), and it is likely that these
566 management arrangements are contributing to the presence of equivocal effects from some
567 of the marine reserves surveyed. Regardless, we observed no effect of marine reserves on
568 non-target species, suggesting the results for fished species are likely driven by the increased
569 fishing pressure outside of marine reserves in the areas surveyed.

570

571 A stronger effect of marine reserve protection was observed for biomass when compared to
572 the abundance of fished species, suggesting that marine reserves across Australia potentially
573 benefit large-bodied fishes. Size-related responses of populations to protection from fishing
574 are common (Russ et al. 2005; McClanahan et al. 2007, 2019) and are generally regarded as
575 a more sensitive metric compared to abundance (Nash & Graham 2016; Goetze et al. 2017).
576 This is due to the preferential targeting of large individuals by fishers (Birkeland & Dayton
577 2005), resulting in greater impacts to biomass than abundance. Our results also demonstrate
578 the value of stereo-BRUVs when monitoring, which provide an accurate measure of fish length
579 that can be converted to biomass (Harvey et al. 2002, 2007; Langlois et al. 2012). The build-
580 up of fish biomass within marine reserves across Australia demonstrates how this strategy of
581 protection of large-bodied fish can provide benefits in terms of increased fecundity and
582 therefore spill over of larvae/eggs into fished areas (McClanahan & Mangi 2000; Evans & Russ

583 2004; Abesamis & Russ 2005; Evans et al. 2008). However, to have a positive effect at the
584 population scale, such reserves would have to be extensive. Note it is important to consider
585 the spatial scale of the marine reserves in comparison to the area under effective fisheries
586 management, as there are numerous harvest control measures that may be applied and
587 marine reserves are just one tool that have an increasingly important role, particularly in
588 countries where governance is less effective. We also observed variation in the importance of
589 covariates between metrics, with the size of marine reserves included in top models for
590 targeted abundance (in line with the literature; Claudet et al. 2008; Edgar et al. 2014), but not
591 for biomass. This may be partly driven by a lack of biomass data in some of the largest marine
592 reserves surveyed (e.g. in the Great Barrier Reef) and the greater influence of other factors
593 (e.g. depth, connectivity and age). Size and distance-based connectivity also shared ~55%
594 and 35% of their variance for abundance and biomass respectively, due to size being
595 incorporated within the distance-based connectivity metric, suggesting that this measure of
596 connectivity is likely explaining variation due to size as well as proximity to other marine
597 reserves.

598

599 Despite compliance with marine reserve rules and regulations being considered one of the
600 most important drivers of conservation success globally (Guidetti et al. 2008; McClanahan et
601 al. 2009; Edgar et al. 2014), we found compliance was a poor predictor of effect sizes for fish
602 abundance or biomass. Our results reflect a relatively high level of marine reserve and
603 fisheries management across Australia compared to other countries, where reserves may vary
604 from ‘paper parks’ (offering little protection in the water) to strictly enforced no-entry zones
605 (Costello & Ballantine 2015). Although this is an endorsement of current management
606 strategies in some parts of Australia, a large proportion of marine reserves (~66%) provided
607 no discernible benefits to fished species and some less than areas open to fishing (~5%),
608 which suggests improvement of enforcement and compliance may be required. However, this
609 result is also explained by the extensive size range of marine reserves across Australia (<0.1
610 to >100,000 km²; Department of Agriculture, Water and the Environment 2020) and the need
611 for marine reserves to be large and deep enough to provide significant benefits to fished
612 species (Claudet et al. 2008; Edgar et al. 2014). Similarly, distance to boat ramp and gravity
613 were not included in top models or regarded as important variables for explaining variation in
614 effect sizes of marine reserves. This contrasts with global studies where conservation success
615 is typically dependent on the gravity of human impacts (Cinner et al. 2016, 2018). Australia is
616 dominated by reefs with lower levels of gravity compared to other countries, so the range of
617 human impacts considered here was likely not large enough to have a significant impact on
618 marine reserve effectiveness. Moreover, recreational and commercial fishing can be high in
619 rural locations where resident human populations are low (e.g. the Gascoyne region of
620 Western Australia; Ryan et al. 2019), information that may not be captured by the Gravity
621 measure. Finally, our top models explained a small proportion of the overall variance in effect
622 size, although still above the average for ecological meta-analyses (Møller and Jennions
623 2002). Nonetheless large amounts of unexplained variance in effect size suggests factors not
624 considered here (e.g. management effectiveness; Gill et al. 2017 and the life-history and
625 ecological characteristics of taxa considered; Claudet et al. 2010) are likely contributing to the
626 ability of marine reserves to provide conservation benefits.

627

628 While marine reserves that preclude fishing are relatively common within multi-use marine
629 parks in Australia, a large proportion of coastal waters (~70%) are not incorporated into marine
630 parks. We identified two large spatial gaps in the presence of marine parks and marine

631 reserves within state waters, from (1) the Northern Territory to Northern Queensland and (2)
632 the southern coast of Western Australia and the Great Australian Bight. Notably the gap on
633 the south coast of Australia covers a large proportion of the Great Southern Reef, which has
634 been identified as a global biodiversity hotspot and provides extensive economic benefits to
635 the tourism and fisheries industries (Bennett et al. 2016). We also identified no distance-based
636 connectivity between marine reserves within Victoria and Tasmania, suggesting the potential
637 for enhancement of existing management strategies and network designs. Roberts et al.
638 (2020) made a similar suggestion and found that Australia's marine reserve system is not
639 functioning as a connected network due to breaks in the connectivity of reef habitat. It will be
640 important to consider natural breaks in connectivity when planning for marine reserves
641 networks (e.g. lack of habitat suitable for fished species), given it may not be practical or
642 beneficial to implement marine reserves separated by less than 50km (as recommended here)
643 in these circumstances. We also found that state and marine region did not influence the
644 success of marine reserves, with positive effect sizes observed across all major states (apart
645 from Tasmania where only one reserve was sampled) suggesting that this conservation
646 strategy can be successful in both tropical and temperate waters.

647

648 By using a national database of BRUVs to comprehensively assess marine reserves across
649 Australia, we demonstrate that they provide significant benefits to fished species and we
650 identify factors that can improve marine reserve design and management globally. We provide
651 new insights to marine reserve design that suggest depth and connectivity are important
652 factors for achieving conservation gains. Although the benefits of marine reserves generally
653 increase with age, this effect was not common in shallow waters, supporting the
654 recommendation that marine reserves should be representative of a broad range of habitats
655 across depths (Ballantine 2014). Similarly, marine reserves that are connected provide
656 benefits that may extend to an entire ecosystem over time. Ongoing implementation and
657 enhancement of comprehensive networks of marine reserves will, however, depend on
658 effective engagement and consultation with all stakeholders on socio-economic and access
659 issues. This will be especially important given increasing anthropogenic pressures and
660 competition for the use of resources. We demonstrate that marine reserves provide an
661 effective conservation strategy for temperate and tropical fished species within an overarching
662 marine biodiversity conservation framework, provided they are fully protected (no-take) and
663 have been designed to optimise connectivity, size and cover a large depth range.

664

665 **Acknowledgements and Data**

666

667 Thanks to the Great Barrier Reef Marine Park Authority compliance team, Parks Victoria,
668 Fisheries NSW managers, operations, compliance, and research staff for information on
669 compliance and Brooke Gibbons for data cleaning and management. We would also like to
670 thank Mike Cappo for his contribution to the BRUV workshop and foundation work on BRUVs.
671 We acknowledge funding for the workshop from Curtin University, a Community of Practice
672 grant from the Australian Institute of Marine Science and from the Global FinPrint Project
673 funded by Paul G Allen Philanthropies. We thank everyone that contributed to the data in
674 GlobalArchive, which was supported by the Australian Research Data Commons (ARDC) and
675 synthesis work was supported through the ARDC's Marine Research Data Cloud project.
676 Thank you to Tiffany Tailor for the design of the infographic and Juliet Corley for fish images.
677 The authors have no conflicts of interest associated with this work.

678

679

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