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Disentangling the response of fishes to recreational fishing over 30 years within a fringing coral reef reserve network



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ABSTRACT

Few studies assess the effects of recreational fishing in isolation from commercial fishing. We used meta-analysis to synthesise 4444 samples from 30 years (1987–2017) of fish surveys inside and outside a large network of highly protected reserves in the Ningaloo Marine Park, Western Australia, where the major fishing activity is recreational. Data were collected by different agencies, using varied survey designs and sampling methods. We contrasted the relative abundance and biomass of target and non-target fish groups between fished and reserve locations. We considered the influence of, and possible interactions between, seven additional variables: age and size of reserve, one of two reserve network configurations, reef habitat type, recreational fishing activity, shore-based fishing regulations and survey method. Taxa responded differently: the abundance and biomass inside reserves relative to outside was higher for targeted lethrinids, while other targeted (and non-targeted) fish groups were indistinguishable. Reef habitat was important for explaining lethrinid response to protection, and this factor interacted with reserve size, such that larger reserves were demonstrably more effective in the back reef and lagoon habitats. There was little evidence of changes in relative abundance and biomass of fishes with reserve age, or after rezoning and expansion of the reserve network. Our study demonstrates the complexities in quantifying fishing effects, highlighting some of the key factors and interactions that likely underlie the varied results in reserve assessments that should be considered in future reserve design and assessment.

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1. Introduction

Anthropogenic activities continue to expand worldwide, threatening natural systems and the ecosystem services they provide (Barlow et al., 2018). As a result, 'protected areas' that seek to balance extractive activities with other socio-ecological values are increasingly being used to manage terrestrial and marine systems (Jenkins and Joppa, 2009; Sala et al., 2018). Many studies have assessed the conservation effects of marine reserves (reviewed by Mosquera et al., 2000; Russ, 2002), including quantitative syntheses of regional and global studies, with most finding higher abundance and size of targeted species within reserve boundaries in the case of 'no-take', or highly protected reserves (Lester et al., 2009). The large majority of these findings are from regions with commercial fisheries, and less is documented about the impacts of recreational fisheries, despite several studies flagging the potentially high impacts of these fisheries (McPhee et al., 2002; Coleman et al., 2004; Cowx and Cooke, 2004; Lewin et al., 2006). No-take reserves are a key tool for assessing the impacts of fishing (Ballantine, 2014) and while there are a handful of empirical studies that have demonstrated the effects of fishing, using inside outside comparisons, on targeted invertebrates (Shears et al., 2006; Babcock et al., 2007) and finfish (Denny et al., 2004) a comprehensive assessment including reserves with different characteristics over long time frames is lacking. The magnitude of differences inside to outside reserves has been correlated with their design, in particular size and age, with larger and older reserves typically resulting in greater abundance and/or size of targeted fishes than reserves that are smaller or newly established (Claudet et al., 2008; Edgar et al., 2014). The effects of reserves vary among biomes, locations and taxa of interest (Côté et al., 2005; Claudet et al., 2010; Mora and Sale, 2011) and there are examples of reserves having negligible effects on targeted fish communities (McLaren et al., 2015). In addition to size and age of reserves, explanations for this variability include high levels of cross-boundary movement by fishes (Pillans et al., 2014) and minimal to no difference in fishing activity between reserve and fished areas due to accessibility and/or non-compliance by fishers (Bergseth et al., 2017), all of which make disentangling the true effects of fishing more complicated.

Ideally assessments of the influence of reserves are based on replicated studies across multiple comparable reserves with long time series of biological data before and after reserve establishment (Underwood, 1993; Russ, 2002; Osenberg et al., 2011). Yet such data are typically beyond the scope of single research programs, necessitating the integration of multiple datasets. 'Adaptive management,' involving changes to the number, size or boundaries of reserves in response to new scientific information, changes in fishing pressure or changing social attitudes (McCook et al., 2010) further complicates long-term assessments. Ongoing improvement of ecological sampling methods and technologies has resulted in new survey methods being introduced to monitoring (Goetze et al., 2015): video based methods (baited remote underwater video (BRUV) and diver operated video (DOV)) are now commonly used alongside or in place of the previously more common underwater visual census (UVC) (Mallet and Pelletier, 2014). Therefore, evaluations of reserves that have long-term datasets must have the capacity to incorporate and evolve with changes in reserve design and survey methods (Claudet and Guidetti, 2010). Other factors, including differences in habitat and benthic structure, have been shown to affect outcomes of reserve evaluation (Miller and Russ, 2014; Rees et al., 2018b) and while these factors have been studied independently, few assessments consider multiple factors simultaneously, including possible interactions (Edgar et al., 2014). Differences in fishing pressure outside of reserves will also directly impact inside to outside comparisons, yet data that quantify localised variation in fishing activity at the scale of marine parks and reserve networks are rarely available (Lewin et al., 2006).

Here, we synthesise a unique 30-year dataset from within a multiple-use marine park at Ningaloo Reef, Western Australia. The type of

fishing activity at Ningaloo Reef (almost exclusively recreational) in combination with a highly protected and regulated network of reserves that have undergone significant expansion during the study period, offers the opportunity to advance on previous studies and inform on the potential impacts of recreational fisheries. We integrate data from numerous agencies with varied survey designs and methods, and therefore use a meta-analytical approach to compare the abundance and biomass of select targeted and non-targeted tropical reef fish inside reserves with adjacent fished areas. We tested two hypotheses: (1) the relative abundance and biomass of targeted fish taxa will be greater inside reserves than outside due to recreational fishing activity; and (2) the observed relative abundance and biomass will vary with survey method, age and size of reserve, spatial variability in fishing activity (including shore-based fishing) and/or habitat. Our study offers four main novelties. First, the effect of recreational fishing on targeted species is assessed in isolation from commercial fishing. Second, we explicitly consider potential interactions between variables. Third, the influence of changes in the reserve network is considered in the context of the increasingly common adaptive management. Fourth, we consider the influence of shore-based fishing, which has rarely been investigated. We therefore provide advances on previous work that are of importance for future planning and assessment of protected areas.

2. Material and methods

2.1. Study region

Data for this study are from the Ningaloo Marine Park (henceforth, the Park) on the western Australian coastline (22°S, 113°E; Fig. 1). The Park covers the majority of Ningaloo Reef (a World Heritage site), which is a fringing coral reef almost 300 km in length. The reef



Fig. 1. The Ningaloo Marine Park and Muiron Islands Marine Management Area boundaries (dotted lines) with the location of sanctuary zones (referred to as reserves in the present study) shown in green along the Ningaloo coast of Western Australia under the a) initial (1987–2005) and b) current (2005–2017) zoning schemes. Tantabiddi Well and Winderabandi Point are indicated with red markers as spearfishing is prohibited between these locations. The Osprey reserve is also indicated. In b) blue regions indicate zones on the coastal boundaries of the reserves where shore-based fishing is allowed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

encompasses a sheltered lagoon that is highly accessible by shore-based fishers and those operating recreational vessels (Smallwood and Beckley, 2012). Despite a relatively small permanent human population, this area is a popular tourism destination for recreational fishers (Sumner et al., 2002; Smallwood and Beckley, 2012; Mitchell et al., 2018). There have not been any major commercial fishing activities within the marine park since the 1970s, (for summary see pg. 78, CALM (2005) and pg. 70, DPIRD (2017)). Recreational spearfishing has additional restrictions of varying degrees outside of the reserves, with spearfishing prohibited along a 70 km stretch of coast between Tantabiddi Well and Winderabandi Point, and spearfishing for Labridae and Serranidae prohibited throughout the Park (DPIRD, 2018) (Fig. 1).

A network of eight no-take reserves was established in April 1987 to cover 10%, ~22,400 ha, of the total Park (Fig. 1a) (CALM, 1989). In 2005, the majority of the existing eight reserves were expanded in size and 10 new reserves were added (Fig. 1b), increasing the reserve coverage to 88,365 ha (34% of the Park). At the same time, three reserves, covering 1929 ha, were established as a part of the 28,616 ha Muiron Islands Marine Management Area (MIMMA), immediately adjacent to the northern boundary of the Ningaloo Marine Park (CALM, 2005). Together, the Park and the MIMMA form a continuous network of reserves (CALM, 2005). There is some variation in the regulations along the boundaries of the 21 current reserves, complicating terminology and analysis, with eight reserves allowing shore-based fishing from their coastal boundaries (Fig. 1b, Appendix A, CALM, 2005). According to recent classifications of marine reserves, the two forms of reserves in the present study, those with shore-based fishing prohibited and those where it is allowed, would classify as Fully Protected Areas and Highly Protected Areas, respectively (Horta e Costa et al., 2016), both of which would be expected to provide protection for fished species (Zupan et al., 2018). We explicitly include consideration of the effect of shore-based fishing in our analyses.

2.2. Survey data

Data from all major research and monitoring programs surveying fish in the Park over the last 30 years (1987–2017) were collated (Appendix B) to create a large synthesis of information. Locations of individual samples are given as Appendix C. Three different survey methods were used to census fish: Baited Remote Underwater stereo-Video (BRUV), Diver Operated stereo-Video (DOV) and Underwater Visual Census (UVC) (Langlois et al., 2010; Murphy and Jenkins, 2010). The majority (90%) of surveys also estimated the length of fish (an in situ estimate of total length for UVC, and fork length measured from stereo-video for DOV and BRUV), which allowed estimates of biomass using formulae from FishBase (Froese, 2018) (Appendix B).

Data were organised hierarchically with a sample (individual UVC or DOV transect or BRUV deployment) being the lowest level of replication. Samples were classified to the next hierarchical level and termed a 'comparison pair', based on the criteria: (i) that there were at least two samples inside and two samples outside a given reserve, (ii) these samples were collected within 2 weeks of each other, (iii) samples were collected > 200 m from within or outside of the reserve boundaries (excluding one reserve, the small size of which meant this was not a logical rule), (iv) samples were collected using the same survey method within one of four *habitat* categories (see Table 1). Data satisfying these conditions consisted of 4444 samples classified into 305 relative abundance comparison pairs. These data covered seven of the initial eight reserves and 16 of the 21 current reserves (Appendix B).

2.3. Fish groups

We consider three main fish groups common at Ningaloo Reef, at family or subfamily and species level (Appendix D) which differ in terms of their behaviour and representation in fisheries catch reports.

This included: parrotfishes (Scarinae), which are not typically targeted by fishers in Australia, and two groups which are highly targeted by recreational fishers in the region (Ryan et al., 2013; Ryan et al., 2015) that have different behaviours; emperors (Lethrinidae; mobile roving predators) and groupers (Epinephelinae; mostly site-attached ambush predators). Previous work has indicated both Epinephelinae and Lethrinidae are vulnerable to fishing and many species in both subfamilies are targeted across the Indo-Pacific (Abesamis et al., 2014). Species level analyses included two species from Lethrinidae: the spangled emperor, Lethrinus nebulosus, which is recognised as the most highly targeted species in the region, consistently featuring at the top of the estimated catch for the bioregion over the 30-year study period, and the vellow-tailed emperor. L. atkinsoni, a species that is anecdotally retained by fishers and featured as the 6th most common species recorded in the 1998/9 catch survey, but was a minor component in subsequent surveys (Sumner et al., 2002; Ryan et al., 2013; Ryan et al., 2015). The Chinaman Rockcod, Epinephelus rivulatus (Epinephelinae) was also considered, with catches comparable to those of L. nebulosus across the catch reports (Ryan et al., 2013; Ryan et al., 2015). Individual species were not considered from the Scarinae subfamily due to inconsistencies in the accuracy of identification of species from this family.

2.4. Meta-analysis

We used a mixed-effects meta-analytical approach to assess the effect of the reserves on fish abundance and biomass. We calculated effect sizes as log-ratios for each of the comparison pairs inside to outside the reserves (Claudet et al., 2008) (see Appendix E for formulas). A constant was added to the mean abundance (c = 0.5) and mean biomass (c = 100 g) to allow calculation of the log ratio in cases where fish were absent either inside or outside (i.e. zero values). We ran a sensitivity analysis on the value of the constant (Appendix F) to determine these values. The size of the constant impacted the magnitude of the effect size, but in general did not influence the significance. Nonetheless, the exact magnitude of the overall effect size should be interpreted with caution. In cases where both the inside and outside mean count of fish were zero, the samples were excluded from the analysis. Effect sizes were weighted by the inverse of the sum of the within- and amongstudy variances (Appendix E). Weighted effect sizes and variances were calculated using the metafor package (Viechtbauer, 2010) in the statistical program R (R Core Team, 2017) with the variance estimator set to "REML" restricted maximum likelihood estimator. Overall effect sizes were comparable for both abundance and biomass and for simplicity we presented the abundance results as these were available for a larger dataset, providing biomass results in Appendix H.

2.5. Sources of variability

We considered seven variables that might mediate the response of fish abundance and biomass to the presence of the reserves (Table 1): (i) the number of years between when a sample was collected and when the zoning went into place; (ii) initial or current *zoning scheme* (see Fig. A1); (iii) survey *method*; (iv) four coarse *habitats* with distinct coral and algae assemblages: 'exposed reef slope', 'reef flat', 'back reef & lagoon coral', and 'lagoon algae'; (v) spatial area of a reserve; (vi) an estimate of fishing pressure outside of individual reserves; (vii) the presence of shore-based fishing zones adjacent to some reserves. Data were explored following the protocol of Zuur et al. (2010) and transformed to normalise their distribution where appropriate (see Table 1).

As all effect sizes were heterogeneous (Appendix G), we explored the influence of the seven variables using weighted mixed-effects categorical meta-analyses and meta-regression, considering each variable as a moderator in isolation to determine which variables explained significant heterogeneity in the overall effect size (see Appendix E for formulas). We also investigated *reserve identity* to allow comparison between individual reserves. Given there were correlations among the

Table 1Description and summary of the	seven variables used in analysis.			
Variable (transformation used in analyses)	Description	Description of variable levels		Source
Years protection	Years between zoning and data collection	Samples were classified to a single reserve based on their location. In cases reserves size was increased, samples inside the old reserve area were classification the extended area were classified as 'current' zoning. Years prote the number of years between zoning and sampling.	where rezoning meant that a fied as 'initial' zoning, while ection was then calculated as	(CALM, 2005; CALM, 1989)
Zoning scheme	Factor describing the two major reserve networks during the study period	Initial 2005-present and the convertigation to sampling. Initial 1987-2005, 8 no-take zones (Fig. 1a) Current 2005-present, 18 no-take (excepting tahone fishing) at Manizon tahan disk Manizon tahan fish	nd 3 no-take zones in the	(CALM, 2005; CALM, 1989) (also see Appendix A)
Survey method	Factor describing the major survey methods used to collect fish count and size data	UVC Underwater visual census, collected along transect lib. UVC Underwater visual census, collected along transect lib. (25 × 5 m, 50 × 5 m, 100 × 10 m or 250 × 10 m). vanorkel. Fish counted and length estimated in situ. BRUV Baited remote underwater stereo-video deployments, location, fish counted and length estimated post hoc. DOV Diver operated stereo-video, collected along a transect lib. Cation, fish counted and length estimated post hoc. DOV Diver operated stereo-video, collected along a transect (5 m in width and varying between 25 and 50 m leng estimated post hoc operated stereo-video, collected along a transect (5 m in width and varying between 25 and 50 m leng estimated post hoc operated stereo-video.	nes of set length and width lost on SCUBA, some via (30 or 60 min) point friom video thine of set length and width th) fish counted and length	For more information on methods see Appendix B
Habitat	Factor describing four major habitat types which have differences both in the dominant benthic community and wave exposure	Exposed reef slope The ocean side of the fringing reef, where the reef slo majority of wave energy is received majority of wave energy is received Reef flat Shallow (~1-3 m deep), shoreward from the reef cre Reef flat Shallow (~1-3 m deep), shoreward from the reef cre Back reef & lagoon From where the reef flat breaks into more patchy rescoral Back reef & lagoon From where the reef flat breaks into more patchy rescoral Lagoon algae Sheltered from wave energy and including some large Corral Sheltered shallow water lagoon, sandy bottom often, forming seaweed of the genera Szyassum and Szyass	pes to deeper water and the ss for tens to hundreds of ora spiecifera on limestone ef and sand environments, e coral bonmies dominated by fleshy canopy storsis	Classified by authors, (see Collins et al., 2003)
Reserve size (square –root)	Area (ha) of each reserve at time of survey	50-44,752ha Mean: 6031 ha: Median: 1756 ha		(CALM, 2005; CALM, 1989)
Boat fishing* (log-transformation)	A mean estimate of the number of vessels recreationally fishing at sites outside of reserves	Mean density of vessels observed fishing during aerial surveys in peak sea sample latitude and longitude was assigned the value of the underlying sy Smallwood and Beckley (2012). For surveys inside the reserves is was assur 0. Range: 0–0.625 vessels fishing per 9 km ² Mean: 0.12; Median: 0.112, Median: 0.112, Median: 0.112, Median: 0.112, Median: 0.112, Median: 0.112, Median: 0.111 *Not available for the Muiron Islands Other estimates of fishing activity exist (Sumner et al., 2002) but this met of resident	uson in 2007. Each survey aatial data in Fig. 4 of ned that fishing activity was tric was deemed the most	(Smallwood and Beckley, 2012)
Shore fishing	Factor describing whether or not a reserve has shore fishing zones on its coastal boundary	Allowed Shore fishing is allowed along the entire, or part of treserve (26% of data) Prohibited No shore fishing is permitted anywhere in the reserved	the coastal boundary of the e (74% of data)	(CALM, 2005)

variables and potential interactions and non-linear effects, we then used weighted full-subsets generalised additive mixed modelling (FSSgam) (Fisher et al., 2018) to investigate the relative importance of each variable in explaining variability in the overall effect size for each fish group. The response variable, effect size e, was modelled with a Gaussian distribution using gam() in the mgcv package in R (Wood, 2011). Years protection and boat fishing were included as continuous smoothers in the FSSgam to allow for non-linear relationships. The distribution of reserve size was not much improved by transformation and sqrt (reserve size) was therefore included in the model set as a linear predictor. Reserve identity was highly collinear with other variables (in particular reserve size), and therefore, rather than including this as a random effect, a smoother of the mean latitude of comparison pairs was included in all models (and as part of the null model). This yielded comparable results to including reserve identity as a random effect. Interactions between the factor variables habitat and shore fishing and the continuous variables reserve size and years protection were tested. In all models the smoothing parameter was limited to a simple spline, allowing only monotonic relationships (k = 3) for all continuous variables except for latitude, which was unlimited. Summed AICc weights were used as a metric of variable importance to investigate the relative importance of each predictor variable across the full set of models (Anderson and Burnham, 2002). Variables included in the most parsimonious model (fewest variables and lowest estimated degrees of freedom within two units of the AICc) were plotted to visualise the shape and direction of relationships between the variables and the effect size. We interpret results of variable importance and the top models with caution and consider the results of the mixed-effects meta-analyses and meta-regression alongside the results of the FSSgam.

Lastly, given the importance of temporal patterns in investigations of protected areas, we explicitly investigate data from the Osprey reserve (see Fig. 1), the best temporally replicated reserve in the dataset. Using available and relatively consistently collected UVC and DOV data we estimated mean fish density as count per transect area. We tested for significant linear and quadratic relationships between the density of *L. nebulosus* and survey year then fitted generalised additive mixed models to illustrate trends.

3. Results

When compared to areas open to fishing, Lethrinidae were on

average 57% more abundant (78% more biomass) inside the reserves $(e = 0.45 \pm 0.12, 95\%$ CI, Fig. 2a), however the effect was heterogeneous ($Q_T = 2002.6$, df = 301, p < 0.001, Table G1). The most parsimonious model for Lethrinidae abundance consisted of an interaction between habitat and reserve size (Table 2), with the same true for biomass (Appendix H). The categorical meta-analysis supported the importance of *habitat* for relative abundance; showing it explained significant heterogeneity among effect sizes ($Q_M = 39.5$, df = 3, p < 0.001, Table G2) with the most positive effect identified in *back* reef & lagoon coral sites with an average of 93% more Lethrinidae inside the reserves ($e = 0.66 \pm 0.14$, 95%CI) (Fig. 2a, Fig. G1) at sites in this habitat. On the reef flat Lethrinidae were 53% more abundant inside the reserves ($e = 0.42 \pm 0.32$, 95%CI) while there was no significant effect on the exposed reef slope and a negative effect in the lagoon algae habitat (Fig. G1). The interaction of reserve size and habitat was evident as an increase in effect size with increasing reserve size in the back reef & lagoon coral habitat versus no clear trends in the other habitats.

Lethrinus nebulosus were on average 42% more abundant (86% more biomass) inside reserves than outside ($e = 0.35 \pm 0.15$, 95%CI, Fig. 2a). The effect was heterogeneous ($Q_T = 1971.1$, df = 256, p < 0.001, Table G1). The most parsimonious model included the interaction between habitat and reserve size with these two variables also having the highest variable importance across the full-subsets model set (Table G3, Fig. 2b). The same was true in the biomass analysis (Appendix H). Habitat explained significant heterogeneity for relative fish abundance (Q_M = 32.5, df = 3, p < 0.001, Table G2) and *L. nebulosus* were on average 84% more abundant within back reef & lagoon coral sites inside the reserves ($e = 0.61 \pm 0.17$, 95%CI), whereas no differences were observed for the reef flat or exposed reef slope sites and a negative effect was observed for lagoon algae sites (Fig. G1). As for Lethrinidae, the interaction of reserve size and habitat was evident by an increase in the effect size with increasing reserve size in the back reef & lagoon coral habitat and no clear effects in the other habitats.

On average, the abundance of *L. atkinsoni* was 40% higher (60% more biomass) inside reserves than outside ($e = 0.34 \pm 0.09$, 95%CI). The effect was heterogeneous ($Q_T = 1739.7$, df = 279, p < 0.001, Table G1). The most parsimonious model included *zoning scheme* and *method*, which also had the highest importance according to weighted AICc (Fig. 2b, Table 2). These two variables also explained significant heterogeneity according to the categorical mixed-effects meta-analyses. Predictions indicated that the BRUV *method* contributed the most to the



Fig. 2. a) Relative fish abundance inside to outside the reserves (back-transformed weighted mean effect sizes) with 95% confidence intervals), for the six fish groups: Lethrinidae, Lethrinus nebulosus, L. atkinsoni, Epinephelinae, Epinephelus rivulatus and Scarinae. Effect sizes are significant when the confidence intervals do not overlap 1.0. Open dots correspond to non-significant effects (i.e. no effect). Sample sizes are given in Table F1. Triangular points show the predicted effect size when habitat was included as a moderator variable in the meta-analysis, for the habitat with the largest mean effect size (orange represents the back reef & lagoon coral, and blue represents the reef flat). b) Importance scores based on summed Akaike weights corrected for finite samples (AICc) from full-subsets analyses exploring the influence of seven variables on the overall effect size for each fish taxa: 1 is highly important while 0 is not important. Red X symbols mark the variables that were included in the most

parsimonious models for each fish taxa (also see Table 2 and Fig. 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Top Generalised Additive Mixed Models (GAMMs) for predicting the effect size, e, for abundance from full-subsets analyses for the six fish groups. The difference between the lowest reported corrected Akaike Information Criterion (Δ AICc), AICc weights (ω AICc), variance explained (\mathbb{R}^2) and estimated degrees of freedom (EDF) are reported for model comparison. Model selection was based on the most parsimonious model (fewest variables and lowest EDF) within two units of the lowest AICc. This model is shown in bold text.

Fish group	Model	ΔAICc	ωAICc	R ²	EDF
LETHRINIDAE	Habitat + Years protection by Habitat + Size by Habitat	0.00	0.31	0.14	14.6
	Years protection + Habitat + Size by Habitat	0.17	0.28	0.13	10.7
	Habitat + Size by Habitat	0.19	0.28	0.12	9.0
L. nebulosus	Habitat + Size by Habitat	0.00	0.57	0.17	9.0
L. atkinsoni	Method + Zoning scheme	0.00	0.19	0.08	6.3
	Habitat + Method + Zoning scheme	0.09	0.18	0.09	9.0
	Boat fishing + Method + Zoning scheme	0.71	0.14	0.08	7.4
	Habitat + Method + Size	1.41	0.10	0.08	8.0
	Habitat + Size + Years protection by Habitat	0.00	0.18	0.11	14.4
	Years protection + Boat fishing + Size	0.92	0.11	0.08	8.3
EPINEPHELINAE	Years protection + Size	1.51	0.08	0.08	7.3
E. rivulatus	Boat fishing + Zoning scheme	0.00	0.60	0.17	8.9
SCARINAE	Boat fishing + Shore fishing	0.00	0.16	0.03	4.0
	Boat fishing + Zoning scheme	0.80	0.11	0.03	4.2
	Years protection + Habitat + Size by Habitat	1.25	0.08	0.05	10.5
	Habitat + Size by Habitat	1.84	0.06	0.04	9.0

positive effect size of *L. atkinsoni* (Fig. 3c), though this was not significant, nor were the differences between initial and current zoning schemes, though there was a slightly higher effect size from the older zoning scheme. Multiple variables explained significant heterogeneity for *L. atkinsoni* according to the categorical meta-analysis and the meta-regression (Table G2), including *habitat* ($Q_M = 14.6$, df = 3, p < 0.001, Table G2). *Reef flat* sites had 94% higher abundance, ($e = 0.66 \pm 0.26$, 95%CI) and *back reef & lagoon coral* sites 43% higher abundance ($e = 0.36 \pm 0.12$, 95%CI) inside the reserves. There were no significant effects for the other habitats (Fig. G1). The biomass analysis for *L. atkinsoni* indicated that *years protection* may interact with *habitat*, and that on the reef flat the effect size was higher and showed a parabolic pattern with *years protection* (Fig. H2).

The effect size for Epinephelinae abundance was significantly negative with 9% fewer fishes inside than outside the reserves $(e = -0.09 \pm 0.08, 95\%$ CI), although this result was heterogeneous $(Q_T = 1125.7, df = 276, p < 0.001, Table G1)$. Variable importance scores showed no variables with high importance relative to the Lethrinidae and *L. nebulosus* model sets. *Reserve size* and *years protection* were present in the most parsimonious model (Fig. 2b, Table 2), while for the biomass it was *method* and *boat fishing* (Appendix H). There were weak increasing trends for both *reserve size* and *years protection*, however the lack of strongly important or consistent variables in these model sets means the results should be interpreted cautiously.

On average there was no significant difference inside to outside the reserves for *E. rivulatus* abundance ($e = -0.06 \pm 0.09$, 95%CI), though the effect was heterogeneous ($Q_T = 477.3$, df = 166, p < 0.001, Table G1). *Zoning scheme* and *boat fishing* had the highest variable importance across the model set and featured in the most parsimonious model. The effect size transitioned from no effect for low boat fishing activity, to a positive effect when there was high boat fishing activity, but the confidence intervals did not show this trend to be significant. The initial reserve network (in place longer) had a more positive effect than the newer reserves, but again this was not significant (Fig. 3e).

The control group, Scarinae, showed no significant difference inside to outside the reserves ($e = -0.01 \pm 0.11$, 95%CI) and this effect was heterogeneous ($Q_T = 1701.1$, df = 260, p < 0.001, Table G1). All variables had low importance according to AICc (Fig. 2b, Table 2) and while *boat fishing* and *shore fishing* appear in the most parsimonious model we interpret this with caution. In the biomass analysis the most parsimonious model had *habitat* only (Appendix H).

In the full-subsets analysis *reserve size* and *habitat* appeared with the highest variable importance (for Lethrinidae and *L. nebulosus*) while

other variables - survey *method*, *years protection*, *zoning scheme* and *shore fishing* - had low importance across all six fish groups. In many cases the heterogeneity statistics from the mixed-effect meta-analysis models supported the findings of the full-subsets analysis, but for some variables such as *shore fishing*, the meta-analysis indicated this variable was important, explaining significant heterogeneity for all fish groups, except for *L. nebulosus*.

The temporal investigation for the most highly targeted fish, *L. nebulosus*, at Osprey reserve gave results that generally confirmed what was found in the overall analysis, showing effect sizes that are mostly positive though time, with higher abundance and biomass inside than outside (Fig. 4). There were no strong or significant patterns with time, except for the abundance density outside of the reserve, which had a significantly negative linear trend (p = 0.032). Generalised additive model fits indicated that, particularly in the latter half of the study period, both abundance and biomass may have declined both inside and outside the Osprey reserve, while there is some indication that abundance initially increased inside of the reserve following establishment. However, confidence in these trends is low and the gam fits were not statistically different from null models (except for abundance density outside the reserve, p = 0.048).

4. Discussion

Across the 30 year synthesis higher abundance and biomass of certain targeted fish taxa inside the reserves suggests that recreational fishing can have significant effects in isolation from commercial harvest, as also shown in some previous studies (Denny et al., 2004; Shears et al., 2006; Babcock et al., 2007). We found the extent of this effect was variable among targeted taxa and influenced by a range of other factors. While our analyses revealed higher relative abundance and biomass of lethrinids (Lethrinus nebulosus and L. atkinsoni) inside reserves, no significant effect was found for the abundance of Epinephelus rivulatus, and a small negative effect was detected for the epinephelids as a group. All effects were heterogeneous, which was not surprising given the size and complexity of the synthesised dataset (including differences in size and age of reserves) and given that fish responses to reserves are known to vary with taxon-specific, ecological and zoning factors (Barrett et al., 2007; Claudet et al., 2010; Edgar et al., 2014). Here we advance previous findings with the largest meta-analysis on recreational fishing in isolation from commercial fishing, illustrating the new information that can be gained from synthesising existing data, though we do not discount the advantages of strategic and consistent monitoring data. We show that it is important for assessments of



Fig. 3. Predicted relative fish abundance inside to outside reserves (back-transformed predicted weighted effect sizes) with 95% confidence intervals for the six fish groups – a) Lethrinidae; b) *Lethrinus nebulosus* c) *L. atkinsoni*; d) Epinephelinae; e) *Epinephelus rivulatus*; f) Scarinae – as a function of variables present in the most parsimonious models (Table 2) from full-subsets GAMM analysis. Ribbons and error bars represent 95% confidence intervals.

reserves to take into account habitat effects, and potential interactions with factors such as reserve size or age, as well as variability in fishing activity, or differences in survey method, in order to avoid oversimplified conclusions on how fish abundance and biomass respond to management.

Some previous studies in the Park have linked higher abundance and biomass of targeted species inside reserves to protection from fishing (Westera, 2003; Babcock et al., 2008; Fitzpatrick et al., 2015); though results of other studies are more equivocal (Wilson et al., 2012; Wilson et al., 2018a). The reasons behind the disparate conclusions are unclear, but may be due to limited and/or varied spatial and temporal scales of the individual studies, different survey methodologies, the confounding influence of habitat, or high variability in target species abundance distributions. We also investigated the regulations on shore-



Fig. 4. Effect sizes through time for a) abundance and b) biomass from comparison pairs for the Osprey reserve and estimated density of c) abundance and d) biomass inside and outside the reserve through time. Ribbons indicate 95% confidence intervals on generalised additive models.

based fishing on the coastal boundaries of reserves, with the hypothesis that this may influence the ability of the reserves to maintain higher abundance and biomass of fishes. There were mixed results with the full-subsets analysis indicating this variable had low importance, while the meta-analysis showed it did explain significant heterogeneity, and indicated effect sizes were larger (though not significantly) when shore fishing was prohibited. However, this factor was likely correlated with other variables not available in the present study, such as accessibility to reserves. High correlation between fish recruitment and larger natural cycles (El Niño Southern Oscillation) has also been suggested as a reason for inconsistencies in fishes response to reserves (Wilson et al., 2018b). In the present study we found high variability in the relative abundance of lethrinids among the different reserves, which can partially account for the varied conclusions of previous studies at smaller spatial scales (Fig. G2). Nonetheless, when all data were pooled the average effect was clearly positive for abundance and biomass of the three lethrinid groups. However, the magnitudes of the positive effects were small (max 57% higher inside) relative to studies in other parts of the world (Watson and Ormond, 1994; Russ et al., 2015). A significant positive response for L. atkinsoni (40% higher), similar to that of L. nebulosus (42%) was not expected, given L. atkinsoni does not feature highly in catch reports (Ryan et al., 2017), possibly indicating it may be more influenced by recreational angling than previously recognised.

Known differences in behaviour between lethrinid and epinephelids taxa did not correlate with their response to reserves as expected. Lethrinids are known to have large home ranges relative to many epinephelids, including *E. rivulatus*, and are therefore more likely to move across reserve boundaries (Mackie and Black, 1999; Pillans et al., 2014; Babcock et al., 2017), with the expectation that they may experience lower levels of protection than epinephelids. However, we only observed positive responses for the lethrinids. It is possible that lower counts of epinephelids than lethrinids in the dataset (Table D1) may have reduced the power to detect an effect in the former group, or there are other factors that have not been captured in our analyses.

The age of no-take reserves has been shown to be a significant positive correlate of relative fish abundance for targeted species (Claudet et al., 2008; Edgar et al., 2014; Zupan et al., 2018). Demonstrated increases in effect size with time help attribute positive effect sizes to the presence of a protected area, rather than other factors (Russ et al., 2015). In the present study there was negligible evidence of changes in effect sizes with age of reserve. Where relationships were present, the shape of the trend was generally parabolic, showing an increase initially, before subsequent decrease around 2005, though no relationships were significant. This was supported by examining data for L. nebulosus, from the best temporally replicated reserve, Osprey, where again no clear temporal patterns were found. Potentially of concern for managers was the significantly negative decline in L. nebulosus density outside of the Osprey reserve, and a slight increase followed by a decrease inside this reserve. However the confidence intervals on all temporal patterns were large. These findings are in contrast with previous studies, for example Russ et al. (2015) showed lethrinids continued to increase in density inside reserves in the Philippines on time scales of 8-30 years. In the present study rezoning in 2005 made temporal analyses more complex, though by including zoning scheme as a variable we partly addressed this. Effect sizes were not strongly influenced by this variable, implying that the effect sizes were broadly consistent across the initial and current reserve networks. Where zoning scheme did feature for L. atkinsoni, the older reserves had a more positive effect, as expected.

The absence of a strong temporal link with effect size must be considered when interpreting the positive effect sizes, however there are various factors which may have contributed to the absence of a strong relationship. First, while there is limited evidence of a reduction in fishing activity within the Park (Ryan et al., 2015, 2017) a shift in fishing activity to areas offshore (> 100 m depth) (West et al., 2015; Mitchell et al., 2018), which are not part of the current survey data, is likely. Second, the mobile behaviour of lethrinid fishes may be capping the levels of the observed effect size, if a proportion of their population is travelling further than the reserve boundaries. Pillans et al. (2014) found that approximately 60% of tagged lethrinid individuals moved at scales greater than the average reserve size over a year period. Third, illegal fishing within the reserves may also limit a temporal increase in effect size, as Smallwood and Beckley (2012) found 8-12% of observed vessels were fishing inside reserves in the Park in 2007. Fourth, we do not discount that the unevenness of sampling though time, with some years being more highly sampled than others (Fig. B2) potentially influenced our capacity to detect a trend if it were present. The analysis of L. nebulosus density at Osprey showed that the temporal patterns inside and outside reserves can be complex and not always captured by the overall effect size. Parallel declines or increases in density occurring

both inside and outside are masked from the effect size, and such declines have been observed in other fisheries closures on the western Australian coast (Bornt et al., 2015).

Though our study only had a very coarse level of habitat classification available, our results support previous studies (Miller and Russ, 2014; Rees et al., 2018a; Rees et al., 2018b), showing the importance of habitat when assessing the ability of reserves to support target species abundance. We further demonstrate interactions between habitat and reserve size, showing that conclusions on both the magnitude and direction (positive or negative) of observed effects are influenced by this interaction. In the case of L. atkinsoni biomass we also found an interaction between habitat and reserve age, though the models were not as strong. Previous studies have demonstrated the positive influence of larger and older reserves (Halpern and Warner, 2002; Claudet et al., 2008; Edgar et al., 2014; Zupan et al., 2018), however the interaction with habitat has not previously been explored. Furthermore, it is noteworthy that effect sizes were greatest in the back reef & lagoon coral habitat for L. nebulosus, while for L. atkinsoni, the effect was greatest on the reef flat, a result that may be attributed to these habitats being preferred by the adults of each species respectively (Babcock et al., 2008; Wilson et al., 2017). This is important when considering potential changes to habitat inside or outside of reserves, as Russ et al. (2015) showed that changes in benthic habitat due to disturbance could markedly influence the effect of reserves for lethrinids. We advise that reserves must incorporate adequate amounts of the essential habitats of the species or communities they are designed to protect, and assessment of reserve effectiveness must account for possible interactions between habitat and reserve size and age.

While habitat was particularly important for the lethrinid groups, it was not found to be an important predictor for Epinephelinae or E. rivulatus. Again, this was contrary to expectations given the often high site fidelity of Epinephelinae (Mackie and Black, 1999). However, the relatively coarse habitat classification available for our analyses likely did not adequately capture the habitat requirements for this group. Previous work has shown E. rivulatus is strongly associated with macroalgal habitats at Ningaloo Reef (Wilson et al., 2012) but that variability in the quality of macroalgal habitats can be substantial and have major implications for fish abundance (Fulton et al., 2014; Wilson et al., 2014; Lim et al., 2016). Furthermore, Beckley and Lombard (2012) found that deeper habitats seaward of the reef have relatively lower spatial protection from recreational fishing, despite these habitats potentially supporting a high biomass of epinephelids (Babcock et al., 2008). It is thus plausible that habitats outside of the reserves were more appropriate for Epinephelinae, particularly prior to re-zoning in 2005, which could explain the overall negative and null effects for these groups. A much better understanding of the habitat requirements, electivity and movement across seascapes by targeted taxa and appropriate 'micro-habitat' classifications are needed to more fully understand these results.

Where the boat fishing variable appeared in models for E. rivulatus, there were subtle positive trends in effect size as fishing activity increased, i.e. where boat fishing was most prevalent the effect size was greater. Our metric for fishing activity is unlikely to be representative across the 30 years of data, as it was an estimate from 2007 (Smallwood and Beckley, 2012), yet still showed some importance. We think this is a particularly important factor when assessing reserves, as variability in fishing activity (spatial or temporal) makes it very difficult to disentangle the true effect of the reserves if this variability is not quantified. We suggest that finer-scale spatiotemporal data on the pressures outside, and indeed inside, of reserves would clarify reserve assessments, both in the case of the present study but also more generally in any assessment of spatial protection. In the case of marine reserves, quantitative standardised data on fishing activity at the scale of individual reserves should be prioritised alongside the collection of ecological data.

Synthesising data from multiple survey methods leads to larger

datasets, and the advent of video-based methods in the last decades (e.g. BRUV and DOV) has increased the diversity of methods used to monitor fish. Contrary to expectations, in general, survey method did not strongly influence the effect size. The strongest effect sizes (Lethrinidae and L. nebulosus) were consistently detected regardless of the survey method. L. atkinsoni exhibited a more positive effect when surveyed by remote video as compared to diver-based methods, which may be partly explained by fish behaviours associated with both the attraction to bait and avoidance of divers (Watson et al., 2005; Goetze et al., 2015), particularly on SCUBA (Radford et al., 2005). On balance, we did not distinguish a single survey method as optimal, and in most cases it was appropriate to compare data from the three methods for the effect size calculation. This is likely possible because of the nature of our effect size, which, as a ratio, is more robust to different units of measurement. However, this cannot provide the same level of information as standardised temporal data on fish density. We therefore suggest that monitoring programs should prioritise resurveying existing monitoring sites with comparable methodology to build more robust time-series data, else adopt the method(s) that are best suited to surveying the taxa of interest.

5. Conclusions

There were two major challenges in addressing the aims of this study. The first stemmed from the nature of the available data, as while we showed that new information can be gained from collaboration and the synthesis of disparate data, a lack of consistent temporal data meant it was not possible to understand the temporal changes to the fish populations. This was demonstrated by some complex trends in the estimated fish density inside and outside the Osprey reserve that underlay the overall effect size. Therefore, the value of consistent monitoring across time and space is unequivocal, particularly given a likely increase in adaptive management complicating temporal assessments. Indeed at Ningaloo, the management plans of a marine park in commonwealth waters directly seaward of the Ningaloo Marine Park has recently been updated. Our findings suggest that consistent monitoring, producing data that can be compared to that of the present study should be implemented for this new Park. The second challenge was explored by Underwood (1995), who argued that ecological research can better aid management if management interventions are treated as testable hypotheses. No-take marine reserves can provide experiments with which to test hypotheses regarding the effects of fishing (Langlois and Ballantine, 2005). However, our study has highlighted that variability in 'experimental design,' resulting from a range of complexities including spatial and temporal variability in fishing activity, shore fishing zones adjacent to no-takes areas and modifications to reserve design over time, makes determining the long-term outcomes of these experiments difficult. We suggest that in order to best analyse across such complicated experimental designs it is necessary to account for (i) habitat; (ii) potential interactions between habitat and reserve size and age; and (iii) variability in fishing activity outside of reserves and compliance inside reserves. Regarding the last point, integration of the collection of fishing activity data with the collection of ecological data is likely to help interpret the true effects of reserves. The two are clearly intertwined and having data on both the pressure and the response is essential for holistic assessments of the efficacy of spatial management interventions.

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Appendices. Supplementary data

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