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

Abstract

While there are numerous studies that have used no-take marine reserves (NTMRs) to understand the effects of commercial fishing, much less is known about the influence of NTMRs in regions subject to recreational fishing. We used meta-analysis to synthesise data from 4,444 samples from 30 years (1987-2017) of fish surveys, inside and outside a large network of NTMRs in the Ningaloo Marine Park, Western Australia, where the major fishing activities are recreational. The 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 NTMR locations. We considered the influence of, and possible interactions between, seven additional variables: age and size of NTMR, one of two reserve network configurations, reef habitat type, the level of recreational fishing activity, shore-based fishing regulations and survey method. Taxa responded differently: commonly targeted lethrinids had clear higher average abundance and biomass inside NTMRs, while the abundance/biomass of other targeted (and non-targeted groups) were indistinguishable inside to outside. Reef habitat was an important factor governing lethrinid response to protection, and we showed this variable can interact with reserve size, with larger NTMRs only demonstrably more effective than smaller ones in the back reef/lagoon habitats. There was little evidence of changes in relative abundance/biomass with reserve age, or before and after rezoning and expansion of the NTMR network. Our study demonstrates the complexity of fish responses to protection and fishing, and also highlights some of the key factors and interactions that likely underlie the varied results found to date in NTMR assessments, and that should thus be considered in future reserve design and assessment.

Keywords

Marine protected area; MPA; fisheries; coral reef; Ningaloo; adaptive management; recreational fishing; *Lethrinus*

1. Introduction

Anthropogenic activities continue to expand worldwide, particularly in the tropics, 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 & Joppa 2009; Sala et al. 2018). Many studies have assessed the conservation effects of no-take marine reserves (NTMR) (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 (Lester et al. 2009). The large majority of these findings are from regions with commercial fisheries operating, 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 & Cooke 2004; Lewin et al. 2006). NTMRs 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 NTMR 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 NTMRs vary among biomes, locations and taxa of interest (Côté et al. 2005; Claudet et al. 2010; Mora & Sale 2011) and there are examples of NTMRs having negligible effects on targeted fish communities (McLaren et al. 2015). In addition to size and age of NTMRs, 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 across no-take 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 NTMRs 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 & Pelletier 2014). Therefore, evaluations of NTMRs must have the capacity to incorporate and evolve with changes in reserve design and survey methods (Claudet & Guidetti 2010). Other factors, including differences in habitat and benthic structure, have been shown to affect outcomes of NTMR evaluation (Miller & 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 typical NTMR 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 regulated network of NTMRs 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 NTMRs with adjacent fished areas. We tested two hypotheses: (1) the relative abundance/biomass of targeted fish taxa will be greater inside NTMRs than outside due to recreational fishing activity; and (2) the observed relative abundance/biomass will vary with survey method, age and size of NTMR, 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 NTMR network are 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 (NMP) on the western Australian coastline (22°S, 113°E). 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 encompasses a sheltered lagoon that is highly accessible by shore-based fishers and those operating recreational vessels (Smallwood & Beckley 2012). Despite a relatively small permanent human population, this area is a popular tourism destination for recreational fishers (Sumner et al. 2002; Smallwood & 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 NTMRs, with spearfishing prohibited along a 70km stretch of coast between Tantabiddi Well and Winderabandi Point, and spear fishing for Labridae and Serranidae prohibited throughout the Park (DPIRD 2018) (Fig. 1).

A network of eight NTMRs was established as part of the Park in April 1987 to cover 10% of the total marine park area ~22,400 ha, (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 NTMR coverage to 88,365 ha (34% of the NMP). At the same time, three NTMRs, covering 1,929 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 NMP (CALM 2005). Together, the NMP and MIMMA form a continuous network (CALM 2005). There is some variation in the regulations along the boundaries of the 21 current NTMRs, complicating terminology and analysis, with eight NTMRs allowing shore-based fishing from their coastal boundaries (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). In the present study we refer to all reserves as NTMRs for comparisons ‘inside’ to ‘outside’, though 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 NMP over the last 30 years (1987 – 2017) were collated (Appendix B) to create a very 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 & 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 formulas from FishBase (Froese 2018) (Appendix B).

Data were organised hierarchically with a sample (individual transect or a 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 NTMR, (ii) these samples were collected within 2 weeks of each other, (iii) samples were collected more than 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 4,444 samples classified into 305 relative abundance comparison pairs and 3,892 samples classified into 268 relative biomass comparison pairs. These data covered seven of the initial eight NTMRs and 16 of the 21 current NTMRs (Appendix B).

2.3 Fish groups

We consider three main fish groups common at Ningaloo Reef, at family/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 yellow-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 NTMRs on fish abundance and biomass. We calculated effect sizes as log-ratios for each of the comparison pairs inside to outside the NTMRs (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 an appropriate value. 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 were zero, the samples were excluded from the analysis. Effect sizes were weighted by the inverse of the sum of the within- and among-study 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/biomass to the presence of the NTMRs (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 Figure A1); (iii) survey method; (iv) four coarse *habitats* with distinct coral/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) regulations on shore-based fishing. 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 first 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 NTMRs. Given there were correlations among the variables and potential interactions and non-linear effects, we used weighted full-subsets generalised additive mixed modelling (*FSSgam*) (Fisher et al. 2018 A simple function for full-subsets multiple regression in ecology with R. *Ecology and Evolution*) 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 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 & 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. AICc can overfit models (REF) so 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 NTMR (see Fig. 1), the best temporally replicated NTMR 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 and fitted generalised additive mixed models.

3. Results

When compared to areas open to fishing, Lethrinidae were on average 57% more abundant (78% more biomass) inside NTMRs (*e* = 0.45±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 NTMRs (*e* = 0.66±0.14, 95%CI) (Fig. 2a, Fig. G1) in this habitat. On the *reef flat* Lethrinidae were 53% more abundant inside the NTMRs (*e* = 0.42±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 NTMRs than outside (*e* = 0.35 ±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 NTMRs (*e* = 0.61±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% more abundant (60% more biomass) inside NTMRs than outside (*e* = 0.34±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. These two variables explained significant heterogeneity according to the categorical mixed-effects meta-analyses. Predictions indicated that the BRUV *method* contributed the most to the positive effect size of *L. atkinsoni* (Fig. 3c), though this was not significant, nor were the differences between initial and current zoning, showing 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±0.26, 95%CI) and *back reef & lagoon coral* sites 43% higher abundance (*e* = 0.36±0.12, 95%CI) inside the NTMRs. 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 NTMRs (*e* = -0.09±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, 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±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 fish group, Scarinae, showed no significant difference inside to outside NTMRs (e = -0.01±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 *habitat* made up the most parsimonious model (Appendix H).

The temporal investigation of effect sizes for the most highly targeted fish, *L. nebulosus*, at Osprey NTMR did not show strong or significant patterns with time, except for the abundance density outside of the NTMR which had a significantly negative linear trend (Fig 4). These results generally confirm what was found for the full meta-analysis for *L. nebulosus*, showing effect sizes that are mostly positive across time, with higher abundance inside than outside. Trends, particularly in the latter half of the study period indicate that both abundance and biomass may have declined both inside and outside the NTMR, while there is some indication that abundance initially increased inside of the NTMR following establishment, however confidence in these trends is low.

4. Discussion

Across the 30 year synthesis higher abundance and biomass of certain targeted fish taxa inside NTMRs 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 NTMRs, 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 NTMRs 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 NTMRs to take into account habitat effects, and potential interactions with factors such as reserve size or age, as well as variability in fishing activity and subtle elements of reserve design (e.g. partial fishing restrictions) in order to avoid oversimplified conclusions on how fish abundance/ biomass respond to management.

Recreational fishing, specifically angling, is the only major fishing activity within the marine park. Some previous studies in the Park have linked higher abundance/biomass of targeted species inside NTMRs to protection from fishing (Westera 2003a; Babcock et al. 2008; Fitzpatrick et al. 2015); though results of other studies are more equivocal (Wilson et al. 2012; Wilson et al. 2018b). 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. High correlation between fish recruitment and larger natural cycles (El Niño Southern Oscillation) has also been suggested as a reason for these inconsistencies (Wilson et al. 2018a). In the present study we found high variability in the relative fish abundances of lethrinids among the different NTMRs, which can at least partly account for the varied conclusions of previous studies of 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. The magnitudes of the positive effects were small (max 57% higher inside) relative to studies in other parts of the world (Watson & 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), suggesting it may be more susceptible to recreational angling that previously recognised.

Known differences in behaviour between lethrinid and serranid taxa did not correlate with their response to NTMR 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 NTMR boundaries (Mackie & 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 higher counts of lethrinids than epinephelids in the dataset may have reduced the power to detect an effect in the latter 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) and 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 NTMR, 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 NTMR, and a slight increase followed by a decrease inside this NTMR. 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 NTMRs 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 NTMR 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 (>100m 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 NTMR boundaries. Pillans et al. (2014) found that approximately 60% of lethrinid individuals move at scales greater than the average NTMR 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 NTMRs in the Park in 2007. Third, 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 NTMRs 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 & Russ 2014; Rees et al. 2018a; Rees et al. 2018b), showing the importance of habitat when assessing the ability of NTMRs 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 for the relative abundance of Lethrinidae and *L. nebulosus* 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 & 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 NTMRs for lethrinids. We advise that NTMRs must incorporate adequate amounts of the essential habitats of the species or communities they are designed to protect, and assessment of NTMR 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 & 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 NTMRs 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 & Beckley 2012), yet still showed some importance. We think this is a particularly important factor when assessing NTMRs, as variability in fishing activity (spatially and temporally) makes it very difficult to disentangle the true effect of the NTMRs if this variability is not quantified. We suggest that finer-scale spatiotemporal data on the pressures outside, and indeed inside, of reserves would clarify NTMR 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 NTMRs should be prioritised alongside the collection of ecological data.

Synthesizing 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 inside to outside, as shown by density patterns inside and outside at Osprey, underlying the overall effect size for this NTMR. 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

We have presented a comprehensive meta-analysis of NTMR assessments using a variety of survey methods over 30 years as a case study to show what can be learnt from collaboration and the synthesis of disparate data spanning adaptive management changes. Adaptive management is likely to become more common, indeed at Ningaloo, a new Australian Marine Park, in commonwealth waters directly seaward of the Ningaloo Marine Park of the present study has recently been implemented (1/1/18). 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, across different habitats. More broadly, we suggest that comparisons inside to outside NTMRs, and indeed protected areas in general, can be improved by accounting for (i) habitat; (ii) potential interactions between habitat and reserve size and age; and (iv) variability in fishing activity outside of reserves and compliance inside reserves. While there is much to learn by synthesising existing data, there are important limitations in the ability of meta-analytical techniques to provide quantification of temporal changes to overall fish populations, and here we found no strong evidence of temporal in effect size. Using two diver-based methods we showed that the patterns in estimated fish density inside and outside and reserves can be complex and not fully captured by effect sizes. Therefore, there is a strong need to make monitoring more meaningful by ensuring data are being consistently recorded across time and space. Further to this, integration of the collection of fishing activity data with the collection of ecological data is likely to help interpret the true effects of NTMRs. 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. A key message for managers designing or adapting NTMRs is the need to account for the preferred habitat of the species of interest and how this may interact with NTMR size or age. Targeting relevant habitats, refining measures of fishing activity and standardising methodologies will vastly improve our ability to assess the effects of NTMRs.

Appendices

Appendix A – Additional information on individual reserves and rezoning
Appendix B – Data summary
Appendix C – Geographic locations of individual surveys
Appendix D – Information on fish groups
Appendix E – Formulas used for calculating effect sizes
Appendix F – Sensitivity analysis for cases of one-armed zero events
Appendix G – Meta-analysis statistics
Appendix H – Biomass results

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Figures

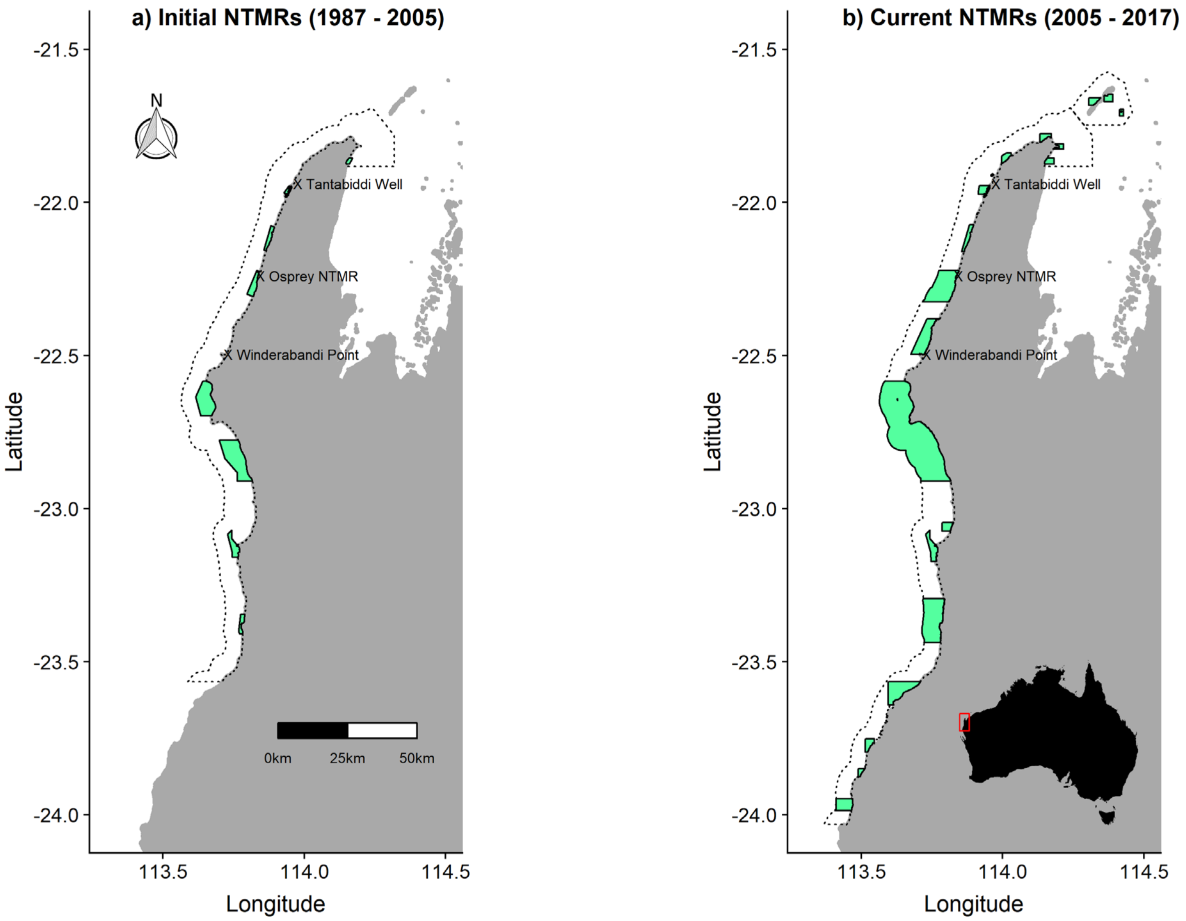

Figure 1 The Ningaloo Marine Park (NMP) and Muiron Islands Marine Management Area boundaries (dotted lines) with the location of sanctuary zones (referred to as NTMRs in the present study) shown in green along the Ningaloo coast of Western Australia under the a) initial (1987 – 2005) and b) current (2005 - 2017) zoning schemes. Tantabiddi Well and Winderabandi Point are shown as spearfishing is prohibited between these locations. The Osprey NTMR is also indicated.

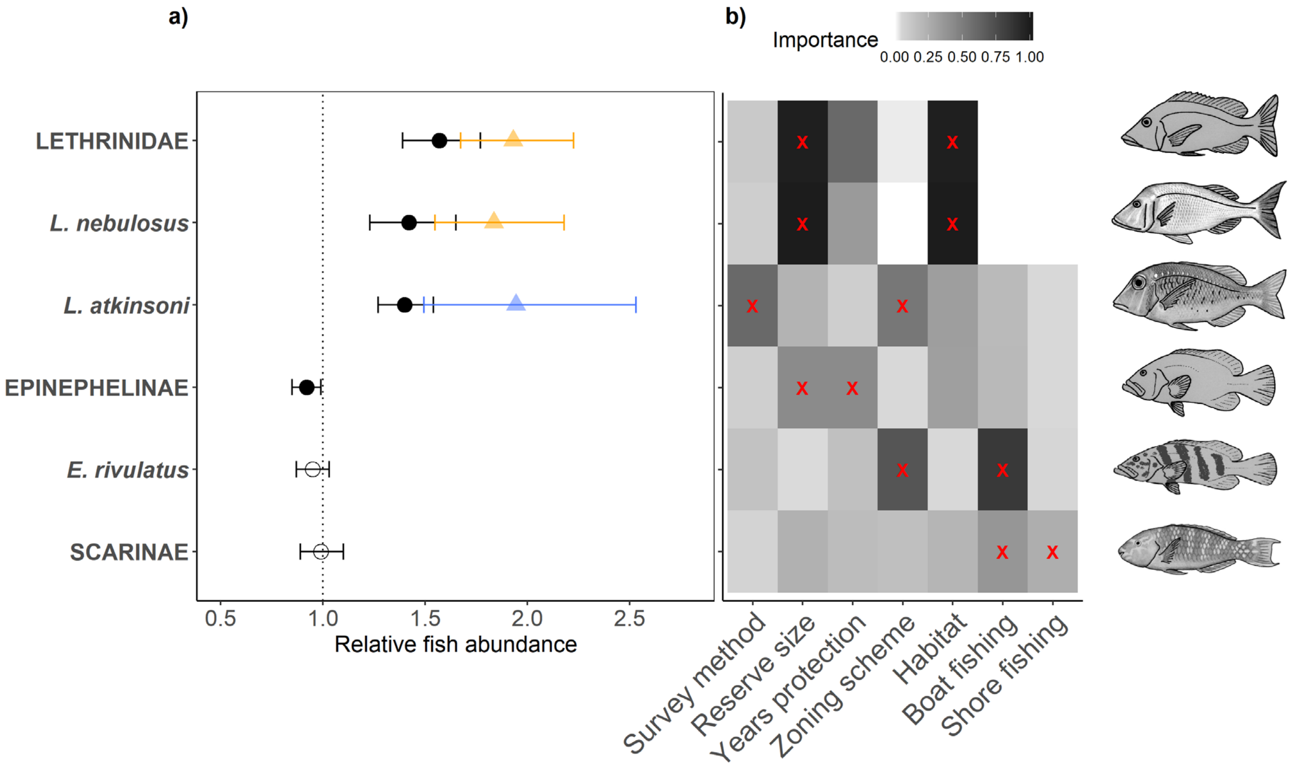

Figure 2. a) Relative fish abundance inside to outside NTMRs (back-transformed weighted mean effect sizes) with 95% confidence intervals), for the six fish groups: Lethrinidae, *Lethrinus nebulosus*, *L. atkinsoni,* Epinephelinae, *Epinephelus rivulatus* and Scarinae. Effect sizes are significant when 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 (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).

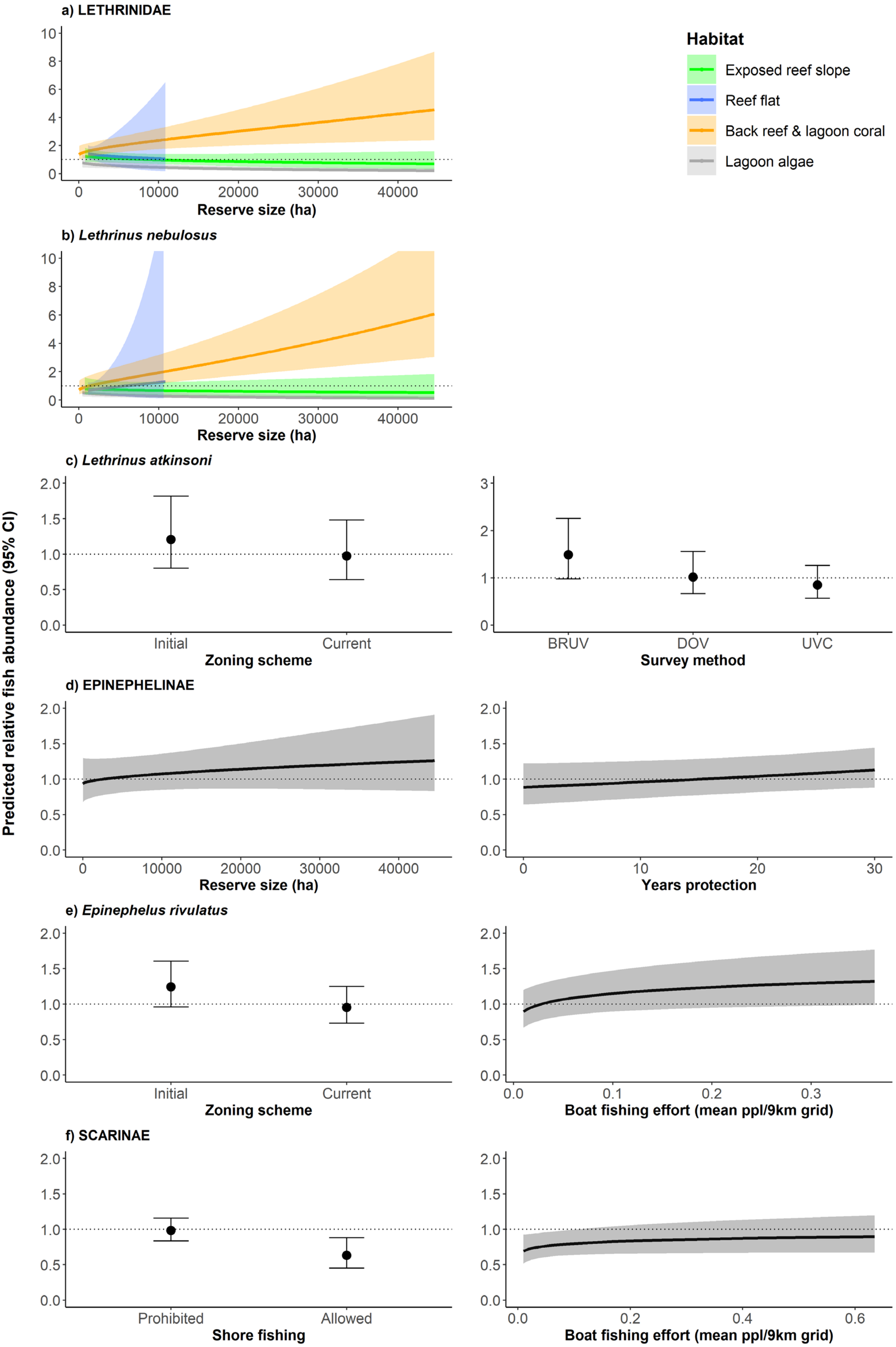

Figure 3. Predicted relative fish abundance inside to outside NTMRs (back-transformed predicted weighted effect sizes) with 95% confidence intervals) for the six fish groups – a) Lethrinidae; b) *Lethrinus nebulosus* c) *Lethrinus atkinsoni;* d) Epinephelinae; e) *Epinephelus rivulatus;* f) Scarinae for abundance– as a function

of variables present in the most parsimonious models (Table 2) from full-subsets GAMM analysis. Ribbons represent 95% confidence intervals

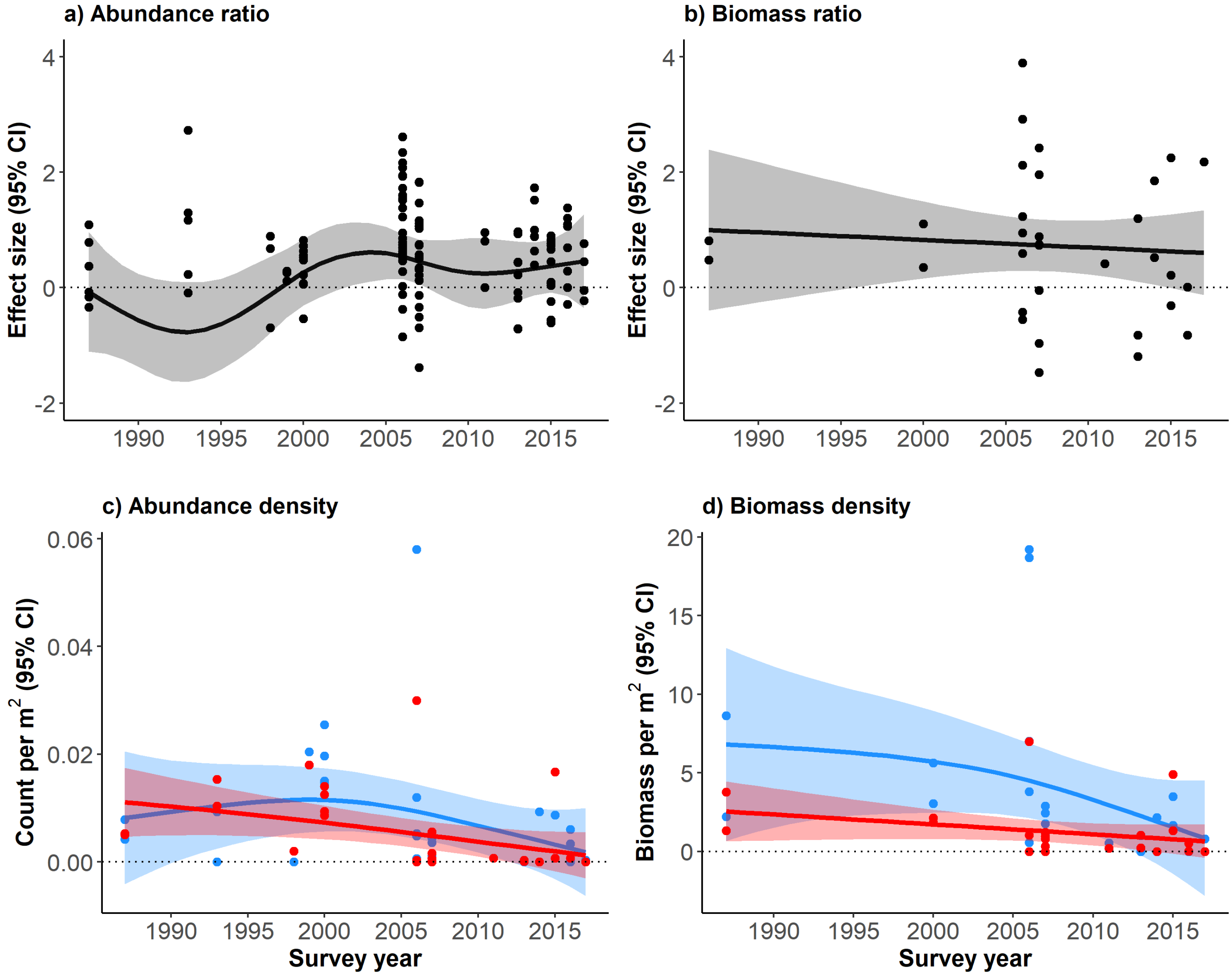

Figure 4. Effect sizes for a) abundance and b) biomass from comparison pairs for the Osprey NTMR through time and estimated density of c) abundance and d) biomass inside and outside the NTMR through time. Ribbons indicate 95% confidence intervals on generalised additive models.

Table 1. Description and summary of the seven variables used in analysis

Variable (transformation used in analyses)	**Description**	**Summary/ description of variable levels**		**Source**
Years protection	Years between zoning and survey data collection	A survey is classified to a single reserve based on its location. In cases where rezoning means that a reserves size was increased, a survey falling inside the old area is classified as the pre-zoning reserve, while if the survey falls in the extended area it is classified as the post-zoning reserve. Years since protection is calculated on the same principal relating to the initial zoning or the rezoning dependent on survey location. 0 - 30 years from time of survey to reserve implementation.		(CALM 2005) (CALM 1989)
Zoning scheme	Factor describing the two major spatial	*Initial*	1987-2005, 8 no-take zones, see Fig. 1a	(CALM 2005) (CALM 1989)

	zonings implemented in the Ningaloo Marine Park	*Current*	2005-present, 18 no-take (excepting shore fishing) and 3 no-take zones in the Muiron Islands Marine Management Area, see Fig. 1b	(Appendix A)
Survey method	Factor describing major survey methods used to collect the fish count and size data	*UVC*	Underwater visual census, collected along transect lines of set length and width (25 x 5 m, 50 x 5 m or 100 x 10 m, 250 x 10 m). Most on SCUBA, some via snorkel. Fish counted and length estimated *in situ.*	For more information on methods see Appendix B
		BRUV	Baited remote underwater stereo-video deployments, (30-60 minutes) point location, fish counted and length estimated *post hoc* from video	
		DOV	Diver operated stereo-video, collected along a transect line of set length and width (5 m in width and varying between 25 and 50 m length), fish counted and length estimated *post hoc* from video	
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 slopes to deeper water and the majority of wave energy is received	Classified by authors, (see Collins et al. 2003)
		Reef flat	Shallow (~2-3m deep), shoreward from the reef crest for tens to hundreds of meters, typically dominated by the plate coral *Acropora spiecifera* on limestone bedrock	
		Back reef & lagoon coral	From where the reef flat breaks into more patchy reef and sand environments, sheltered from wave energy and including some large coral bommies	
		Lagoon algae	Sheltered shallow water lagoon, dominated by fleshy canopy forming seaweed of the genera *Sargassum* and *Sargassopsis*.	
Reserve size (square –root)	Area (ha) of each no-take reserve at time of survey	50 – 44752 hectares 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 the outside reserve survey sites	Mean density of vessels observed fishing during aerial surveys in peak season in 2007. Each survey sample latitude and longitude was assigned the value of the underlying spatial data in Fig. 4 of Smallwood and Beckley (2012). For surveys inside the NTMRs is was assumed that fishing activity was 0. 0 - 0.625 vessels fishing per 9 km^2 Mean: 0.12; Median: 0.11 * Not available for the Muiron Islands Other estimates of fishing activity exist (Sumner et al. 2002) but the metric chosen was deemed the most detailed		Smallwood and Beckley (2012)
Shore fishing	Factor describing whether or not shore fishing permitted in a reserve	*Allowed*	Shore fishing is allowed along the entire, or part of the coastline side of the reserve (26% of data)	(CALM 2005)
		Prohibited	No shore fishing is permitted anywhere in the reserve (74% of data)	

Table 2. Top Generalised Additive Mixed Models (GAMMs) for predicting the response ratio inside to outside NTMRs, $\bar{E}$, for abundance from full subset analyses for the abundance of the six fish groups. Difference between the lowest reported corrected Akaike Information Criterion (ΔAICc), AICc weights (ωAICc), variance explained (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.log + 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

Appendix A *– Additional information on individual reserves and rezoning*

Maps of individual reserves can be found in CALM (1989), pgs. 55, for the 1987-2005 zoning and (CALM 2005), pgs. 89-96, for the 2005-current zoning. Table A1 details individual reserves, their year of establishment, size, and the regulations on shore-based fishing on the coastal edges of the reserves. As well, the number of inside outside comparisons and the total number of surveys are given for each reserve.

Table A1. Features of historical and current reserves in the Ningaloo Marine Park

	Reserve	Management area	Year of Establishment	Size (ha)	Shore fishing	Total number comparison pairs	Total number of samples
2005 – PRESENT MANAGEMENT (CURRENT)	3 Mile	Ningaloo Marine Park	2005	395	N	0	0
	Bateman	Ningaloo Marine Park	2005	1111	N	1	12
	Bundegi rezoned	Ningaloo Marine Park	1987/2005	696	N	3	24
	Cape Farquhar	Ningaloo Marine Park	2005	5326	N	3	31
	Cloates/ Dugong rezoned	Ningaloo Marine Park	1987/2005	44752	P	17	268
	Gnaraloo Bay	Ningaloo Marine Park	2005	1021	N	2	39
	Jurabi	Ningaloo Marine Park	2005	754	Y	9	78
	Lakeside	Ningaloo Marine Park	2005	8	N	0	0
	Lighthouse Bay	Ningaloo Marine Park	2005	763	P	9	136
	Mandu rezoned	Ningaloo Marine Park	1987/2004	1349	N	12	110
	Mangrove rezoned	Ningaloo Marine Park	1987/2005	1135	N	27	429
	Maud rezoned	Ningaloo Marine Park	1987/2005	2151	P	10	133
	Murat	Ningaloo Marine Park	2005	490	Y	0	0
	North Muiron	Muiron Islands Marine Management Size	2005	828	N	4	66
	Osprey rezoned	Ningaloo Marine Park	1987/2005	9513	P	7	54
	Pelican rezoned	Ningaloo Marine Park	1987/2006	10864	P	28	454
	South Muiron	Muiron Islands Marine Management Size	2005	784	N	4	54
	Sunday Island	Muiron Islands Marine Management Size	2005	317	N	0	0
	Tantabiddi	Ningaloo Marine Park	2005	50	N	8	98
	Turtles	Ningaloo Marine Park	2005	2461	N	0	0
	Winderabandi	Ningaloo Marine Park	2005	5526	Y	7	52
1987 – 2005 MANAGEMENT (INITIAL)	Bundegi	Ningaloo Marine Park	1987	297	N	20	333
	Cloates	Ningaloo Marine Park	1987	6257	N	16	186
	Dugong	Ningaloo Marine Park	1987	8852	N	0	0
	Mandu	Ningaloo Marine Park	1987	1163	N	50	1001
	Mangrove	Ningaloo Marine Park	1987	403	N	2	14
	Maud	Ningaloo Marine Park	1987	1806	N	36	652
	Osprey	Ningaloo Marine Park	1987	1756	N	44	701
	Pelican	Ningaloo Marine Park	1987	908	N	7	66
	3 Mile	Ningaloo Marine Park	2005	395	N	0	0

The rezoning of the eight NTMRs in 2005, with the addition of new reserves and the expansion of the existing reserves required that data be clearly classified to account for this. Figure A1 shows an example of how samples were referenced based on their spatial location to the initial or current reserves and the time period of sampling.

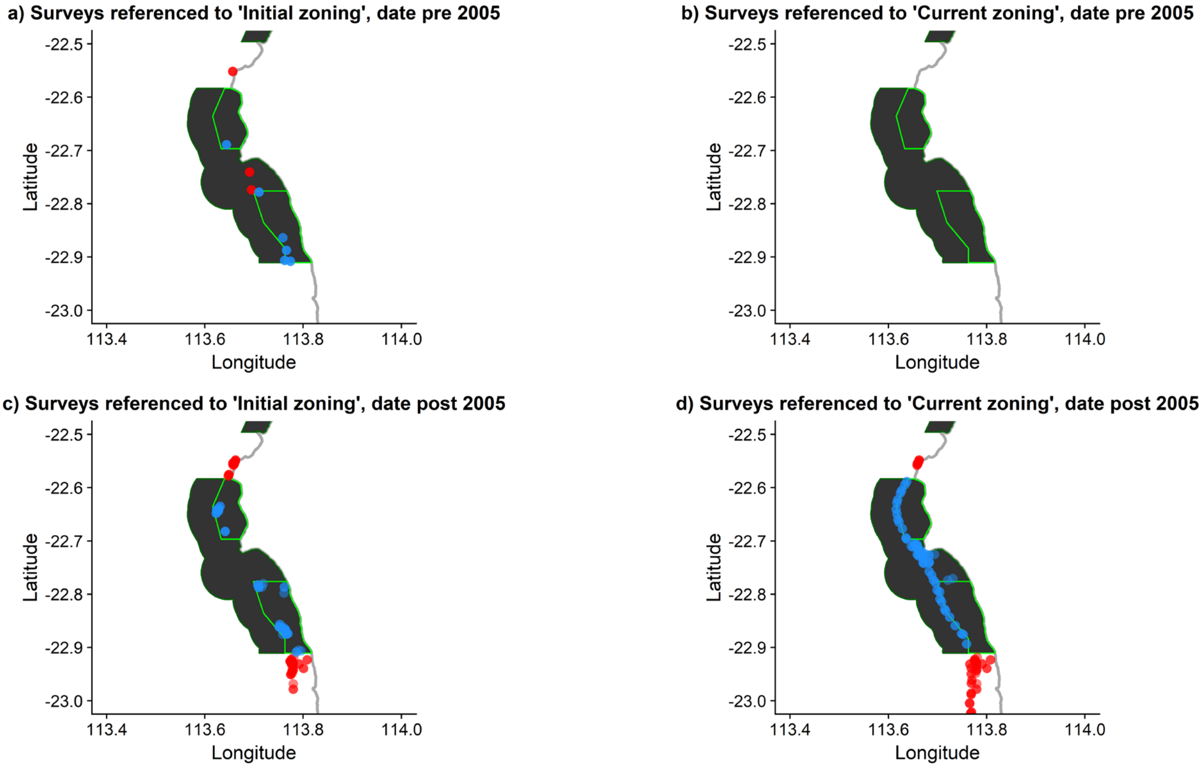

Figure A1. Example classification of ‘initial’ and ‘current’ zoning. The boundaries of the initial 1987 – 2005 reserves, Cloates and Dugong, are indicated by a green outline, while the current reserve (2005 – 2017) is shown in black which combined the two initial reserves into one larger reserve, ‘Cloates/Dugong rezoned’ (also see Table 1). Pre 2005, surveys were classified as inside/outside based on their spatial relation to initial reserves (green outline). Post 2005, surveys were classified as inside/outside based on their spatial relation to the current reserves (black). If an inside reserve is within the initial boundaries, but surveyed post 2005, it was referenced as initial as shown in c). If a sample was collected at a site within the new area of the rezoned reserve post the rezoning, it was referenced as current as seen in d).

Appendix B– Data summary

Suitable data were identified through searches on Google Scholar and research databases compiled by the Department of Biodiversity, Conservation and Attractions. In addition, relevant researchers from universities, research institutions, industry and citizen science programs operating in Western Australia were contacted to source unpublished data. Nine major custodians contributed data to this study. Table B1 summarises the survey methods used by each custodian, the number of samples collected, the temporal span of data, the reserves surveyed and directs to further reading for more information. Figure B2 graphically illustrates the important data constraints.

Table B1. Summary of data contributions

Data custodian	Total number of surveys	Reserves surveyed	Maximum temporal span of surveys	Main survey methods	More information available:
Australian Institute of Marine Science – Woodside Energy (AIMS-Woodside)	183	Bundegi, Bundegi rezoned, Cloates, Cloates/Dugong rezoned, Mandu, Mangrove rezoned, Maud, North Muiron, Osprey, Pelican rezoned, Tantabiddi	1993 -2014	Underwater Visual Census : 50 x 5 m	(Depczynski et al. 2015)
Ben Fitzpatrick	345	Mandu, Osprey	2006 - 2007	Baited Remote Underwater stereo-Video	(Fitzpatrick et al. 2015)
Commonwealth Industrial and Scientific Research Organisation (CSIRO)	18	Bundegi, Bundegi rezoned, Cape Farquhar, Cloates, Cloates/Dugong rezoned, Gnaraloo Bay, Jurabi, Lighthouse Bay, Mandu, Mandu rezoned, Mangrove, Mangrove rezoned, Maud, North Muiron, Osprey, Osprey rezoned, Pelican, Pelican rezoned, South Muiron	2006 - 2017	Underwater Visual Census, 4 main sizes: 1) Either a singular, or three, 25 × 5 m transects per site. 2) 30 × 5 m transects 3) 50 × 5 m transects 4) 100 × 10 m transects at a site	(Babcock et al. 2008)
Western Australian Department of Biodiversity, Conservation and Attractions (DBCA)	1237	Bundegi , Cape Farquhar, Cloates, Cloates/Dugong rezoned, Jurabi, Lighthouse Bay, Mandu, Mangrove rezoned, Maud, Maud rezoned, North Muiron, Osprey, Pelican, Pelican rezoned, Tantabiddi, Winderabandi	2010 - 2016	Diver Operated stereo-Video: six replicate 50 x 5 m belt transects per site; or nine replicate 30 x 5 m belt transects per site	(Wilson et al. 2012; Holmes et al. 2013; Wilson et al. 2018b)
Mark Westera	257	Mandu, Maud, Osprey	1999 - 2000	Baited Remote Underwater stereo-Video, 30 minute deployments at 12 replicate locations in each zone, Underwater visual census using snorkel, 250 x 10 m transects	(Westera 2003a, b)
Reef Life Survey (RLS)	291	Bateman, Bundegi, Cloates, Maud, Maud rezoned, Pelican rezoned	2010 - 2017	Underwater Visual Census, 50 x 5 m transects	(see http://reeflifesurvey.com/files/2008/09/rils-reef-monitoring-procedures.pdf).
Tony Ayling	60	Osprey	1987		(Ayling & Ayling 1987)
The University of Western Australia	325	Cloates, Cloates/Dugong rezoned, Mandu rezoned, Mangrove rezoned, Osprey, Osprey rezoned, Pelican rezoned, Winderabandi	2014 - 2015	Baited Remote Underwater stereo-Video, generally 60 minute deployments	(McLean et al. 2016)
Joint data custodians WA Department of Biodiversity, Conservation and Attractions, Australian Institute of Marine Science, Australian National University	587	Cloates/Dugong rezoned, Mandu, Mangrove rezoned, Maud, Maud rezoned, Pelican, Pelican rezoned,	2013 - 2015	Underwater Visual Census, 4 main sizes: 1) Either a singular, or three, 25 × 5 m transects per site. 2) 30 × 5 m transects 3) 50 × 5 m transects 4) 100 × 10 m transects at a site	(Fulton et al. 2014)

In most surveys biomass had been calculated by the respective data custodians from the estimated or measured fish length. In these cases the provided values were used (with the reasoning that different survey methods may warrant slightly different biomass calculations). In cases where length data was available but biomass had not been calculated the fish counts and length estimates were converted to biomass (kg) using constants and formulas from Fishbase (www.fishbase.org).

$$Biomass = e^{\ln(a)+b\times\ln(L)}$$

where *L* is the estimated total length of the fish and *a* and *b* are constants for the species or family in question. In cases where data provided fork length measurements, these were converted to total length using the formula from FishBase:

$$TL = c + d \times FL$$

where *TL* is estimated total fish length, *FL* is the measured fork length from BRUV or DOV video and *c* and *d* are parameters specific to the fish species in question.

More data was available for some NTMRs and years, with increased sampling after 2005 (Appendix B).

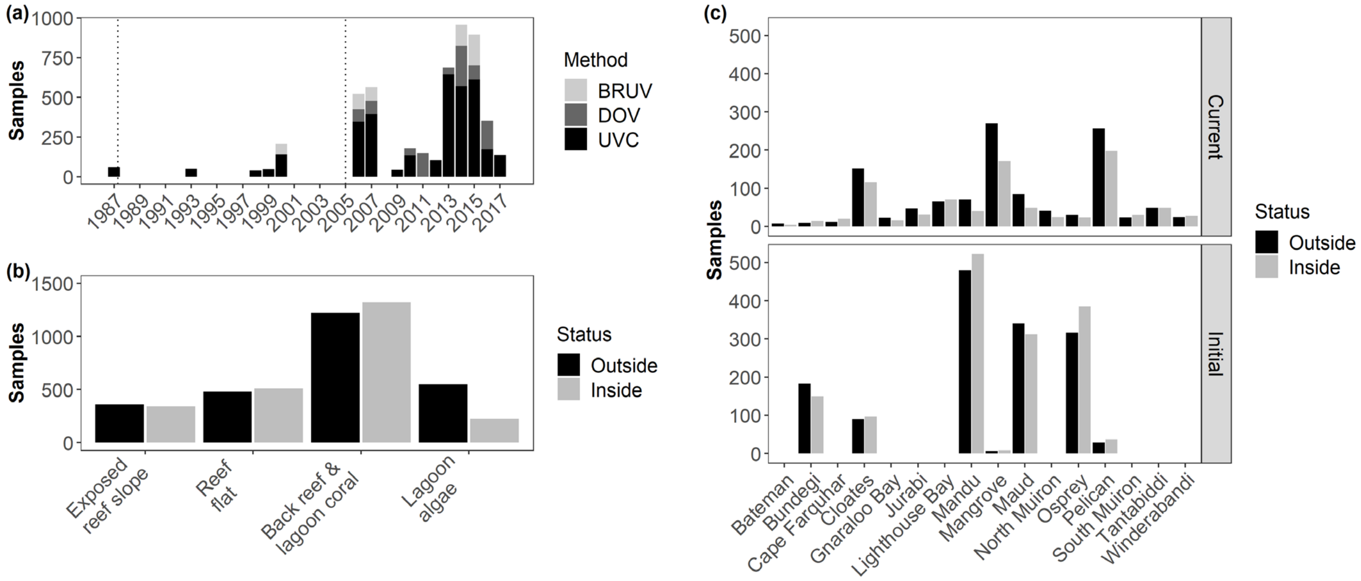

Figure B2. Temporal and spatial distribution of samples: a) number of samples by year, with shade indicating the type of survey method (BRUV, Baited Remote Underwater stereo-Video, DOV, Diver Operated stereo-Video and UVC, Underwater Visual Census); b) distribution of samples inside and outside NTMRs for each of the four major habitats; c) distribution of samples inside and outside for each NTMR under both the initial and current zoning.

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***Appendix C –** Geographic locations of individual samples*

Kml file for viewing samples in GoogleEarth

Appendix D: *Fish groups*

Analyses were conducted at the family/subfamily level and species level. Investigation of patterns at the family/subfamily level allowed the inclusion of data from targeted but rare species.

Table D1. Total count of fish groups across all data

Taxa	**Total count across synthesised data**
LETHRINIDAE	10307
L. nebulosus	4183
L. atkinsoni	4765
EPINEPHELINAE	4012
E. rivulatus	1119
SCARINAE	44931

Genera included in the family/ sub-family analysis that were sampled in the synthesised data are summarised below.

Lethrinidae

- *Gnathodentex aureolineatus*
- *Gymnocranius euanus*
- *Gymnocranius grandoculis*
- *Gymnocranius griseus*
- *Gymnocranius spp.*
- *Lethrinus amboinensis*
- *Lethrinus atkinsoni*
- *Lethrinus genivittatus*
- *Lethrinus harak*
- *Lethrinus laticaudis*
- *Lethrinus lentjan*
- *Lethrinus microdon*
- *Lethrinus miniatus*
- *Lethrinus nebulosus*
- *Lethrinus obsoletus*
- *Lethrinus olivaceus*
- *Lethrinus ravus*
- *Lethrinus rubrioperculatus*
- *Lethrinus semicinctus*
- *Lethrinus variegatus*
- *Lethrinus spp.*
- *Monotaxis grandoculis*

Epinephelinae *

- *Aethaloperca rogaa*
- *Anyperodon leucogrammicus*
- *Cephalopholis* spp.
- *Cephalopholis argus*
- *Cephalopholis boenak*
- *Cephalopholis cyanostigma*
- *Cephalopholis formosa*
- *Cephalopholis miniata*
- *Cephalopholis sexmaculata*
- *Cephalopholis sonnerati*
- *Cromileptes altivelis*
- *Epinephelus* spp.
- *Epinephelus areolatus*
- *Epinephelus bilobatus*
- *Epinephelus coeruleopunctatus*
- *Epinephelus coioides*
- *Epinephelus corallicola*
- *Epinephelus fasciatus*

- *Epinephelus fuscoguttatus*
- *Epinephelus hexagonatus*
- *Epinephelus lanceolatus*
- *Epinephelus macrospilos*
- *Epinephelus maculatus*
- *Epinephelus malabaricus*
- *Epinephelus melanostigma*
- *Epinephelus merra*
- *Epinephelus polyphekadion*
- *Epinephelus quoyanus*
- *Epinephelus rivulatus*
- *Epinephelus tauvina*
- *Epinephelus tukula*
- *Plectropomus leopardus*
- *Plectropomus maculatus*
- *Plectropomus* spp.
- *Variola albimarginata*
- *Variola louti*

* Note that there is current discussion of whether Epinephelinae may be better classified as its own family, Epinephelidae (Ma & Craig 2018), however we have chosen to name it as its subfamily here.

Scarinae

- *Calotomus carolinus*
- *Calotomus spinidens*
- *Cetoscarus ocellatus*
- *Chlorurus bleekeri*
- *Chlorurus microrhinos*
- *Chlorurus sordidus*
- *Hipposcarus longiceps*
- *Leptoscarus vaigiensis*
- *Scarus chameleon*
- *Scarus dimidiatus*
- *Scarus flavipectoralis*
- *Scarus frenatus*
- *Scarus ghobban*
- *Scarus globiceps*
- *Scarus niger*
- *Scarus oviceps*
- *Scarus prasiognathos*
- *Scarus psittacus*
- *Scarus rivulatus*
- *Scarus rubroviolaceus*
- *Scarus schlegeli*
- *Scarus* spp.

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Appendix E: *Formulas used for calculating effect sizes*

For each inside/ outside comparison pair a log response ratio (*e*) (Hedges et al. 1999) was calculated as the ratio of the mean abundance/ biomass inside to outside a NTMRfor comparison pair *i* and fish group *j* as

$$e_{ij} = \ln\left(\frac{\bar{X}_{ij,I}}{\bar{X}_{ij,O}}\right)$$

where and $\bar{X}_{ij,I}$ and $\bar{X}_{ij,O}$ are the mean abundance or biomass inside (I) and outside (O) a NTMR. Therefore, a positive e_{ij} implies a greater fish abundance/ biomass inside the NTMRs than outside. A log response ratio was appropriate because it is independent of the actual unit of measurement across the different survey methods.

The variance of e_{ij} was also quantified (i.e. the within-study variance, where a study is a comparison pair), given that sampling error plays an important role in introducing variability in the overall outcome of a meta-analysis:

$$v_{ij} = \frac{\sigma_{ij,I}^2}{\left(n_{ij,I}\bar{X}_{ij,I}^2\right)} + \frac{\sigma_{ij,O}^2}{\left(n_{ij,O}\bar{X}_{ij,O}^2\right)}$$

Here, v_{ij} is calculated from the standard deviation, σ_{ij} , sample size, n_{ij}, and mean $\bar{X}_{ij}$ for inside (I) and outside (O) for comparison pair *i* and fish group *j*.

Effect sizes were weighted by the inverse of the sum of the within- and among-study variances, w_{ij},. The within-study variance (where a study is a comparison pair) was the sum of the variances associated with each mean in the log-ratio. The among-study variance was calculated using the *metafor* package (Viechtbauer 2010) in the statistical program R (R Core Team 2017).

$$w_{ij} = \frac{1}{v_{ij}}$$

This weighting minimized the influence of studies with low statistical power, and increased the influence of studies with high statistical power, meaning that each inside/ outside replicate did not contribute equally to the final pooled outcome. Weighted meta-analyses of this sort are considered to increase the precision and power of meta-analyses (Osenberg et al. 1999) and was an appropriate approach in the present study as there was a large distribution of sample sizes and variance associated with the inside/ outside comparison pairs. The weighted cumulative effect size for fish group *j*, $\bar{E}_j$, was obtained as

$\bar{E}_j = \frac{\sum_{i=1}^{n_{ij}} w_{ij}e_{ij}}{\sum_{i=1}^{n_{ij}} w_{ij}}$ with associated variance, $\bar{v}_j = \frac{1}{\sum_{i=1}^{n_{ij}} w_{ij}}$.

where w_{ij} and e_{ij} are defined above. The overall heterogeneity (Q_t) for fish group *j* was calculated as

$$Q_{t,j} = \sum_{i=1}^{n_{ij}} w_{ij}\left(e_{ij} - \bar{E}_j\right)^2$$

and its significance was tested against the χ^2 distribution with $n_{ij} - 1$ degrees of freedom.

We used a random-effects model to calculate $\bar{E}_j$ and $Q_{t,j}$ using the *metafor* package in R through the call rma(e_{ij}, v_{ij}, method = “REML”, data =) following the suggestions in Viechtbauer (2005) that the REML, restricted maximum likelihood estimator for variance, strikes a good balance between unbiasedness and efficiency.

We ran mixed-effects categorical analyses and meta-regression to examine how the seven additional variables (Table 1, main text) mediated the overall effect size $\bar{E}_j$. For a given level (*L)* of the factor, a weighted cumulative effect size was calculated as

$$\bar{E}_{L,j} = \frac{\sum_{i=1}^{n_{Lj}} w_{ij}\, e_{ij}}{\sum_{i=1}^{n_{Lj}} w_{ij}}$$

Where n_{Lj} is the number of comparison pairs in level, *L,* of the factor, and e_{ij} and w_{ij} are defined above. The heterogeneity of the model explained by the factor (Q_m) was calculated as

$$Q_{m,j} = \sum_{i=1}^{n_{Lj}} w_{ij}\left(\bar{E}_{L,j} - \bar{E}_j\right)^2$$

The significance of Q_m was tested against the χ^2 distribution with $n_{Lj} - 1$ degrees of freedom

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***Appendix F -** Sensitivity analysis for case of one-armed zero events*

Cheng et al. (2016) define two scenarios relating to zero events: zero-event and double-zero-event. In the present study there were both double-zero-events (a zero mean abundance/biomass for both inside and outside) and zero-events (zero mean abundance/biomass for either the inside or the outside), summarised in Table 1. In both cases, lnR cannot be computed due to division by zero and/or logarithm of zero. The former case are often removed from meta-analyses, while the latter is often handled via the addition of a small constant (Bradburn et al. 2007; Spittal et al. 2015). The total number of comparisons (n) used in the final calculated of the weighted average effect size is given.

In the present study the species examined can be encountered infrequently on a survey. As well, one of the key species, *Lethrinus nebulosus*, is a schooling species which, when it occurs, can be present in larger numbers. Consequently there are many zero counts in the data which needed to be explicitly considered.

Table F1. Summary of total number of comparisons and zero events

	Fish Group	Total number of possible comparisons	Double-zero events	Zero-events	Final sample size (n) in calculation of mean weighted effect size
ABUNDANCE	**LETHRINIDAE**	305	4	151	301
	L. nebulosus	305	48	162	257
	L. atkinsoni	305	25	101	280
	EPINEPHELINAE	305	28	110	277
	E. rivulatus	305	138	210	167
	SCARINAE	305	44	46	261
BIOMASS	**LETHRINIDAE**	268	4	49	264
	L. nebulosus	268	45	143	223
	L. atkinsoni	268	21	86	247
	EPINEPHELINAE	268	15	87	253
	E. rivulatus	268	112	180	156
	SCARINAE	268	45	48	223

Double-zero-events were removed from analysis. For the remaining data a constant of 0.5 fish (half the smallest unit in the abundance analysis) was added to both the inside and outside mean counts, while for biomass a constant of 100 grams was added to both the inside and outside mean biomass.

Given there is no clear protocol for the size of the constant used to deal with zeros in a *ln*R meta-analysis, we conducted a sensitivity analysis on the value of the constant. We ran the sensitivity analysis for the abundance data for the six taxa examined. We tested constant values, *c*, ranging from *c* = 0.01 to *c* = 1 in 0.01 increments.

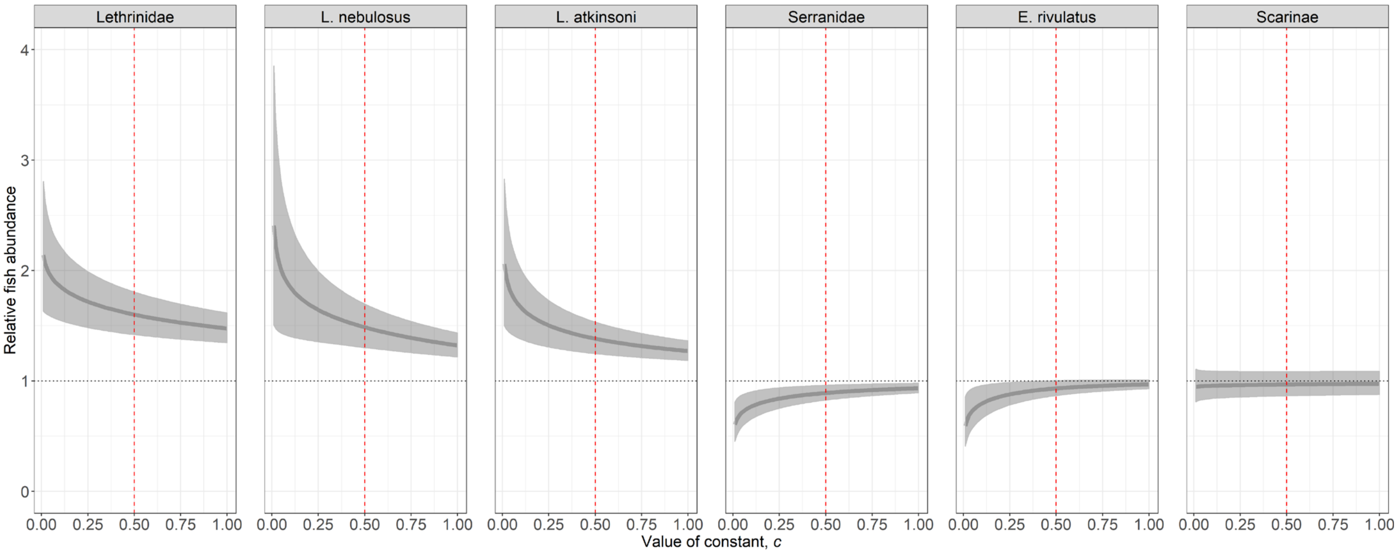

Figure F1. Sensitivity analysis for the size of the constant added to inside/outside mean abundance showing the resulting transformed mean weighted effect size, exponential of $\bar{E}$, and 95% confidence interval (*CI*) for values of constant *c* ranging from 0.01 to 1 in 0.01 increments. a) Lethrinidae, b) *L. nebulosus*, c) *L. atkinsoni,* d) Epinephelinae, e) *E. rivulatus*, f) Scarinae. The mean effect sizes are considered significant when the confidence intervals do not include one.

It is clear that the size of the constant used influenced the mean overall effect size. For example, the magnitude of $\bar{E}$ for *L. nebulosus* total abundance varied from $\bar{E}$ = 0.73 (0.54) when c = 0.01 to $\bar{E}$ = 0.28 (0.08) when c = 1. However, while the constant size impacted the magnitude of the effect size, it did not influence the significance, except for *E. rivulatus,* which had the highest count of zero-events, and transitioned from marginally negative to not significantly different from one. From this analysis we decided a constant of 0.5 would be an adequate, and conservative addition for the calculation of *ln*R in this analysis. Given the high levels of inherent variability expected in fish count data (Samoilys et al. 1995; Cappo & Brown 1996) and additional variation from uncontrolled variables, even with addition of a constant, overall differences in abundance would have to be consistent in order to observe statistical significance. Nonetheless, we urge caution in the interpretation of the magnitude of the overall effect.

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Appendix G - *Meta-analysis statistics*

Table G1. Total heterogeneity statistics

	ABUNDANCE			BIOMASS		
Fish group	**Q_T**	**df**	***P***	**Q_T**	**df**	***P***
LETHRINIDAE	2002.57	300	<0.001	2318.26	263	<0.001
L. nebulosus	1971.07	256	<0.001	2886.99	222	<0.001
L. atkinsoni	1739.71	279	<0.001	1928.65	246	<0.001
EPINEPHELINAE	1125.65	276	<0.001	1307.49	252	<0.001
E. rivulatus	477.33	166	<0.001	590.76	155	<0.001
SCARINAE	1701.09	260	<0.001	1224.57	222	<0.001

Table G2 and G3 summarise the results of weighted mixed-effects meta-analyses for all seven variables and for *reserve identity* modelled individually. Figure 1 shows the predicted effect size for the cases where the moderator reserve identity explained a significant amount of heterogeneity for *habitat* so that it can be directly compared to the overall effect sizes in Figure 2 (main text).

Table G2. Mixed-effects models heterogeneity statistics for abundance data

		ABUNDANCE					
		*Model heterogeneity**			*Residual heterogeneity*		
	Fish group	**Q_m**	**df**	***P***	**Q_e**	**df**	***P***
HABITAT	LETHRINIDAE	39.46	3	**<0.001**	1622.38	297	<0.001
	L. nebulosus	32.51	3	**<0.001**	1574.07	253	<0.001
	L. atkinsoni	14.55	3	**<0.001**	1614.93	276	<0.001
	EPINEPHELINAE	0.31	3	0.96	1117.33	273	<0.001
	E. rivulatus	5.39	3	0.15	467.33	163	<0.001
	SCARINAE	6	3	0.11	1589.43	257	<0.001
METHOD	LETHRINIDAE	4.09	2	0.13	1975.79	298	<0.001
	L. nebulosus	0.71	2	0.7	1946.56	254	<0.001
	L. atkinsoni	7.85	2	**0.02**	1676.16	277	<0.001
	EPINEPHELINAE	4.35	2	0.11	1094.35	274	<0.001
	E. rivulatus	0.98	2	0.61	474.68	164	<0.001
	SCARINAE	0.01	2	0.99	1633.03	258	<0.001
RESERVE SIZE	LETHRINIDAE	3.8	1	0.05	1959.06	299	<0.001
	L. nebulosus	0.01	1	0.94	1970.56	255	<0.001
	L. atkinsoni	8.11	1	**<0.001**	1688.35	278	<0.001
	EPINEPHELINAE	1.58	1	0.21	1112.23	275	<0.001
	E. rivulatus	0.47	1	0.49	477.08	165	<0.001
	SCARINAE	0.02	1	0.88	1701.09	259	<0.001
YEARS PROTECTION	LETHRINIDAE	0	1	0.95	2001.07	299	<0.001
	L. nebulosus	0.92	1	0.34	1949.89	255	<0.001
	L. atkinsoni	1.86	1	0.17	1736.82	278	<0.001
	EPINEPHELINAE	0.42	1	0.52	1115.08	275	<0.001
	E. rivulatus	5.43	1	**0.02**	462.46	165	<0.001
	SCARINAE	0.83	1	0.36	1689.03	259	<0.001
ZONING SCHEME	LETHRINIDAE	0.83	1	0.36	2002.31	299	<0.001
	L. nebulosus	0.87	1	0.35	1961.63	255	<0.001
	L. atkinsoni	8.43	1	**<0.001**	1696.16	278	<0.001
	EPINEPHELINAE	1.1	1	0.29	1100.82	275	<0.001
	E. rivulatus	13.43	1	**<0.001**	440.94	165	<0.001
	SCARINAE	3.82	1	0.05	1680.66	259	<0.001
BOAT FISHING	LETHRINIDAE	1.15	1	0.28	1987.99	295	<0.001
	L. nebulosus	0.7	1	0.4	1960.92	251	<0.001
	L. atkinsoni	0.55	1	0.46	1698.56	275	<0.001
	EPINEPHELINAE	0.01	1	0.92	1099.86	271	<0.001
	E. rivulatus	4.79	1	**0.03**	457.62	162	<0.001
	SCARINAE	5.9	1	**0.02**	1670.41	255	<0.001
SH OR E FIS	LETHRINIDAE	7.09	1	**0.01**	1953.98	299	<0.001
	L. nebulosus	0.16	1	0.69	1966.75	255	<0.001
	L. atkinsoni	9.03	1	**<0.001**	1689.1	278	<0.001

	EPINEPHELINAE	3.9	1	**0.05**	1060.95	275	<0.001
	E. rivulatus	6.16	1	**0.01**	461.9	165	<0.001
	SCARINAE	5.59	1	**0.02**	1674.58	259	<0.001
RESERVE IDENTITY	LETHRINIDAE	43.22	21	**<0.001**	1746.07	279	<0.001
	L. nebulosus	48.82	21	**<0.001**	1665.43	235	<0.001
	L. atkinsoni	35.29	20	**0.02**	1494.98	259	<0.001
	EPINEPHELINAE	54.33	21	**<0.001**	880.04	255	<0.001
	E. rivulatus	68.95	20	**<0.001**	344.61	146	<0.001
	SCARINAE	27.81	21	0.15	1484.39	239	<0.001
SURVEY YEAR	LETHRINIDAE	2.39	1	0.12	1994.3	299	<0.001
	L. nebulosus	0	1	0.99	1962.36	255	<0.001
	L. atkinsoni	5.75	1	**0.02**	1674.53	278	<0.001
	EPINEPHELINAE	0.5	1	0.48	1115.22	275	<0.001
	E. rivulatus	3.59	1	0.06	468.95	165	<0.001
	SCARINAE	21.29	1	**<0.001**	1579.86	259	<0.001

* Total heterogeneity is provided in Table G1

Table G3. Mixed-effects models heterogeneity statistics for abundance data

		BIOMASS					
		*Model heterogeneity**			*Residual heterogeneity*		
	Fish group	**Q_m**	**df**	***P***	**Q_e**	**df**	***P***
HABITAT	LETHRINIDAE	41.75	3	**<0.001**	2082.5	260	<0.001
	L. nebulosus	29.38	3	**<0.001**	2743.83	219	<0.001
	L. atkinsoni	17.13	3	**<0.001**	1714.19	243	<0.001
	EPINEPHELINAE	1.21	3	0.75	1296.97	249	<0.001
	E. rivulatus	2.53	3	0.47	517.38	152	<0.001
	SCARINAE	22.86	3	**<0.001**	1038.84	219	<0.001
METHOD	LETHRINIDAE	2.46	2	0.29	2140.53	261	<0.001
	L. nebulosus	0.63	2	0.73	2829.86	220	<0.001
	L. atkinsoni	7.79	2	**0.02**	1720.61	244	<0.001
	EPINEPHELINAE	12.37	2	**<0.001**	1258.74	250	<0.001
	E. rivulatus	5.9	2	0.05	586.26	153	<0.001
	SCARINAE	1.16	2	0.56	1193.63	220	<0.001
RESERVE SIZE	LETHRINIDAE	1.3	1	0.25	2318.18	262	<0.001
	L. nebulosus	0.1	1	0.75	2886.72	221	<0.001
	L. atkinsoni	1.97	1	0.16	1925.76	245	<0.001
	EPINEPHELINAE	3.78	1	0.05	1307.41	251	<0.001
	E. rivulatus	1.32	1	0.25	571.52	154	<0.001
	SCARINAE	0.59	1	0.44	1220.28	221	<0.001
YEARS PROTECTION	LETHRINIDAE	0.01	1	0.94	2312.18	262	<0.001
	L. nebulosus	0.71	1	0.4	2882.59	221	<0.001
	L. atkinsoni	3.13	1	0.08	1924.77	245	<0.001
	EPINEPHELINAE	0.12	1	0.73	1307.3	251	<0.001
	E. rivulatus	5.01	1	**0.03**	587.67	154	<0.001
	SCARINAE	0.02	1	0.89	1218.81	221	<0.001
ZONING SCHEME	LETHRINIDAE	0.44	1	0.51	2314.92	262	<0.001
	L. nebulosus	0.54	1	0.46	2883.99	221	<0.001
	L. atkinsoni	9.59	1	**<0.001**	1925.41	245	<0.001
	EPINEPHELINAE	0.04	1	0.83	1307.27	251	<0.001
	E. rivulatus	9.96	1	**<0.001**	587.78	154	<0.001
	SCARINAE	3.09	1	0.08	1222.86	221	<0.001
BOAT FISHING	LETHRINIDAE	0.18	1	0.67	2313.23	258	<0.001
	L. nebulosus	0.04	1	0.84	2879.67	217	<0.001
	L. atkinsoni	0.14	1	0.7	1923.96	243	<0.001
	EPINEPHELINAE	0.82	1	0.37	1287.94	247	<0.001
	E. rivulatus	3.75	1	0.05	578.7	151	<0.001
	SCARINAE	0.57	1	0.45	1193.33	217	<0.001
SHORE FISHING	LETHRINIDAE	2.19	1	0.14	2295.06	262	<0.001
	L. nebulosus	0	1	0.96	2606.71	221	<0.001
	L. atkinsoni	5.25	1	**0.02**	1927.59	245	<0.001
	EPINEPHELINAE	0.38	1	0.54	1268.07	251	<0.001
	E. rivulatus	3.05	1	0.08	580.64	154	<0.001
	SCARINAE	5.78	1	**0.02**	1168.18	221	<0.001
RESERVE IDENTITY	LETHRINIDAE	29.09	21	0.11	2019.62	242	<0.001
	L. nebulosus	27.02	21	0.17	1941.89	201	<0.001
	L. atkinsoni	33.93	20	**0.03**	1846.92	226	<0.001
	EPINEPHELINAE	58.1	21	**<0.001**	987.83	231	<0.001
	E. rivulatus	49.47	20	**<0.001**	503.04	135	<0.001

	SCARINAE	33.11	21	**0.04**	1046.15	201	<0.001
SURVEY YEAR	LETHRINIDAE	2.39	1	0.12	1994.3	299	<0.001
	L. nebulosus	0	1	0.99	1962.36	255	<0.001
	L. atkinsoni	5.75	1	**0.02**	1674.53	278	<0.001
	EPINEPHELINAE	0.5	1	0.48	1115.22	275	<0.001
	E. rivulatus	3.59	1	0.06	468.95	165	<0.001
	SCARINAE	21.29	1	**<0.001**	1579.86	259	<0.001

* Total heterogeneity is provided in Table G1

Figure G1 shows the transformed predicted effect sizes as relative fish abundance by *habitat* while Figure G2 shows this for *reserve identity*.

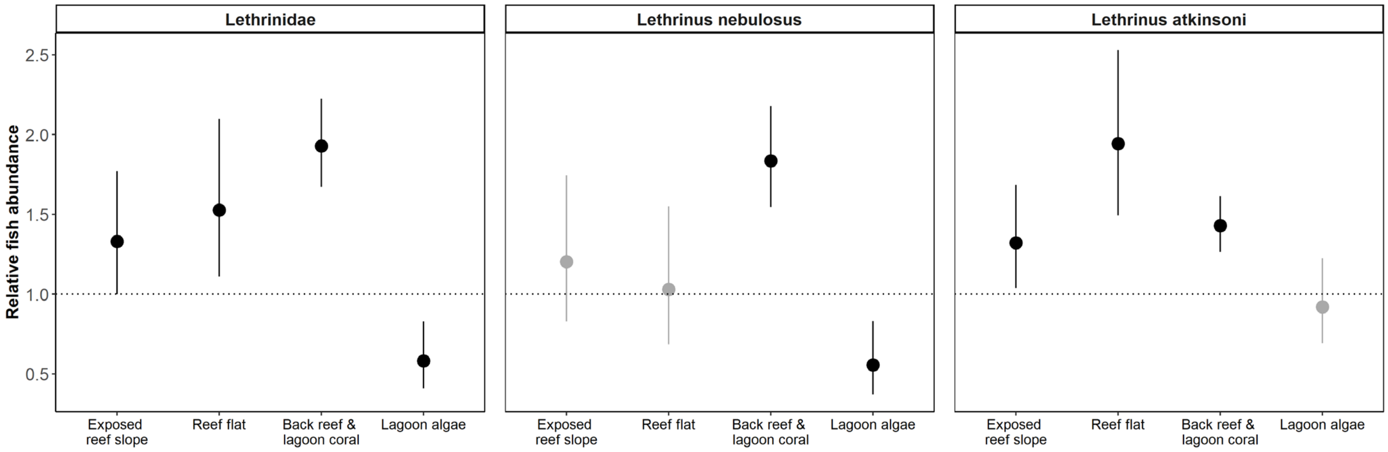
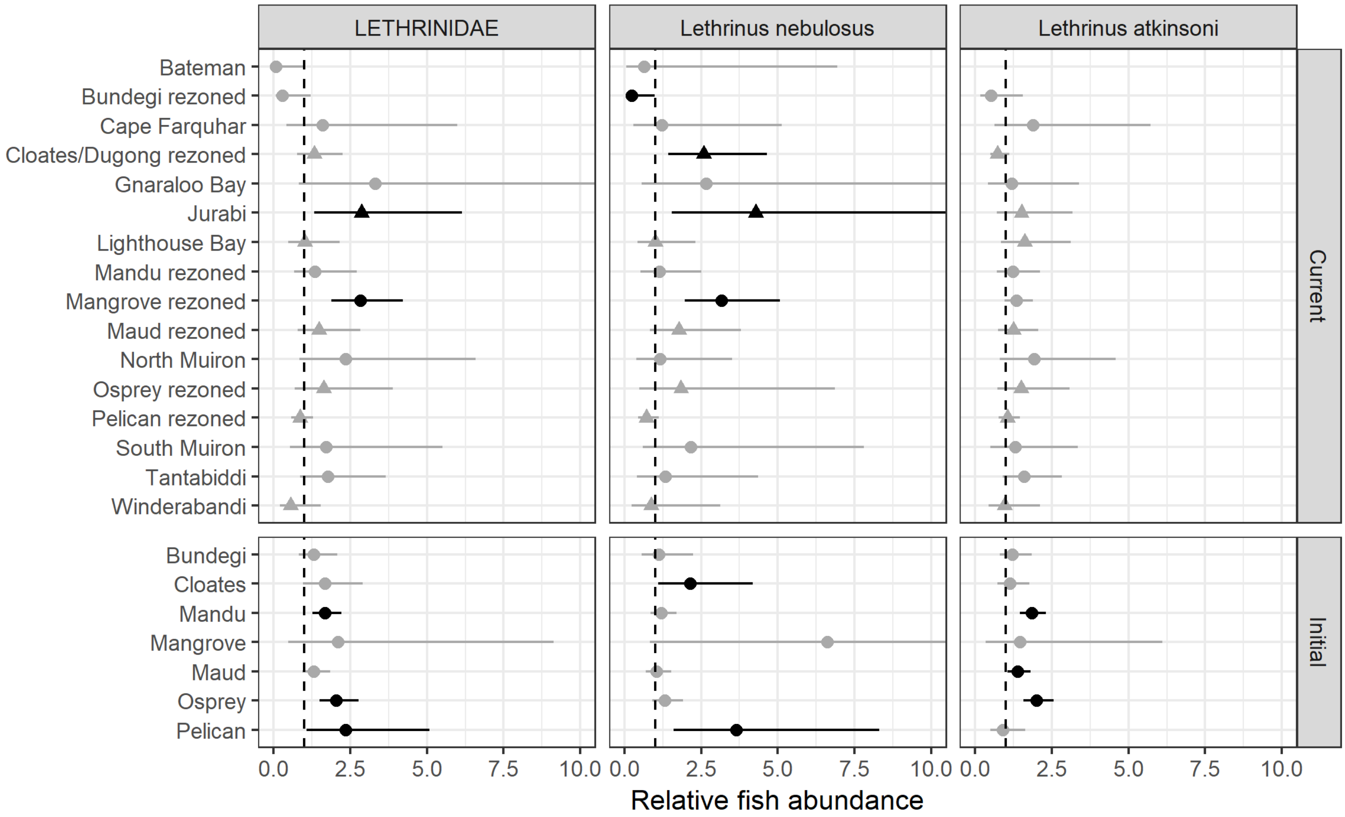


Figure G1. Relative fish abundance inside to outside NTMRs (back-transformed weighted mean effect sizes) with 95% confidence intervals) for the Lethrinidae, *Lethrinus nebulosus*, and *L. atkinsoni*, the fish groups for which *habitat* explained a significant amount of variation. Effect sizes are considered significant when the confidence intervals do not include one. Black dots correspond to significant effects while grey dots correspond to non-significant effects.

Figure G2 is included to show that there is heterogeneity between individual NTMRs and because it may be useful to managers of the Ningaloo Marine Park.



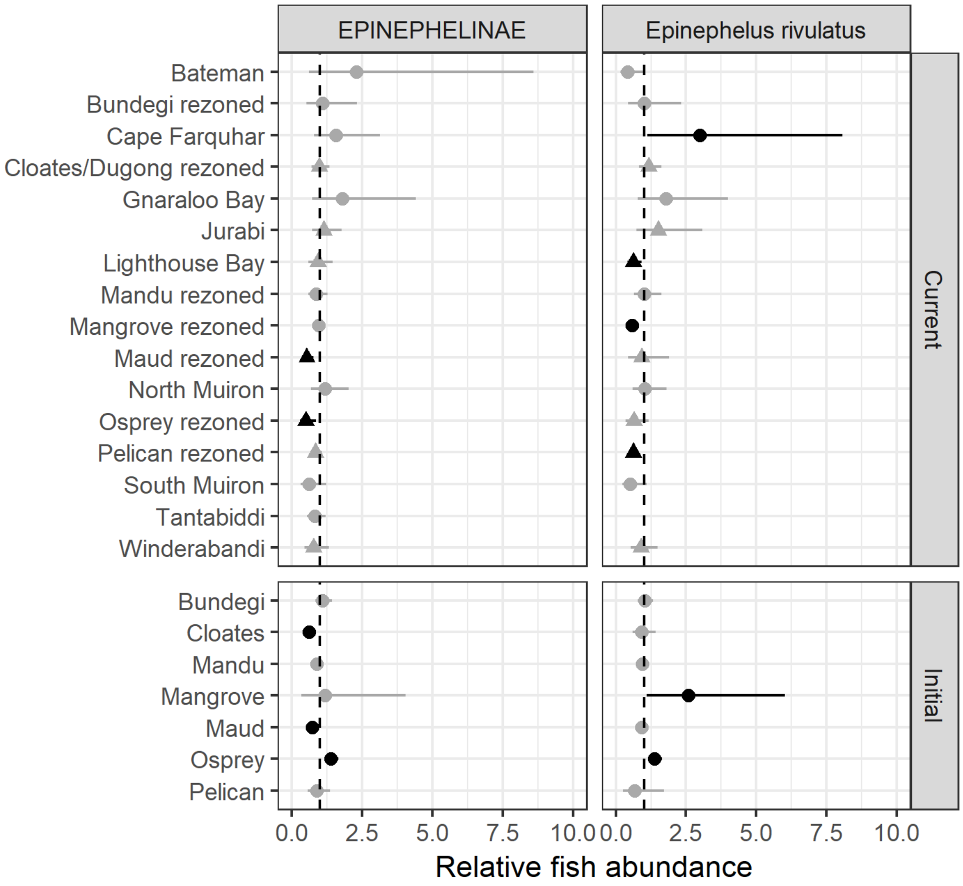


Figure G2. Relative fish abundance (Transformed weighted mean effect sizes ($exp(e)$) with 95% confidence intervals (*CI*)), for the Lethrinidae, *Lethrinus nebulosus*, *Lethrinus atkinsoni,* Epinephelinae and *Epinephelus rivulatus,* the fish groups for which *reserve identity* explained a significant amount of variation. Results are categorised into panels based on the initial or current zoning. Point shape indicates whether shore fishing is allowed or prohibited along the coastal edge of the reserve (circle = prohibited; triangle = allowed). Effect sizes are considered significant when the confidence intervals do not include one. Black dots correspond to significant effects while grey dots correspond to non-significant effects.

Appendix H – Biomass results

Table H1. Top Generalised Additive Mixed Models (GAMMs) for predicting the response ratio inside to outside NTMRs, $\bar{E}$, for biomass from full subset analyses for the abundance of the six fish groups. Difference between the lowest reported corrected Akaike Information Criterion (ΔAICc), AICc weights (ωAICc), variance explained (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 + Size by Habitat**	0	0.855	0.17399	9
L. nebulosus	Habitat + Years protection by Habitat + Size by Habitat	0	0.443	0.19863	14.51
	Habitat + Size by Habitat	0.857	0.289	0.17016	9
	Years protection + Habitat + Size by Habitat	1.301	0.231	0.17594	10.66
L. atkinsoni	Habitat + Method + Years protection by Habitat	0	0.29	0.10828	12.98
	Habitat + Years protection by Habitat	0.39	0.238	0.09662	10.67
	Habitat + Method + Zoning scheme	1.273	0.153	0.08162	8
EPINEPHELINAE	Years protection + Boat fishing + Method	0	0.196	0.09835	7.81
	Boat fishing + Method	0.516	0.152	0.09171	6.68
	Years protection + Method	1.092	0.114	0.09192	7.24
	Method	1.198	0.108	0.08585	5.88
	Boat fishing + Method + Shore fishing	1.751	0.082	0.09098	7.61
	Boat fishing + Method + Zoning scheme	1.955	0.074	0.09064	7.71
E. rivulatus	**Boat fishing + Method + Zoning scheme**	0	0.546	0.17358	12.31
	Years protection + Boat fishing + Method	1.457	0.264	0.16292	11.96
SCARIDAE	Years protection + Habitat + Size by Habitat	0	0.271	0.12181	16.44
	Habitat	1.354	0.138	0.05738	5
	Years protection + Habitat + Size	1.406	0.134	0.09791	13.04
	Habitat + Zoning scheme	1.698	0.116	0.06077	6
	Habitat + Size by Habitat	1.889	0.106	0.07496	9
	Habitat + Size	1.952	0.102	0.06103	6.28

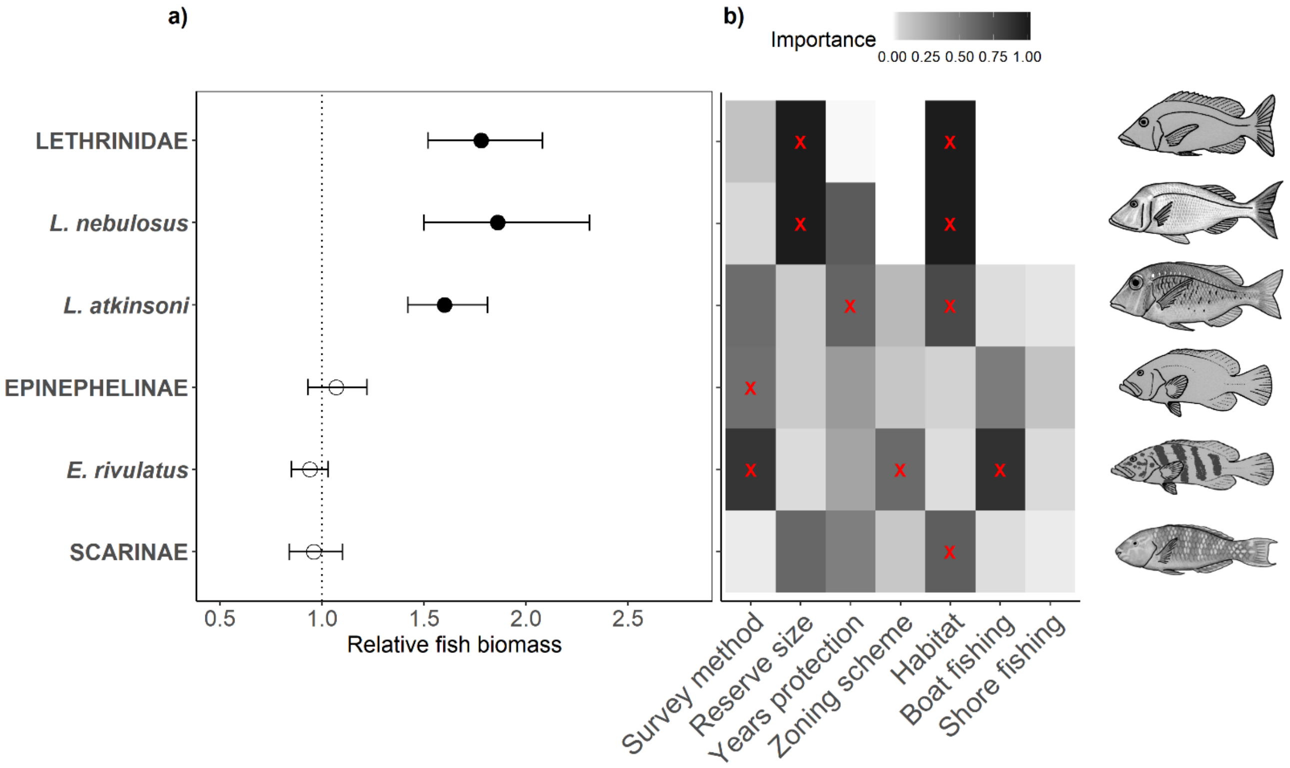


Figure H1. a) Relative fish biomass (Transformed weighted mean effect sizes ($exp(\bar{E})$) with 95% confidence intervals (*CI*)), for the relative abundance of the six fish taxa: Lethrinidae, *Lethrinus nebulosus*, *L. atkinsoni,* Epinephelinae, *Epinephelus rivulatus* and Scarinae. Effect sizes are considered significant when the confidence intervals do not include one. Open dots correspond to non-significant effects. Sample sizes are given in Appendix G. 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. *Reserve size* was square-root transformed and *boat fishing* was log-transformed in all models. Red X symbols mark the variables that were included in the most parsimonious models for each fish taxa (also see Table H1 and Fig. H2).

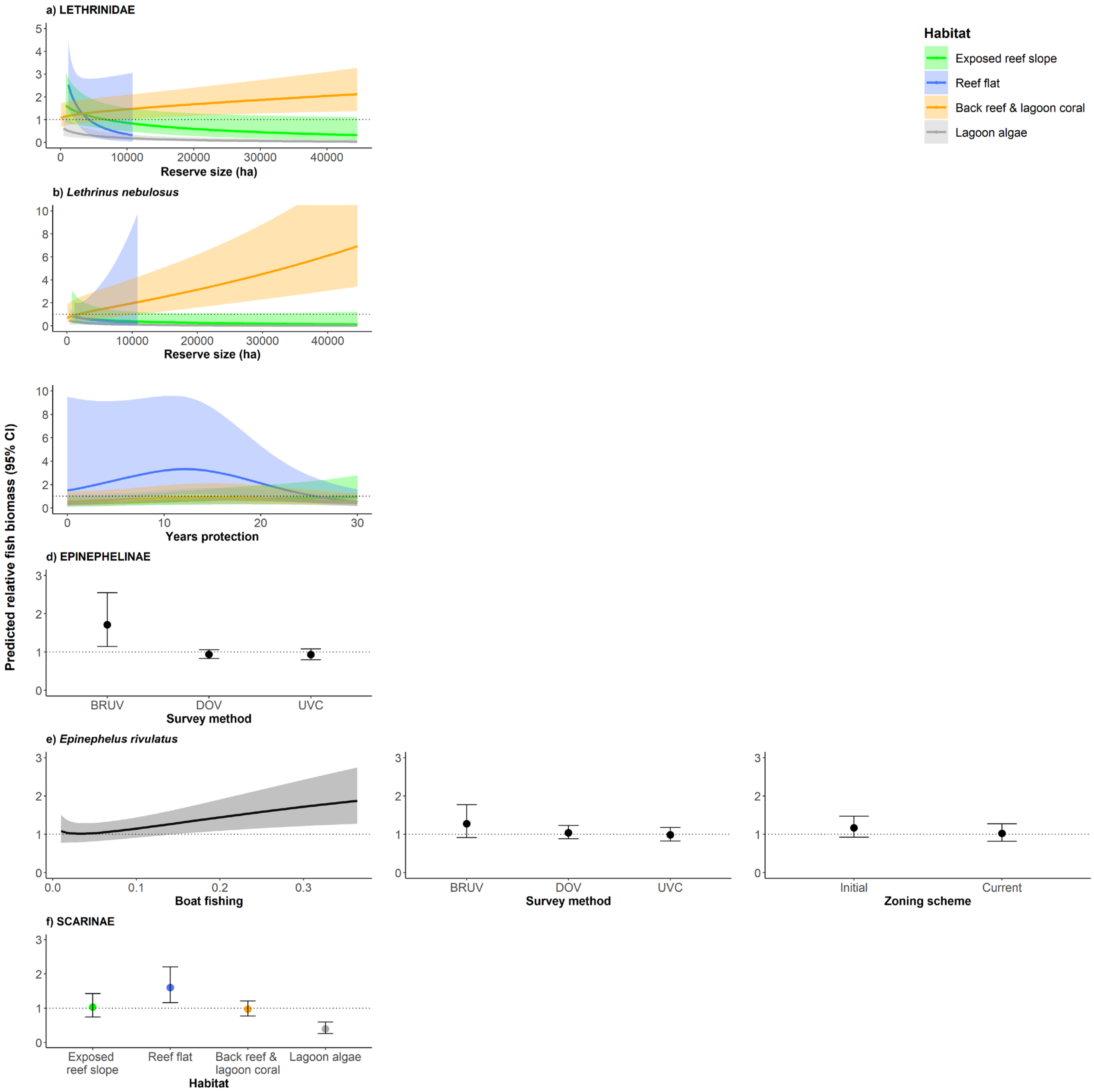


Figure H2. Predicted relative fish biomass inside to outside NTMRs (back-transformed predicted weighted effect sizes) with 95% confidence intervals) for the six fish groups – a) Lethrinidae; b) *Lethrinus nebulosus* c) *Lethrinus atkinsoni;* d) Epinephelinae; e) *Epinephelus rivulatus;* f) Scarinae for abundance– as a function of variables present in the most parsimonious models (Table G4) from full-subsets GAMM analysis. Ribbons represent 95% confidence intervals