A coherent, representative, and bioregional marine reserve network shows consistent change in rocky reef fish assemblages

N. A. KNOTT1, J. WILLIAMS1, D. HARASTI2, H. A. MALCOLM3, M. A. COLEMAN3, B. P. KELAHER4, M. J. REES1, A. SCHULTZ3, AND A. JORDAN2

1Fisheries Research, NSW Department of Primary Industries, Huskisson, New South Wales 2540 Australia
2New South Wales Department of Primary Industries, Port Stephens Fisheries Institute, Taylors Beach Road, Taylors Beach, New South Wales 2316 Australia
3Fisheries Research, NSW Department of Primary Industries, Coffs Harbour, New South Wales 2400 Australia
4National Marine Science Centre and Marine Ecology Research Centre, Southern Cross University, Coffs Harbour, New South Wales 2450 Australia

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Abstract. Worldwide, several countries have established coherent, representative, and large-scale networks of marine reserves to conserve biodiversity. Very few have, however, published systematic assessments of the ecological responses to this network protection, hindering broad understanding of their generality, utility, and efficacy. We present data collected from systematic sampling of rocky reef fish assemblages at sites across a network of 27 no-take marine reserve areas (NTMR) and 27 partially protected areas (PPA) nested within multiple marine parks (regional networks) across three Australian bioregions spanning >1000 km of coastline (7° latitude) to test the generality of ecological change across this network. We also sampled 18 reference areas (outside of the marine parks) to provide an independent assessment of potential NTMR effects and also to assess whole marine park effects. Baited remote underwater video (BRUV) was used to sample fishes between depths of 20–40 m over austral winters in four years (2010, 2011, 2015, and 2016). Despite substantial bioregional differences in fish assemblages, large and consistent effects of NTMR protection were detected across all bioregions for a key commercially and recreationally harvested species, *Chrysophrys auratus* (pink snapper). There were substantial increases in relative abundance of *C. auratus* in NTMR compared with fished zones through time (effect sizes >150%). The wider assemblage of targeted fish (excluding *C. auratus*) only showed relatively small effects of protection (~11%) with trends observed for site-attached wrasses (labrids) and planktivores (e.g., commercially fished *Scorpius lineolata*) that are recreationally and commercially harvested. Furthermore, the relative abundance of non-target or by-catch species generally did not differ among management zones across the bioregional network. These results highlight how NTMR can be used to assess the ecological effects of fishing and wider environmental management, and can be incorporated into ecosystem-based management for reef species more generally. Importantly, the provision of robust evidence of the performance and generality of NTMR over large-spatial scales (e.g., bioregions) provides greater confidence in the expected outcomes from marine reserve networks as a conservation management approach.

Key words: biological diversity; great southern reef; marine protected area; temperate reefs.

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†E-mail: Nathan.Knott@dpi.nsw.gov.au
INTRODUCTION

In response to the documented and perceived degradation of the marine environment (Lotze et al. 2006, 2018, Halpern et al. 2008), most countries around the world are implementing a range of management actions to protect and conserve the biological diversity and social values of these ecosystems (Crain et al. 2009, Spalding et al. 2013, Long et al. 2015). One of the major approaches to conservation management has been the use of marine reserves (Fenberg et al. 2012, Ballantine 2014, Jessen et al. 2017). Signatories to the United Nations Convention on Biological Diversity 1992 (CBD) committed to developing nationally representative systems of marine reserves (specifically referred to as protected areas; Toropova et al. 2010), with each nation aiming to protect at least 10% of their coastal waters by 2012 (Spalding et al. 2008). Despite this, many countries struggled to achieve the 10% protection target (Watson et al. 2014, Spalding and Hale 2016) and the proposed targets were refined and pushed back to 2020 (Aichi Target 11; Spalding et al. 2013, Spalding and Hale 2016).

Several countries have, however, developed representative systems of marine reserves over large sections of their coastlines (e.g., Australia, USA, New Zealand, Mexico, Spain, Italy, France, Portugal, Philippines; Lowry et al. 2009, Fenberg et al. 2012, Horigue et al. 2012, Gleason et al. 2013, Ballantine 2014, Batista and Cabral 2016, Fitzsimons and Wescott 2016, Jessen et al. 2017). Recently, the importance of coherence of marine reserve networks within and among jurisdictions has been highlighted (Gleason et al. 2013, Johnson et al. 2014, Batista and Cabral 2016). Coherent marine reserve networks are strategically designed systems of multiple no-take marine reserves (NTMR; i.e., IUCN II or higher classification; Dudley 2008) and partially protected areas (PPA; i.e., IUCN III; Dudley 2008) placed along a coastline to representatively conserve species and habitats with consistent management approaches (e.g., regulations, planning, enforcement, education; Grorud-Colvert et al. 2014). This coherent design and management sets them apart from “ad hoc or regional” marine reserve networks (Grorud-Colvert et al. 2014). Despite the significant resources required to establish and manage coherent networks of marine reserves, there are very few published assessments of the ecological responses to such comprehensive protection (Ahmadia et al. 2015, Addison et al. 2017, Gill et al. 2017).

As a major aim of the UN Convention on Biological Diversity is to have nationally representative systems of reserves, ideally an entire network of marine reserves should be assessed rather than as individual reserves (Gaines et al. 2010, Guidetti et al. 2014, Batista and Cabral 2016). Providing whole network assessments have several potential benefits. Firstly, the generality of marine reserves has often been assessed via meta-analyses of data from studies generally consisting of single pair comparisons of marine reserves and control (reference) sites, and often include studies with major differences in sampling technique, study design, and replication, while the studied reserves themselves may be very different from one another in terms of design, enforcement, management, jurisdiction, and social license (Halpern and Warner 2002; Halpern 2003; Micheli et al. 2004; Claudet et al. 2008; García-Charton et al. 2008; Stewart et al. 2009; Fox et al. 2014; Haddaway and Rytwinski 2018). Carrying-out whole coherent network assessments using standardized methods, however, avoids many of these confounding issues (Barrett et al. 2007, Edgar et al. 2009, Edgar and Barrett 2012). Secondly, whole network assessments provide an opportunity to better gauge the generality of ecological change associated with reserves and quantify spatial variation in these changes over large-spatial scales. This is particularly important in the meta-analysis context, where publication bias may lead to overestimating the effects of marine reserves or their consistency (Claudet et al. 2008, Molloy et al. 2009, Caveen et al. 2012). Thirdly, the use of consistent survey methods, reserve design, and management arrangements in a whole network assessment facilitates the unconfounded assessment of ecological changes across bioregions or latitude. To date, assessments of changes in biodiversity across coherent, large-scale networks of marine reserves have only been made in a few places worldwide (Gaines et al. 2010, Grorud-Colvert et al. 2014, Addison et al. 2017), such as the Great Barrier Reef Marine Park (Mapstone et al. 2004, Russ et al. 2008, Heupel...
et al. 2009, McCook et al. 2010, Emslie et al. 2015) and the Californian Marine Protected Area network (Hamilton et al. 2010, Caselle et al. 2015). Other than these examples, the assessment of the generality of effects across coherent networks of marine reserve has been limited and further investigation is timely (Grorud-Colvert et al. 2014, Ahmadia et al. 2015). It should be noted that there have been several excellent large-scale assessments of regional or ad hoc marine reserves across wide ranging regions; however, these studies have involved sampling reserves with a wide variety of management approaches and jurisdictions which are not coherent and are not managed as consistent networks (e.g., Tetreault and Ambrose 2007, Edgar et al. 2009, 2017, Edgar and Stuart-Smith 2009, Edgar and Barrett 2012, Guidetti et al. 2014).

A coherent network of marine reserves has been established on the temperate-subtropical southeast coast of Australia following the signing of the CBD by the Australian federal government and its subsequent adoption of the Australia’s Ocean Policy (Commonwealth of Australia 1998a, b, NSW Fisheries et al. 2001). The east coast state of New South Wales (NSW) initially implemented two marine parks (i.e., Solitary Islands Marine Park and Jervis Bay Marine Park; Fig. 1) in 1998 and four more marine parks were added to form the current NSW state marine reserve network over the following decade (see NSW Fisheries et al. 2001, Read and West 2010, Coleman et al. 2015 for further details). The primary purposes of this network of bioregional marine reserves were to protect biological diversity and maintain ecosystem integrity and function, complemented by a number of secondary purposes to provide for social, cultural, economic, and wider environmental values (Marine Estate Management Act 2014; https://legislation.nsw.gov.au//view/act/2014/72).

The NSW state marine reserve network covers a third of the state’s coastal waters and three of its mainland marine bioregions—spanning 7.9° of latitude (from S28.5° to S36.4°)—covering the warmer subtropical waters of the north of the state to the cooler temperate waters in the south (Fig. 1). Each marine park is composed of a sub-network of replicated NTMR and PPA which representatively include each major habitat type (e.g., rocky reef, seagrass, mangroves, soft sediments; as per the Comprehensive, Adequate and Representative [CAR] principles; NSW Fisheries et al. 2001, Breen et al. 2004, 2005, Banks 2010). The greatest level of protection is provided by Sanctuary Zones (IUCN protected area category II; Dudley 2008; referred to herein as no-take marine reserves, NTMR), where human disturbance is kept to a minimum and it is not permitted to take or harm marine life. NTMR, which represent 6% of the NSW state coastal waters, were often established adjacent to terrestrial national parks and have been sited adjacent to catchments with limited anthropogenic disturbance. Generally, each of the NTMR on the open-coast is relatively large and cover 2–6 km of coastline, with the majority including areas of rocky reef, the extent of which were defined through high-resolution multi-beam acoustic mapping (Jordan 2010). Other major zones are Habitat Protection and General Use Zones (IUCN protected area category VI; Dudley 2008) which permit recreational and many forms of commercial fishing, where the management aim is to allow extraction while minimizing damage to the habitat. These areas were also generally sited adjacent to terrestrial national parks and catchments with limited anthropogenic disturbance. These zones will be referred to herein as partially protected areas (PPA). As the marine parks have compliance officers to enforce the regulations of the marine parks (Kelaher et al. 2015a, but see Harasti et al. 2019), NTMR and PPA effectively represent medium- and large-scale manipulation of human extractive activities (Walters and Holling 1990, Micheli et al. 2004).

Here, we quantify and assess the changes in reef fish assemblages through time across three bioregions within a coherent, representative, and large-scale network of marine reserves. Specifically, we compare the relative abundance and diversity of target and non-target fish species on rocky reefs in NTMR and PPA across much of the NSW state marine reserve network over a six-year time span. Additionally, comparisons were made with external reference areas (REF) located well outside marine parks (generally >10 km). Reference areas provided a counterfactual from which the effects of marine park management can be assessed (both NTMR and PPA) and enabled better interpretation of NTMR responses, while also providing a background
assessments of the state’s rocky reef fish assemblages under general management regulations (e.g., for fishing, pollution, and habitat protection). We sampled fish associated with rocky reefs as they are one of the main components of the biological diversity likely to be affected by marine park management on the open coast, as recreational and commercial fishing are the main human activities directly and consistently managed and prohibited within the NTMR in these environments.

The general prediction we evaluated was that abundances of targeted fish species would increase if significant levels of stressors were reduced by marine park management (i.e., harvesting). This may occur between (1) no-take (NTMR) and fished zones (PPA) within the marine parks (i.e., NTMR > PPA: a zone effect within the marine parks); (2) no-take (NTMR) and fished zones within and outside of the marine parks (PPA + REF) (i.e., NTMR > PPA = REF: a reserve effect but no partial protection effect); (3) as a gradient from no-take to fished areas within the marine parks to fished areas outside of the marine parks (i.e., NTMR > PPA > REF: a reserve and a marine park effect); or (4) only...
between areas inside (NTMR + PPA) and outside (REF) of the marine parks (i.e., NTMR = PPA > REF: a whole marine park effect). Importantly, we predicted that these potential responses would increase in magnitude through time for targeted species, and the effect sizes would vary among bioregions but would show the same proportional responses among zones.

**METHODS**

We sampled 72 rocky reef sites representatively covering the >1000 km of NSW coastline (7° latitude; S29.5°–S36.5°) and most of the mainland NSW state marine reserve network (including four marine parks across three bioregions). The four marine parks (Fig. 1) were Solitary Islands Marine Park (SIMP: zoning commenced August 2002; Tweed-Moreton bioregion abbreviated to Tweed herein); Port Stephens-Great Lakes Marine Park (PSGLMP: zoning commenced April 2007; Manning bioregion); Jervis Bay Marine Park (JBMP: zoning commenced October 2002; Batemans bioregion); and Batemans Marine Park (BMP: zoning commenced October 2008; Batemans bioregion). The NTMR and PPA are representatively distributed in a mosaic throughout each marine park, creating a smaller nested scale network within each marine park. Both of these marine park management zones were generally adjacent to terrestrial national parks and to catchments with limited anthropogenic disturbance.

Fish assemblages were sampled using the non-destructive technique of baited remote underwater video (BRUV; Cappo et al. 2001, Malcolm et al. 2007, Harasti et al. 2015b) on rocky reefs between the depths of 20–40 m. BRUV is a commonly used method to survey fish communities when other methods are unsuitable due to bottom type (e.g., trawl), depth (e.g., SCUBA), or management zone (e.g., no destructive sampling permitted), and Australian standard operating procedures were used (Langlois et al. 2020). We targeted this habitat and depth range as it is the focus of much of the boat-based fishing along the NSW coastline (Lynch 2006, Stewart 2011). We sampled 27 NTMR sites (no-take areas within marine parks), 27 PPA sites (fished areas within marine parks), and 18 REF sites across representative sections of the NSW coastline outside of the marine park systems (external references areas). We considered these sites and zones to be effectively haphazardly placed along the NSW coastlines as they were selected as representative areas within each bioregion and management type along the NSW coastline.

Little information is available on the relative intensity of recreational fishing in PPA, except in the SIMP, where aerial surveys revealed similar fishing intensity among PPA throughout the marine park (NSW Marine Parks Authority 2009). High-resolution mapping of the majority of survey locations (Jordan et al. 2010, Rees et al. 2014) indicates few systematic differences in habitat structure or benthic topography among the marine park zones (Jordan et al. 2010, Rees et al. 2014). Analyses of within video mean relief scores from the rocky reefs (a habitat complexity metric; McLean et al. 2016) indicated that they were very similar among zones (Appendix S1: Fig. S1), although there was slightly lower relief in the REF sites. Similarly, macroalgal cover estimates (measured as per McLean et al. 2016) were similar among zones in the Tweed and Batemans bioregions (Appendix S1: Fig. S1), but was slightly lower in NTMR than the other zones in the Manning bioregion. These differences were relatively very small and considered unlikely to have significant effects on the rocky reef fish assemblages. The similarities of the habitats among zones were expected as all zones within marine parks were initially chosen to be representative of the variety of habitats in the region, although there was generally little available information on diversity, abundance, or sizes of reef fish or habitat structure.

Sampling of the NSW state marine reserve network commenced in the austral winter of 2010 (PSGLMP and BMP zoning plans were 2–3 yr old, and SIMP and JBMP zoning plans were 8 yr old) and then re-sampled in the winter of 2011 to provide a state-wide base from which to assess contemporary ecological patterns, and provide a baseline to assess potential ongoing changes associated with marine park management at a state-wide level. This two-year sample is referred to as period 1. Sampling was re-commenced in the austral winter of 2015 and then again in 2016 and is referred to as period 2. A change related to the marine park management was tested by the
main interaction of period (period 1 and 2) and zone (NTMR vs PPA vs REF). This assessment enabled tests for changes in NTMR despite having all been in place for several years, as any intrinsic differences would not be expected to change differentially through time (e.g., habitat complexity or habitat quality); hence, an increase in fish abundance in the NTMR relative to the other zones could only be attributed to the management action itself.

In each round of sampling, rocky reef fishes at each site were sampled using four simultaneously deployed BRUV units baited with ~500 g of chopped pilchards (*Sardinops sagax*). Each BRUV was deployed on the seafloor for a minimum of 30 min (Harasti et al. 2015a) and was generally separated by 200 m. In each marine park, the number of sites sampled within each zone (NTMR and PPA) varied due to differences in the size of each park, the numbers and sizes of the zones, and availability of suitable rocky reef (Fig. 1): SIMP, NTMR = 6, PPA = 6; PSGLMP, NTMR = 5, PPA = 5; JBMP, NTMR = 4, PPA = 4; and BMP, NTMR = 12, PPA = 12. External reference areas were sampled along sections of the coast between each marine park (REF sites = 3, 3, 4, 4, 4, respectively; Fig. 1) from north to south. These random and nested samples were collected from the same sites in each year of sampling. Also, haphazard and interspersed sampling of management zones was completed to avoid any temporal biases.

Each BRUV unit was constructed as per Malcolm et al. (2007) and SEAGIS (2017), which included a galvanized metal frame containing a video camera (mini DV SONY or digital Canon HG21) pointed at a bait bag mounted horizontally at the end of a 1.5 m long bait arm. Cameras were housed within high-pressure polyvinyl chloride pipe with flat acrylic endpoints yielding a field of view of 110°. Videos of 30-min duration were analyzed using a field of view of 5 m distance from the camera either estimated visually (i.e., with single camera BRUV units) or through stereo-camera measurement (i.e., with stereo-camera BRUV units). For each replicate BRUV deployment, we determined the maximum number of individuals of a particular species in any frame at any point in time, Max N; the total Max N was the sum of Max N for each species (Cappo et al. 2004). Both are estimates of relative abundance that are considered appropriate for BRUV video analyses because they avoid problems associated with counting the same individual fish more than once and correlate well with fish abundances measured via other methods (Willis et al. 2000).

Generalized linear mixed modeling (GLMM) was used to analyze the potential patterns among management zones through time (i.e., periods) and across bioregions. GLMMs were used due to the spatial and temporal structuring of the sampling design, and also because of the unbalanced design and the large number of zeros for many species (Bolker et al. 2009, Zuur et al. 2012). To enable inferences between main effects and interactions an a priori model including the fixed factors zone, bioregion and period was fitted to a suite of response variables. Analyzed response variables included the relative abundance of recreationally and commercially targeted species (e.g., *Chrysophrys auratus* (Sparidae), *Nemadactylus douglasi* (Cheilodactyliidae), *Meuschenia freycineti* (Monacanthidae), *Ophthalmolepis lineolatus* (Labridae); Stewart 2011; Appendix S1: Table S1), all targeted species (as a group; Appendix S1: Table S1) and all non-target species. Targeted species (Appendix S1: Table S1) were defined as those species with a recreational bag or size limit or were reported in the NSW trap and line fishing assessments (West et al. 2015, NSW DPI 2018). All other species were distinguished as non-targeted. To account for spatial autocorrelation and replicate BRUV deployments, we treated “site” as a random factor. Data were pooled across years within each period (1, 2010 + 2011; 2, 2015 + 2016). Generally, plots of estimated means and 95% confidence intervals were provided for period, bioregion, and zone and for some analyses as relevant two-way interactions or main effects in line with the a priori predictions and to allow the generality of any effects to be assessed.

Models were first fitted using a Poisson distribution (the exception being species richness that was fitted using a Gaussian distribution), and the residuals were checked for overdispersion, outliers, and heterogeneity. If a model was considered overdispersed, then the data were explored to determine what factors were driving the overdispersion. If the overdispersion was deemed to be real as in expected outliers or zero
inflation, then the model was re-run with a negative binomial distribution (Zuur et al. 2012). Negative binomial models were run multiple times adjusting the theta value until the deviance and residual degrees of freedom were close to one. In extreme cases, when the negative binomial model was still overdispersed due to zero inflation, models were fitted with a Tweedie distribution using the cplm package (Zhang 2013).

All GLMMs were run using the lme4 package in R (Bates et al. 2015). The emmeans and broom packages were then used to obtain the back-transformed model estimates with 95% confidence intervals for plotting (Robinson and Hayes 2018, Lenth 2019). The lme4 package does not provide p-values as they are deemed unreliable (Bates et al. 2015, http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html). Therefore, inferences were made from the model estimates and the level of uncertainty derived from the 95% confidence intervals that were visualized using plots. Model outputs are provided in the Appendix S1: Table S2.

To examine patterns in species assemblages, we used redundancy analysis (RDA). RDA is related to principal components analyses and is based on Euclidean distance, implying that each species is on an axis orthogonal to all other species, and sites are points in this multidimensional space (Borcard et al. 2018). Schooling species Atypichthys strigatus, Trachurus novaezelandiae, Scorps lineolata, and Chromis hysilepis occurred frequently in very large abundances and may have obscured patterns for the whole assemblage. Hence, analyses were run with and without these species to assess their influence. All species data were Hellinger transformed before doing a forward stepwise model selection using a suite of explanatory factors (bioregion, zoning, and period) to select the factors that best explained the dissimilarity in the species assemblage. The function ordiR2step from the Vegan package in R was used to select the most parsimonious model (Oksanen et al. 2019). Permutation tests were used to test for the statistical significance of each marginal term. A triplot was used to display the strength of the relationships between species assemblage and the explanatory factors that underpin the variation in species assemblage among BRUV deployments.

**RESULTS**

Targeted fish species, as a group, showed increases in relative abundances between no-take marine reserves (NTMR) and fished areas across the two time periods (PPA, REF; Fig. 2a). Chrysophrys auratus (pink snapper) was the main species driver for the effect on targeted species (Fig. 2b).

Chrysophrys auratus increased in the NTMR through time relative to the PPA and REF areas (Fig. 2b), and also showed strong bioregional patterns in abundance (Fig. 2b). This species was most abundant in the Manning bioregion (central; Figs. 1, 2b), followed by the Tweed bioregion in the north (Figs. 1, 2b), while the abundances were much smaller in the southern Batemans bioregion (Figs. 1, 2b). There was also substantial variation in the relative abundance of C. auratus among sites (indicated by large confidence intervals around some of the modeled estimates; Fig. 2b), but despite this and the bioregional differences, there were relatively clear effects of the NTMR in each bioregion (Fig. 2b, Table 1). At the bioregional level, C. auratus exhibited substantial relative increases in the NTMR in the Tweed and Batemans bioregions through time (Fig. 2b, Table 1). In the Tweed bioregion, C. auratus increased by 56% between period 1 and period 2 within the NTMR, while there were no significant increases in the fished areas within or outside of the marine parks (Fig. 2b). A similar effect size for C. auratus was observed in the Batemans bioregion with an increase of 68% in the NTMR, while in the fished areas (PPA and REF), the relative abundance of C. auratus remained similar or decreased across the two time periods (Fig. 2b). The Manning bioregion also had greater relative abundance of C. auratus in NTMR compared with PPA and REF (Fig. 2b). There was, however, no significant difference between periods for the abundance of C. auratus and a possible trend toward a reduction in C. auratus within its no-take reserves (i.e., a 14% decrease). Overall, each bioregion displayed strong effects in relation to NTMR protection for C. auratus, and in two of the three bioregions, this effect continued to increase through time.

Examining the targeted species, with C. auratus excluded, indicated that they were showing an
increase in the NTMR sites relative to the fished areas (Fig. 2c). This effect, however, was much smaller in magnitude than observed for *C. auratus*. The modeled estimates indicated that there was a small increase in the relative abundance of the other targeted species in NTMR compared with the fished areas between the two time periods (Fig. 2c). The magnitude of the general effect was a relative increase of 11% more targeted fish in NTMR than in fished areas. A range of species contributed to this relatively small effect, and all exhibited bioregional variation. Several targeted labrids showed NTMR trends: *Ophthalmolepis lineolatus* (target and also a common by-catch species) tended to only have higher abundances in NTMR in the Manning bioregion (Fig. 3a), but not elsewhere; *Bodianus unimaculatus* was mainly recorded in the Batemans and Manning bioregions (Fig. 3b) and showed a trend of increasing abundance in the NTMR compared with the fished areas; and the large bodied *Achoerodus viridis* displayed a trend toward becoming more abundant in NTMR than in PPA across the bioregions (Fig. 3c), but showed little change in relation to external references areas (REF, Fig. 3c). Targeted cheilodactylids displayed no clear
pattern with \textit{Nemadactylus douglasii} showing a NTMR response in the Tweed bioregion but not in the other bioregions (Fig. 3d) and \textit{Cheilodactylus fuscus} exhibited no zone related patterns (Fig. 3e). Monacanthids (leatherjackets), which are commonly targeted, were not consistently different among zones in any bioregion (Fig. 3f). \textit{Scorpaena jacksoniensis}, another common by-catch species, displayed no consistent patterns of abundance across the management zones (Fig. 3g). Several other common species and groups revealed little consistent differences among zones across bioregions (Appendix S1: Fig. S2). Furthermore, the non-targeted species in the fish assemblages also displayed no patterns of abundance that would be consistent with an effect of NTMR (Fig. 3h).

Examining the fish functional groups more widely revealed little further detail with most groups showing no influence of zoning at this level (Appendix S1: Fig. S3). The carnivorous fishes were the obvious exception; however, this effect was driven by \textit{Chrysophrys auratus} and to a lesser degree some of the targeted labrids (Appendix S1: Fig. S3a, Table S2). Planktivores provided an interesting scenario—at the species level—where \textit{Scorpius lineolata} showed a trend of greater relative abundance in NTMRs than in fished areas, while \textit{Trachurus novaecelandiae} and \textit{Atypichthys strigatus} showed the alternate pattern of being more abundant in the fished areas inside (PPA) and outside (REF) of the marine parks (Fig. 4). Clearly, there was substantial variation among sites (Fig. 4) within each management zone; however, this trend is worthwhile noting and considering further.

There was no apparent effect on the diversity of fish assemblages, as measured by species richness, among zones (Fig. 5a,b). Redundancy analysis on the whole assemblage showed strong bioregionalization and a comparatively subtle influence of management zone (Fig. 6), but with the removal of \textit{C. auratus} from the assemblage the zone influence was diminished greatly. The bioregional differences across the state continued to be clear (Fig. 5a) with the greatest levels of diversity found within the Manning bioregion which is in the central region of the state’s coastline (Fig. 1). Despite the strong bioregionalization, there was no indication of spatial structuring of species richness by management zone as they were well interspersed across the species richness rankings for sites (Fig. 5b). The lack of differences through time indicates that the levels of species diversity at relatively small spatial scales (i.e., per BRUV deployment) appear to be maintained currently across all management zones (Fig. 5a).

\section*{Discussion}

This study presents a rare empirical demonstration of change in rocky reef fish assemblages across a coherent, representative, and large-scale marine reserve network. Clear bioregional patterns existed in the fish assemblages sampled

\begin{table}[h]
\centering
\begin{tabular}{|l|c|c|c|c|c|c|c|c|}
\hline
\textbf{Bioregion} & \textbf{MaxN} & \textbf{Effect size (\%)} & \textbf{Log-effect size ratio} \\
\hline
\textbf{Manning\textsuperscript{†}} & NTMR & Fished & PPA & REF & NTMR vs Fished & NTMR vs PPA & NTMR vs REF & NTMR vs Fished & NTMR vs PPA & NTMR vs REF \\
\hline
\textbf{Tweed\textsuperscript{‡}} & 8.0 & 5.9 & 3.0 & \_ & 36 & 164 & \_ & 0.31 & 0.98 & \_ \\
\hline
\textbf{Period 1} & 4.7 & 1.8 & \_ & \_ & 155 & \_ & \_ & 0.8 & \_ & \_ \\
\textbf{Period 2} & 7.3 & 2.4 & \_ & \_ & 202 & \_ & \_ & 1 & \_ & \_ \\
\textbf{Batemans\textsuperscript{‡}} & 1.3 & 0.9 & \_ & \_ & 42 & \_ & \_ & 0.75 & \_ & \_ \\
\textbf{Period 1} & 2.2 & 0.6 & \_ & \_ & 255 & \_ & \_ & 1.2 & \_ & \_ \\
\textbf{Period 2} & \_ & \_ & \_ & \_ & \_ & \_ & \_ & \_ & \_ & \_ \\
\hline
\end{tabular}
\caption{No-take marine reserve effects for \textit{Chrysophrys auratus} across the NSW network.}
\end{table}

\textbf{Notes:} Dashes indicate that no values were presented.
Relative abundances (MaxN), % effect sizes, and log-effect ratios for \textit{C. auratus}. Abbreviations are NTMR, no-take marine reserve; PPA, partially protected area; REF, external reference area.
\textsuperscript{†} The Fished treatments were statistically different for the Manning bioregion; hence, the PPA and REF means were both presented.
\textsuperscript{‡} There was no statistical difference between PPA and REF, and hence, the mean Max N values for these treatments were pooled.
over 1000 km of the NSW coastline covering more than 7° latitude and 3 coastal bioregions. Importantly, we were able to detect clear and consistent effects of marine reserve protection across multiple bioregions on a key targeted species, *Chrysophrys auratus* (pink snapper). Despite the substantial bioregional differences in the relative abundance of this species, there were clear differences in no-take marine reserves (NTMR) compared with fished areas within and
outside of marine parks (PPA and REF respectively). In two out of three bioregions (Batemans and Tweed), there were substantial increases in *C. auratus* relative abundance in NTMR compared with fished areas through time. This is noteworthy as it indicates that no intrinsic differences in the sites (e.g., reef structure) could explain the increase in abundance, other than protection of NTMR itself, as any other potential explanations for differences among zones would be unlikely to change differentially (i.e., only at the NTMR) through time (Caselle et al. 2015). While at the third bioregion (Manning), there was a general pattern consistent with a NTMR effect through time. It is important to appreciate that the effects of marine reserve protection can, alternatively, be considered as indicating a clear

Fig. 4. Trends in relative abundance patterns for planktivores on NSW rocky reefs compared among management zones. Model means and 95% confidence intervals are shown for zone as a main effect. Pink indicates NTMR; yellow, PPA; and blue, REF.

Fig. 5. Mean fish species richness per site on NSW rocky reefs across management zones and bioregions. (a) Model estimates and 95% confidence intervals for species richness; and (b) species richness at sites ordered from highest to lowest. Pink indicates NTMR; yellow, PPA; and blue, REF.
and measurable impact of recreational and commercial fishing. This is because the main human activity that is modified or managed by NTMR on open coastal rocky reefs is fishing activity. The positive side of this assessment is that only relatively small differences (or weak effects) were detected between NTMR and fished areas for the wider suite of targeted species (excluding *C. auratus*), and there were no apparent wider or indirect effects on non targeted fish species.

*C. auratus* stocks have shown signs of being under considerable pressure (West et al. 2015) as they have been previously assessed as growth overfished (Stewart 2015c, although currently considered to be sustainable: Fowler et al. 2018b, Wortmann et al. 2018) and have had a truncated age structure (i.e., fewer older fish in population than expected; Stewart 2011). Considering this pressure and their residency patterns (Willis et al. 2001, Parsons et al. 2003, Harasti et al. 2015a, Stewart et al. 2019), it is not surprising that this species showed the clearest response to NTMR protection. The consistency of the relative differences and log effects size ratios among bioregions (Table 1) indicates that the NTMR effects for *C. auratus* are general and profound across the state’s coastline, despite the substantial differences in the absolute MaxN values among bioregions. Considering longer periods of time, the changes in the relative abundance of *C. auratus* reported here in this time series reflects the general patterns quantified within specific marine parks across the state (Kelaher et al. 2014, 2015b, e.g., Malcolm et al. 2015a, b, 2018, Harasti et al. 2018a, b) and/or show a maturing of initial patterns (Kelaher et al. 2014, Coleman et al. 2015). Internationally, similar effects of protection have been observed for *C. auratus* in several marine reserves in New Zealand where it is also a dominant species on subtidal rocky reefs (Babcock et al. 1999, Willis et al. 2003, Denny et al. 2004, Smith et al. 2014, Schiel et al. 2018, Appendix S1: Table S3). The New Zealand effect sizes were, however, either similar (Appendix S1: Table S3; Willis et al. 2003) or even larger (Appendix S1: Table S3; Babcock et al. 1999, Denny et al. 2004, Smith et al. 2014) than those observed in the current study (Table 1). This wider context indicates that these NTMR effects are temporally and spatially consistent, both nationally and internationally.
A potential positive from the current study was the relatively small apparent effect of NTMR protection on the wider assemblage of targeted fish species (excluding *C. auratus*) across the NSW coastline. This may indicate that fishing mortality for these species is insufficient to result in measurable differences over the time scales of the current study; or alternatively, aspects of their life-history of these species (e.g., roaming over large-spatial scales; Brodie et al. 2018) may reduce the potential for abundances to increase at the scale of marine park zones. The effect size for the target species (excluding *C. auratus*) was approximately 11% fewer fish in fished areas than NTMR. Several groups appeared to be responsible for this response: labrids (e.g., *Ophthalmolepis lineolatus*, *Bodianus unimaculatus*, *Achoerodus viridis*) and the planktivore, *Scorpa lineolata*. Although the effects were generally small or inconsistent across bioregions, these groups and species should be highlighted for future monitoring to assess any further declines and the potential need for further management action. For labrids, the NTMR effects are most likely to due to recreational and commercial fishing interest in these species in NSW waters (Stewart 2011, Stewart et al. 2015, West et al. 2015) and the likelihood of high levels of residency of labrids over small spatial scales on rocky reefs (Barrett 1995, Edgar et al. 2004, Kingsford and Carlson 2010, Lee et al. 2015). An intriguing pattern appeared with the gregarious reef species, *Scorpa lineolata*, which are targeted by commercial and recreational fishers (Stewart and Hughes 2005, West et al. 2015), as it showed higher relative abundance in NTMR than in fished areas. Commercial landings of this species have declined substantially through time (Stewart and Hughes 2005, Stewart et al. 2015) and this species can live for >50 yr (Stewart and Hughes 2005). Furthermore, there was a trend for the other major planktivores—*Atypichthys strigatus* and *Trachurus novaelandiae*—where they had higher abundances in fished areas than NTMR. The contrasting patterns for these species seemed to support anecdotal reports from commercial fishers that local depletion of *S. lineolata* at certain locations along the NSW coastline had resulted in increases in abundances of *A. strigatus* (Stewart and Hughes 2005) and presumably *T. novaelandiae* (as observed in our study). Closer attention may be needed to monitor the abundances of these species in future to determine whether these effects increase or diminish through time.

In this state-wide comparison, there were no obvious or consistent responses to NTMR protection for a range of other targeted species (West et al. 2015), such as *Nemadactylus douglasii*, *Cheilodactylus fuscus*, and various monacanthids which are (or are likely to be) resident species on NSW rocky reefs (Barrett 1995, Lowry and Suthers 1998, Edgar et al. 2004, Curley et al. 2013, Stewart et al. 2015). *Nemadactylus douglasii* is assessed as a depleted stock (Stewart et al. 2018), and a stock rebuilding plan is to be developed for this species (Stewart and Hughes 2009, Stewart 2015a, NSW DPI 2018); and *Cheilodactylus fuscus* have been observed to often respond to NTMR protection (Barrett et al. 2008, Coleman et al. 2013, Malcolm et al. 2015). In this study, however, the estimates of relative abundance for these species were very similar among zones across most of the bioregions (the only exception being *N. douglasii* in the Tweed bioregion, Fig. 3; and see Malcolm et al. 2018). Similarly, the by-catch species, *Scorpaena jacksoniensis* (Stewart and Hughes 2010), which we suspect are also likely to be highly site-attached, showed no consistent large-scale effects. The consistency of the patterns among zones and/or the similarity of the estimates over the time suggest that this study provides robust estimates of relative abundance for these species. Furthermore, the high level of temporal and spatial replication in this study covering four replicate times and 27 NTMR, 27 PPA, and 18 REF sites indicates that this study should provide robust estimates of relative abundance for these species across the NSW coastline. Hence, we are confident that there appears to be no large-scale, consistent effects of fishing for these species on intermediate reefs (i.e., 20–40 m) along the NSW coastline.

Several commonly targeted species are, however, difficult to assess in relation to NTMR protection due to not being well sampled by our technique (BRUVs) or their movement patterns covering spatial scales much larger than the NTMR. For example, it is possible that *Pseudocaranx georgianus* is likely to move over large areas (Fowler et al. 2018c), much greater than that covered by the NTMR and our estimates of...
their abundances were highly variable and patchy. Nonetheless, the larger marine park scale (as opposed to NTMR alone) may offer protection at an appropriate scale for species such as *P. georgianus* based on the spatial scales over which they move (Fowler et al. 2018a). This species is considered depleting (Fowler et al. 2018a) and could potentially be protected from trawling (Stewart 2015b) within marine park boundaries. Several other species were highly variable, relatively patchy or rare and hence were difficult to assess such as *Rhabdosargus sarba*, *Acanthopagrus australis*, and *Girella tricuspidata*. Also, the reefs sampled here are likely to be too deep and not the core habitat for these targeted species (Kingsford et al. 1991, Kingsford 2002, Curley et al. 2013, Ferguson et al. 2016).

Non-targeted species showed no NTMR effects which potentially may indicate that fishing was not having wide ranging ecological effects on rocky reef fish assemblages either as a result of by-catch or indirect effects (i.e., alterations in the abundances of target species affecting the abundance of non-targeted species via release from competition or predation). Generally, in marine reserve comparisons, non-target species have been found to be unaffected by fishing on temperate reefs (Micheli et al. 2004, Tetreault and Ambrose 2007, Hamilton et al. 2010, Guidetti et al. 2014). It has been argued, however, that these sorts of effects may take long periods of time to develop due to a series of indirect effects that may need to take place and/or due to variable, infrequent, or low levels of recruitment (Babcock et al. 2010). This should be considered and care should be taken to look for signals of potential effects (or recovery, which would indicate an earlier effect), but many of the marine park management rules have been long established (14 yr for SIMP and JBMP) so it may be expected that patterns would have become clear by now. Nonetheless, the issue of shifting baselines (Pauly 1995, Roberts 2007, Clark 2017) can make it difficult to discern whether large-scale changes may already have occurred within these marine environments.

Despite the potential issues surrounding NTMR meta-analyses, it would appear that many of the findings of the current study are consistent with the large-scale meta-analysis findings. Meta-analysis studies have generally found strong effects of NTMR on rocky reef fishes (Mosquera et al. 2000, Côté et al. 2001, Halpern and Warner 2002, Halpern 2003, Micheli et al. 2004, Guidetti and Sala 2007, Claudet et al. 2008, Lester et al. 2009, Stewart et al. 2009, Giakoumi et al. 2017). The current study involving the systematic surveying of rocky reef fishes over large-spatial scales across a coherent network of marine parks also supports these general findings of major effects associated with NTMR. Nonetheless, meta-analyses have consistently reported substantial variation among locations and studies in NTMR effects (Côté et al. 2001, Guidetti and Sala 2007, Claudet et al. 2008, Stewart et al. 2009). Despite the substantial variation in relative abundances among bioregions observed in the current study, the relative effects (and effect size ratios) were generally very similar. In large part, this variation in relative abundance is expected in the fish assemblages and species abundances across latitudes, but as observed in many meta-analyses the relative effects of NTMR indicate that latitude has little to no influence on the relative effects of NTMR (Côté et al. 2001, Lester et al. 2009, Stewart et al. 2009) and the responses were remarkably consistent, as they were in our study. Meta-analysis studies have generally found that effects only occur for targeted fish species, and few indirect effects have been observed for non-target fish species (Mosquera et al. 2000, Côté et al. 2001, Micheli et al. 2004, Claudet et al. 2008). The same results were also found in our study. Similarly, we observed no effects of NTMR on fish diversity, which was relatively consistent with Lester et al. (2009); however, contradicted the findings of several other meta-analysis studies which observed effects on diversity (Côté et al. 2001, Halpern 2003, Stewart et al. 2009). Intriguingly, most meta-analyses have observed no effects of PPA on fishes (Denny et al. 2004, Lester and Halpern 2008, Guidetti et al. 2014, Lubchenko and Groot-Verlent 2015, Giakoumi et al. 2017, Sala and Giakoumi 2018). We also found no indication of any such PPA effect as there were generally no differences between PPA and REF areas along the NSW coastline.

Striking bioregional patterns in fish assemblages were observed across rocky reefs along 7° of latitude of the east Australian coastline exposed to substantially different sea
temperatures (Fig. 1; >1000 km) from subtropical to temperate waters. One of the most interesting species was *C. auratus* which had the highest abundances in the middle bioregion, slightly lower in the north of the state and substantially lower abundances in the south. Nonetheless, strong NTMR responses for this species occurred across all bioregions despite the very different magnitudes of absolute effect sizes (Fig. 2b, Table 1). When these were assessed as relative effect sizes (Table 1), the responses were remarkably similar and indicated a strong level of generality across the bioregions despite the substantial bioregional differences in abundances for this species. In other comparable large-scale studies from the Great Barrier Reef Marine Park (GBRMP) and the California Marine Protected Area network, substantial bioregional patterns have been observed (Mapstone et al. 2004, Russ et al. 2008, Hamilton et al. 2010, McCook et al. 2010, Emslie et al. 2015). In the GBRMP, the major effect was similarly on the main resident, targeted species, coral trout (*Plectropomus* spp.), and red-throated emperor (*Lethrinus miniatus*). Their relative abundances varied greatly across the bioregions, as did their responses to the NTMR among bioregions (Mapstone et al. 2004) with little difference in the north and substantial differences in the south (Mapstone et al. 2004). Differential fishing pressure was argued to be the driver for the different bioregional patterns in NTMR responses (Mapstone et al. 2004, McCook et al. 2010). In California, substantial bioregional patterns were also observed and the effect sizes for targeted species also varied (Hamilton et al. 2010, Caselle et al. 2015). A range of targeted species were observed to contribute to these differences with larger effects in the warmer water bioregions than cooler ones, while effects on non-target species were limited (Hamilton et al. 2010, Caselle et al. 2015). In many ways, the GBR and Californian marine reserve systems the relative effects varied greatly depending on the bioregion. Hence, it appears that the use of similar management approaches (e.g., across a large-scale comprehensive network of marine parks) results in very similar relative effects in the NSW context; however, in California and the GBR more variable responses have been observed. Importantly, this study and those from the GBR and California highlight the importance in having bioregional coverage of monitoring programs to confidently report and understand the ecological responses of marine park management and protection.

The utility of NTMR as environmental references has been highlighted by many researchers (Edgar and Barrett 1999, Russ 2002, Sainsbury and Sumalia 2003, Willis and Millar 2005, Barrett et al. 2007). It would seem that the use of NTMR may allow the assessment of the ecological effects of fishing and could easily be incorporated into ecosystem-based management of reef species. In fisheries more widely (Macpherson et al. 2000, Hilborn et al. 2004, Halpern et al. 2010). Furthermore, the utility of NTMR to assist in quantifying and interpreting large-scale ecological condition change and monitoring would appear obvious (Stuart-Smith et al. 2017, Edgar et al. 2018) and emphasizes the importance of NTMR as scientific reference areas (Hamilton et al. 2010, Edgar and Barrett 2012, Harasti et al. 2019). The reduction in many anthropogenic stressors within NTMR and broader MPA networks provides the opportunity to form a contemporary baseline from which the general condition of the environment can be assessed. The long-term nature of monitoring of NTMR (often a management requirement) means that they can, into the future, provide a useful yardstick to assess long-term changes in the marine environment—which is often not provided by other research programs (i.e., in terms of consistency and scope). In Australia, similar data sets have been used to assess general ecological condition (Australian State of the Environment Reporting; Stuart-Smith et al. 2017) and fishery sustainability (Edgar et al. 2018). This will be particularly important into the future considering the substantial increase in pressures associated with the expansion of human population and development (Crain et al. 2009, Mora and Sale...
including along the NSW coastline (Australian Government 2019). Similarly, the systematic, large-scale, and long-term monitoring of rocky reef assemblages as in the current study program is producing an invaluable record for detecting impacts of climate change (e.g., Vergés et al. 2018).

This study has demonstrated how a whole network assessment of a coherent, representative, and large-scale marine reserves can provide striking evidence of consistent effects across very different bioregions (e.g., subtropical to temperate waters). Such large-scale assessments of marine reserve networks are rarely done, but clearly this should be the aim of world’s best practice for state and national marine reserve systems. The costs associated with these programs can be offset against the substantial gains made from simultaneously assessing or contributing to several overlapping natural resource management priorities (e.g., state of the environment reporting, climate change assessment, stock assessment, and the assessment of wider environmental management) and the broader context and understanding that is provided by such large-scale bioregional assessments. The provision of clear unconfounded evidence of the performance or utility of NTMR over a wide range of environmental gradients (e.g., bioregions) will provide greater confidence in the expected outcome of this management application (Gorurud-Colvert et al. 2014, Edgar 2017). This, in turn, should provide stakeholders with greater certainty and reduce concerns (Navarro et al. 2018) about the implementation of marine reserve networks.

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