



Marine protected areas are linked to higher predation rates by fish in shallow urbanised reefs, but only in no-take reserves

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ABSTRACT: Marine protected areas (MPAs) in which fishing is limited are a widespread management strategy to protect marine ecosystems. While many studies show clear effects of MPAs on fish biomass, much less is known about how protection influences the strength of ecological processes such as herbivory and predation. We characterised fish assemblages and used feeding assays to contrast rates of herbivory and predation by fish in MPAs (no-take and those with partial protection) and in fished sites in Sydney, Australia's largest city. In no-take MPAs, large fish were more abundant, species richness was greater, and the biomass of predatory, herbivorous and all fish combined was higher. In contrast, sites with partial protection were indistinguishable from fished sites. Predation was higher in no-take MPAs than in partially protected MPAs, while herbivory was less influenced by protection status. These results show that protection from fishing within urbanised reefs can facilitate energy flow to higher trophic levels via increases in predation.

KEY WORDS: Marine ecology · Predation · Herbivory · MPA · Fish · Standardised method · Kelp reef

1. INTRODUCTION

Global marine ecosystems face multiple threats due to overfishing, climate change, pollution and habitat decline (Halpern et al. 2008). Overfishing is widely recognised as one of the greatest threats to the world's oceans, causing widespread declines in species richness and productivity, with cascading impacts on ecological communities (Jackson et al. 2001, Brander 2007). Due to these negative impacts, marine protected areas (MPAs), where fishing and other human activities such as mining are prohibited or limited, are increasingly implemented to conserve marine ecosystems (Halpern & Warner 2002).

Although the number of MPAs has grown over the past few decades, they vary widely in levels of protection. Globally, only 6% of MPAs are listed as 'no-take' areas where fishing and extractive activities of any kind are prohibited (Costello & Ballantine 2015). Hence, a large majority of MPAs are only partially protected and still allow some levels of fishing. Studies consistently show the benefits of no-take MPAs having full protection from fishing on metrics such as density, species richness or biomass of fish, whereas partially protected MPAs and openly fished areas rarely differ (Lester & Halpern 2008, Di Franco et al. 2009, Edgar 2011, Currie et al. 2012, Edgar et al. 2014, Giakoumi et al. 2017,

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Sala & Giakoumi 2018, Knott et al. 2021, Turnbull et al. 2021).

No-take zones within MPAs are essentially large-scale mensurative experiments where human extractive activities are prohibited (Knott et al. 2021). Their establishment provides an opportunity to understand the effects of fishing on overall community structure and fish abundance. Many studies show that species targeted by fishing have higher densities within no-take MPAs (Evans & Russ 2004, Guidetti & Sala 2007, Tetreault & Ambrose 2007, Malcolm et al. 2018). MPAs have also provided some of the clearest demonstrations of trophic cascades in temperate reefs by showing how the re-establishment of larger sized predators (inside no-take MPAs) can lead to the recovery of seaweed forests via increased predation on sea urchins that can otherwise overgraze the seaweeds (Shears & Babcock 2002, Guidetti 2006, Clemente et al. 2010). For example, sea urchin densities on no-take New Zealand rocky reefs are now controlled by a higher abundance of predators inside the protected areas, resulting in increased kelp cover (Babcock et al. 1999, Shears & Babcock 2002). Similarly, fishing pressure in unprotected waters in the Mediterranean commonly decreases the abundance of predatory fish, elevating urchin densities and leading to the overconsumption of macroalgae (Sala & Zabala 1996, Guidetti 2006, Clemente et al. 2010). In these case studies, the presence or absence of no-take MPAs influences the state of the ecosystem, which shifts between macroalgal-dominated reefs with a high abundance of predatory fish, and coralline barrens with a high abundance of sea urchins.

Recently, ecologists and conservationists have increasingly focused on quantifying ecological functions and the functional traits of species, in addition to monitoring species abundance and richness, with the aim of better understanding ecosystem processes and services (de Bello et al. 2010). Another functional approach gaining traction is to measure the strength of ecological interactions such as herbivory and predation, which can impact important ecosystem functions and determine community structure (Meyer et al. 2015). Rapid and standardised assessments of ecosystem functions have been proposed to increase the collection of consistent and collaborative data that can be integrated across various ecosystems at global scales (Borer et al. 2014, Meyer et al. 2015). For example, standardised bioassays that estimate ecological processes have been used in experimental studies, including assessments of predation rates on terrestrial invertebrates (Howe et al. 2009), and across global latitudes and elevations (Roslin et al. 2017).

Estimating the strength of trophic interactions is particularly important in marine systems, where top-down effects are a frequent determinant of community structure (Shurin et al. 2002, 2006). Marine herbivory is particularly important, with consumption of primary producers being 3–4 times greater in water than on land (Cyr & Pace 1993, Shurin et al. 2002, 2006), and marine grazers reducing primary producer abundance by 68% on average (Poore et al. 2012). The importance of predation is also evident from the well-known examples of trophic cascades, where declines in predators lead to large increases in herbivores and subsequent overgrazing of primary producers (Estes et al. 1998, Ling et al. 2015).

Global assessments of ecological processes in marine ecosystems have emerged with improved integration of observation, programmes and resources (Benson et al. 2018). For instance, Duffy et al. (2015) developed a standardised bioassay (the 'squidpop') to quantify relative consumption rates of generalist predators in a marine setting. The method has been used to compare consumption pressure between artificial and natural habitats (Rodemann & Brandl 2017), to monitor predation on restored oyster reefs (Gilby et al. 2020) and to test how habitat-formers benefit prey in a soft sediment facilitation cascade (Lanham et al. 2020). On large scales, Whalen et al. (2020) used squidpops to quantify predation in seagrass beds across 105° of latitude in Europe, Asia and the Americas, and Ashton et al. (2022) contrasted predation pressure on benthic marine communities across 115° degrees in the Americas. There is currently no widely accepted standardised method to assess herbivory. Here we used a method analogous to squidpops, where squid prey is replaced by *Ulva* spp. algal fronds, which we have termed 'Ulvapops'. We acknowledge that bioassays such as squidpops or *Ulvapops* are an indirect method that may also indirectly measure other feeding groups such as scavengers (Porter & Scanes 2015). While these bioassay methods do not estimate absolute consumption rates, they provide a good approach to spatially compare relative levels of predation and/or herbivory (Duffy et al. 2015).

In this study, we assessed the effect of protection from fishing on the strength of top-down processes (predation and herbivory rates) on temperate reefs in Sydney, Australia. Within the Sydney metropolitan region, there are 10 small MPAs (locally termed 'aquatic reserves' but referred to as MPAs herein) with varying levels of protection, but only 2 of these are no-take areas where all fishing and collection of marine organisms is prohibited. The remaining par-

tially protected MPAs allow various forms of fishing and collection of marine organisms (Table 1). Given the complexities in doing so, few studies have directly measured the ecological impacts of Sydney's MPAs. We acknowledge that it is impossible to meticulously replicate across MPA zones given inherent variation between MPA sites and often ecological biases in their zonation. Nevertheless, early studies within Sydney's existing MPAs suggest that size and density of targeted fish species are higher in sites partially protected from fishing activities (Curley 2007, Curley et al. 2013). More recently, studies have shown that in Sydney, only full no-take MPAs were distinguishable from nearby fished areas in terms of overall biodiversity, fish abundance and biomass, and that partially protected MPAs were ineffective in meeting many conservation goals (Turnbull et al. 2018, 2021). No studies have directly measured the effect of Sydney's MPAs on the strength of ecological processes.

We use standardised bioassays to compare predation and herbivory rates in shallow waters in Sydney MPAs, with varying levels of protection from fishing, to fished reference sites. To identify important consumers within these communities, we filmed all assays, and fish assemblages were also characterised using underwater visual surveys. Predation rates were hypothesised to be higher under the highest level of protection (i.e. in no-take MPAs), as we expected to find greater fish biodiversity and predatory fish abundance (Knott et al. 2021). As Sydney's partially protected MPAs are known to be ineffective in enhancing biodiversity and fish biomass (Turnbull et al. 2018), we also expected that these sites would show similar levels of predation as fished sites. We expected higher grazing rates and a higher abundance of herbivores inside no-take MPAs only, as has

been found in other no-take MPAs nearby (Ferguson et al. 2016, 2017). Measures of urchin densities and identification of benthic habitat composition were also undertaken to test for potential trophic cascade effects across sites.

2. MATERIALS AND METHODS

2.1. Study sites

The coastal area of Sydney is situated within the Hawkesbury Shelf marine bioregion of New South Wales, in eastern Australia. Subtidal rocky reefs form one main habitat of this coastline, which is largely dominated by the kelp *Ecklonia radiata*, urchin-grazed barrens and sponge gardens in deeper waters (Underwood et al. 1991, NSW Marine Estate Management Authority 2016). The Sydney metropolitan area is the most urbanised and populated coastline in Australia, where recreational fishing pressure is particularly high (West et al. 2015, Rees et al. 2021).

Sydney's MPAs were established between 1980 and 2002 and range from fully closed to varying levels of fishing and extractive activities being allowed. Study sites encompassed 5 MPAs that differ in their level and type of protection and are characterised either as no-take or partially protected (Table 1). These included 2 no-take MPA sites under the highest level of protection (Fig. 1): Cabbage Tree Bay Aquatic Reserve (33.8000°S, 151.2971°E), which is 0.2 km² and was implemented in 2002, and Shiprock Aquatic Reserve (34.0691°S, 151.1297°E), a more estuarine environment located within Port Hacking that is 0.02 km² and implemented in 1982 (<https://www.dpi.nsw.gov.au/fishing/marine-protected-areas/aquatic-reserves>). No extractive activities of

Table 1. Regulations of fishing and collection activities in marine protected area (MPA) study sites in Sydney, Australia. Tick indicates the activity is allowed, cross indicates the activity is prohibited

Aquatic reserve	Size (km ²)	Year established	Line fishing	Spear-fishing	Invert/cunjevoi collection	Abalone collection	Rock lobster collection	<i>Ulva</i> collection	Bait weed collection	Collection of other marine vegetation
Partially protected										
Boat Harbour	0.72	2002	✓	✓	×	✓	✓	✓	✓	×
Gordons Bay	0.43	2002	✓	×	×	✓	✓	✓	✓	×
Long Reef	0.76	1980	✓ ^a	✓	×	×	×	×	×	×
No-take										
Cabbage Tree Bay	0.2	2002	×	×	×	×	×	×	×	×
Shiprock	0.02	1982	×	×	×	×	×	×	×	×

^aOnly hand-held for finfish

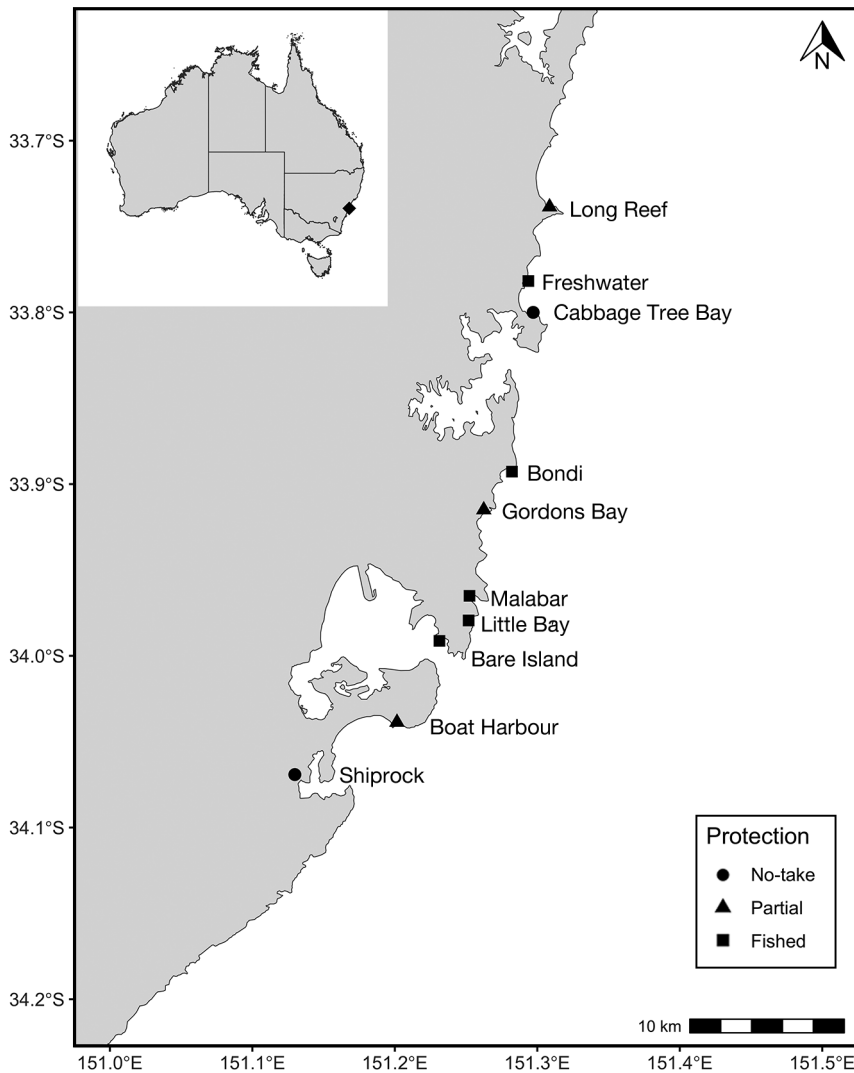


Fig. 1. Study sites along the Sydney, Australia, coastline

any type are allowed at either of these no-take sites. The 3 remaining MPA sites are partially protected (Fig. 1): Long Reef (33.7386° S, 151.3086° E), Boat Harbour (34.0387° S, 151.2015° E) and Gordons Bay (33.9150° S, 151.2624° E), which all allow line fishing and other varying extractive activities (specified in Table 1). Five reference sites situated in fished waters, where fishing is unrestricted, include Freshwater (33.7820° S, 151.2937° E), Bondi (33.8927° S, 151.2822° E), Malabar (33.9651° S, 151.2524° E), Little Bay (33.9794° S, 151.2518° E) and Bare Island (33.9913° S, 151.2313° E) (Fig. 1). The reference sites are geographically interspersed among the MPA sites along the Sydney coastline and mostly capture coastal habitats except for Bare Island, which is inside Botany Bay and represents a slightly more estuarine environment.

2.2. Rates of predation and herbivory

A standardised method was employed to measure rates of consumption at each site. Using the 'squidpop' design of Duffy et al. (2015), dried squid attached to metal poles were used as an assay to measure feeding intensity of predatory fish. Dried squid was cut into equally sized circular pieces (1.3 cm²), tied to fishing line and secured to the top of a pole. To create a similar assay to measure rates of herbivory, the green alga *Ulva* sp. (hereafter referred to as *Ulva*) was used as bait, to create '*Ulvapops*'. *Ulva* is largely restricted to the intertidal zone in Sydney (pers. obs.) and occurs infrequently within the kelp-dominated studied reefs, minimising the chances that the assays would be confounded by naturally occurring *Ulva* nearby. *Ulva* was also chosen for its attractiveness as bait for *Girella tricuspidata*, an abundant herbivorous fish in eastern Australia (Gollan & Wright 2006, Ferguson et al. 2015). Generally, *Ulva* species are regarded as more palatable than dominant habitat-forming brown algae such as kelp (Barrientos et al. 2021). Herbivory rates measured here therefore reflect maximum herbivory rates and are used for comparative purposes only; they do not provide an appropriate metric to

estimate herbivory on dominant brown algae such as kelp. *Ulva* attached to holdfasts was collected at low tide within 1–3 d of use in the field experiment from North Clovelly, Little Bay and Freshwater Beach. Each piece of *Ulva* (initial mean [±SE] area was 51.63 ± 0.81 cm²) was photographed against a white board, with a ruler for scale, at the beginning and end of the experiments to calculate surface area lost after exposure to herbivores. Poles were prepared by securing a piece of 3-ply rope with *Ulva* attached to the top of each pole with duct tape. While herbivory assays often use control replicates where algae are protected from herbivores to account for autogenic changes in area (e.g. due to growth), these changes are generally negligible or very small over a 24 h period. Here we were interested in capturing clear and large signs of herbivory (close to 100% consumption) akin to the

eaten/uneaten measures from the squidpop assays. Due to the irregular shape of *Ulva* fronds and the fact that herbivores generally do not consume their prey completely, we could not apply a binomial eaten/uneaten category to the algal baits, and hence we used changes in area instead, which are easy to measure for *Ulva* due to its laminar growth form.

The experimental method used was adapted from Duffy et al. (2015). In each assay, 25 squidpops were deployed by free diving at each of the 10 sites (2 no-take MPAs, 3 partially protected MPAs and 5 fished sites; Fig. 1). Rods were secured into sandy sediment within or adjacent to shallow rocky reef habitat within a depth range of 2–4 m, in 1 m increments, along a 25 m transect. This method was repeated with an assay of 25 *Ulvapops*, ensuring a distance of at least 3 m from the squidpop assay to reduce attraction of predatory fish to the *Ulvapops*. The *Ulvapop* method aimed to measure herbivory by fish only. Urchins and other invertebrate herbivores are generally confined to rocky reefs and would not have been able to access the *Ulva* bioassays, as the algae were placed on top of poles on sandy substrate. We acknowledge that the proximity of *Ulvapops* to squidpops may affect algal herbivory due to smell of squid and predatory species feeding on squid, but the paired bioassays allowed for greater feasibility of deployment and direct comparison of predation and herbivory rates across sites. At the time of initial deployment of baited poles, a GoPro HERO4 camera attached to a weighted frame was placed near each bioassay so that the frame captured 1–3 rods, following the methods of Duffy et al. (2015). The experimental assays were repeated over 3 consecutive days at each site to estimate 3 measures of predation and herbivory rates. All assays were completed between November 2017 and January 2018, with the timing of assays in no-take, partial and control sites interspersed.

Loss of squid bait was recorded after 1 h and then after 24 h of deployment, as either 'taken', where the entire squid bait was removed, or 'present', where all or part of the bait remained. Only predation was quantified after both 1 and 24 h, as it was expected to be a faster process than herbivory within a temperate ecosystem during summer. After 24 h, baits were counted, and all squidpops were removed and replaced by another assay of 25 pre-prepared squidpops, until 3 assays were complete (i.e. assays were repeated over 3 consecutive days). Similarly, *Ulva* pops were collected after a 24 h deployment and immediately replaced by new *Ulvapops* for 3 consecutive days. After each collection, the *Ulva* pieces

were removed from the rope attachment and photographed using the same method as prior to deployment. The taken/present method was not used with the *Ulva* pieces as they varied initially in size (unlike the squid). Changes in herbivory were instead measured as proportional loss of *Ulva* by surface area using ImageJ software (Schneider et al. 2012).

2.3. Fish abundance and composition at assay sites

Video footage was recorded to characterise the fish communities responsible for the observed loss of baits in the initial hour of deployment for the predation and herbivory assays, as it was expected that feeding would be most concentrated at deployment. The first hour of recording was used to identify fish species consuming the squid and algae bait and provide fish species composition estimates within each study site.

The GoPro videos were analysed to quantify the number of strikes/bites taken by all fish and whether they removed bait, using EventMeasure software (www.seagis.com.au). Fish were identified to species, or to a broader taxonomic grouping in cases of poor visibility, determined by personal observation. Additional fish species, which did not take bait during the fish bite analyses, were identified and quantified to provide an estimate of the entire species assemblage. Fish abundance was measured as MaxN, the maximum number of individuals observed in a single frame, commonly used for underwater video analysis as a conservative measure of abundance (Willis et al. 2000, Cappo et al. 2003). Species richness was also calculated as the number of species observed per video.

2.4. Fish and benthic assemblages at protected and fished sites

We used underwater visual surveys to estimate the abundance, trophic group biomass and species composition of fish assemblages at each site. These surveys were done in the absence of baits, to avoid confounding impacts of changes in fish behaviour due to bait attraction and to capture a broader representation of fish assemblages at sites (Wraith et al. 2013). Urchin densities were also measured to quantify the abundance of an important temperate herbivore that may be heavily influenced by predatory fish (Shears & Babcock 2002).

Surveys were undertaken from March to April 2018 at each of the 10 field sites. Transects were deployed perpendicular to shore (i.e. swum away from the shoreline) alongside rocky reefs and shortened to 25 m due to limited length of continuous reef at some sites. Surveys were undertaken on snorkel due to shallow depths across sites (2–4 m). Three transects were surveyed at each site, at least 10 m apart. Along transects, all mobile, non-cryptic fish species, abundance and length estimates were recorded 5 m on either side of the transect line (Reef Life Survey [RLS] method 1). Urchin species and abundance were recorded along the same transects, 1 m either side of the transect line (modified RLS method 2). Fish and urchin transects were surveyed again over the same area approximately 1 mo later to account for temporal variability in assemblages. Habitat complexity was measured to explain possible differences in fish abundance among sites. Rugosity was estimated with a 6.4 m fine-link chain. The chain was contoured to kelp reef parallel to the transect tape, and a ratio was calculated from the chain length and the straight-line distance of the contoured chain. Two rugosity measurements were taken at each transect, totalling 6 measurements at each site. Benthic surveys were undertaken at each site to test the hypothesis that variation in consumption rates of fish affects habitat composition. Sixteen photo quadrats were taken using a 25 cm × 25 cm frame at each site at random points along the rocky reef, within 20 m of the bioassays. Algal species were identified to species or genus level to quantify diversity, as well as other benthic categories including bare rock, sand, encrusting algae and turfing algae. Density was estimated by a random point generator using Coral Point Cover with Excel extensions (CPCe) software, which calculates the percentage cover of algal groups identified within each photo quadrat (Kohler & Gill 2006).

2.5. Data analysis

A linear mixed-effects model (LMM) with a Gaussian error distribution was run for each of the following response variables: herbivory (surface area of *Ulva* lost per day [$n = 3$], large fish size (≥ 20 cm, underwater visual census [UVC]), habitat complexity and total percent cover of algae. Species richness (both UVC and video) data were analysed using a generalised linear mixed-effects model (GLMM) specifying a Poisson distribution. For pre-

dition, separate analyses were run on the proportion of baits taken from the total array of squidpops within each day ($n = 3$) after both 1 and 24 h. The proportional loss of squid bait was analysed using a GLMM with a binomial distribution for both the 1 and 24 h assays separately. The model was fitted with the response variable as a 2-column matrix of the number of bait absences (i.e. 'successes') and the number remaining, weighted by the total number of replicates for each assay. For herbivory rate, the number of bites per day ($n = 3$) was used as the response variable in a GLMM specifying a negative binomial distribution. The model for large fish size was weighted by abundance (to reduce the potential bias of large but rare species on statistical outputs), and for fish abundance (MaxN), a GLMM with a Poisson error distribution was fitted. For all other response variables, raw data were retained for analysis. In all models, protection status (no-take, partial and fished) was treated as a fixed factor, and sites were included as a random factor nested within protection status. Analyses were run using the R package 'lme4' (Bates et al. 2015) with analyses of deviance used for statistical inference of the fixed factor. Where protection status was a significant predictor for the response variable, Tukey's multiple post hoc comparisons were run using the 'glht' function in the R package 'multcomp' (Hothorn et al. 2008), specifying a chi-squared test to determine which treatments were different. Where group means are presented, these were modelled based on linear models as described above and were calculated using the 'predictions' function in the 'marginaleffects' package in R (Arel-Bundock 2023). For reporting on effect sizes, group means and 95% confidence intervals were estimated from linear models (as described above) using the 'predictions' function, and differences between group means were derived using the 'avg_comparisons' function, both in the 'marginaleffects' package (Arel-Bundock 2023). Where confidence intervals are reported, they are done so in the following notation: mean [lower 95% CI, upper 95% CI].

G. tricuspidata was the only fish species recorded as feeding on the *Ulva* bait across all sites. The rates of herbivory for this species alone were contrasted among sites using a LMM, with protection status (no-take, partially protected and fished) as a fixed factor and site as a random factor (nested within protection status). Formal analyses were not carried out on predation (total bites taken) for individual species of predatory fish due to variability of fish species and

size classes recorded among sites, and a low overlap of fish composition among sites.

The composition of fish from videos was contrasted among sites with permutational multivariate ANOVA using PRIMER-E software (Clarke & Warwick 2001), with protection status as the predictor. Video data containing outliers of large schools of bait fish from the family Atherinidae, confined to 1 control site (Freshwater), were removed from analyses. These fishes feed on zooplankton, so they are not focal predators within the study. However, other planktivore data were retained and included in the supplementary material for a high-level assessment of the relative importance of this trophic group between habitat types, but this was not tested in detail. Abundance totals were log+1 transformed to account for highly abundant species. The fish species counts were standardised by total species abundance to account for the effect of schooling species, and a Bray-Curtis dissimilarity measure was used.

Fish abundance from visual surveys was contrasted among sites using a GLMM with a negative binomial error distribution, with protection status as the predictor variable. Fish biomass (W) was calculated from the allometric growth equation $W = aL^b$, where L is length and the parameters a and b were sourced from FishBase for each of the observed species (Froese & Pauly 2018). In few cases where values were not listed, those of a closely related species were used. Fish species were grouped into 4 broad trophic groups: predators (including piscivores and invertivores), herbivores, omnivores and planktivores, based on dietary information sourced from both FishBase and Fishes of Australia (www.fishesofaustralia.net.au). Total biomass across sites was contrasted using GLMMs, using a gamma regression and a log link function. Independent variables were the same as used in the above analyses, with protection status as a fixed factor and site as a random factor nested within protection status. Biomass for each trophic group was individually tested to compare the effect of protection status on each group, using GLMMs with the same regression and link function as the previous test.

Total urchin densities were contrasted among sites using GLMMs with a Poisson error distribution, using the same independent variables. The composition of fish and algal density in visual surveys was compared among sites with permutational multivariate ANOVA in PRIMER-E, again with the same independent variables. Fish and algal species counts were standardised by the total species abundance and a Bray-Curtis similarity measure was used.

3. RESULTS

3.1. Predation and herbivory

Protection status had a significant effect on squid-pup predation rates by fish after a short time period (1 h, GLMM: $df = 2$, $\chi^2 = 7.684$, $p = 0.021$), but not after an extended time period (24 h, GLMM: $df = 2$, $\chi^2 = 3.626$, $p = 0.163$; Fig. 2, Table 2). Overall, a higher bait loss was recorded in no-take MPAs after 1 h when compared to partially protected sites (modelled difference of 98 [77, 100]%, Tukey's post hoc: $p = 0.038$). There was no statistical significance between no-take and fished sites where squid loss was only 26 [67, 100]% lower in fished sites (Tukey's post hoc: $p = 0.067$) and fished and partial sites were similar (Tukey's post hoc: $p = 0.580$; Fig. 2, Table 2). After 24 h, 100% bait loss was recorded within no-take MPA sites (Cabbage Tree Bay Reserve and Shiprock Reserve) in which bait loss was 28 [0, 56]% higher than in partially protected sites and 28 [6, 50]% more than for fished sites (Fig. 2, Table 2), which differed by 2 [0, 36]%

Herbivory (mean percent algal loss) after 24 h was not statistically different based on protection status (LMM: $df = 2$, $\chi^2 = 2.330$, $p = 0.312$; Fig. 3, Table 2). Both no-take MPA sites and 2 of the 3 partially protected MPA sites (Gordons Bay and Boat Harbour) showed high rates of herbivory where mean (\pm SE) algal loss was over 90% (Cabbage Tree Bay: $93.3 \pm 21.6\%$; Shiprock: $97.6 \pm 21.6\%$; Boat Harbour: $93.3 \pm 12.6\%$; and Gordons Bay: $90.9 \pm 17.6\%$), and algal loss for fished sites was $61.1 \pm 13.4\%$.

3.2. Fish abundance and composition at assay sites

We observed 46 species of fish from video footage in the feeding assays at all sites, largely planktivores and omnivores (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m721p135_supp.pdf). *Atypichthys strigatus* (planktivore) were the main feeders of squidpops (Fig. S1), with 2 omnivorous leatherjackets (*Meuschenia trachylepis* and *Nelusetta ayraudi*) also identified as substantial feeders at some sites (Shiprock, a no-take MPA; and Bare Island, a fished area; Fig. S1), while *Girella tricuspidata* (herbivore) were almost exclusive feeders of the *Ulva*pops. There was a significant effect of protection status on both fish abundance (as measured by the sum of MaxN for each species, GLMM: $df = 2$, $\chi^2 = 15.025$, $p < 0.001$) and species richness (GLMM: $df = 2$, $\chi^2 = 8.739$,

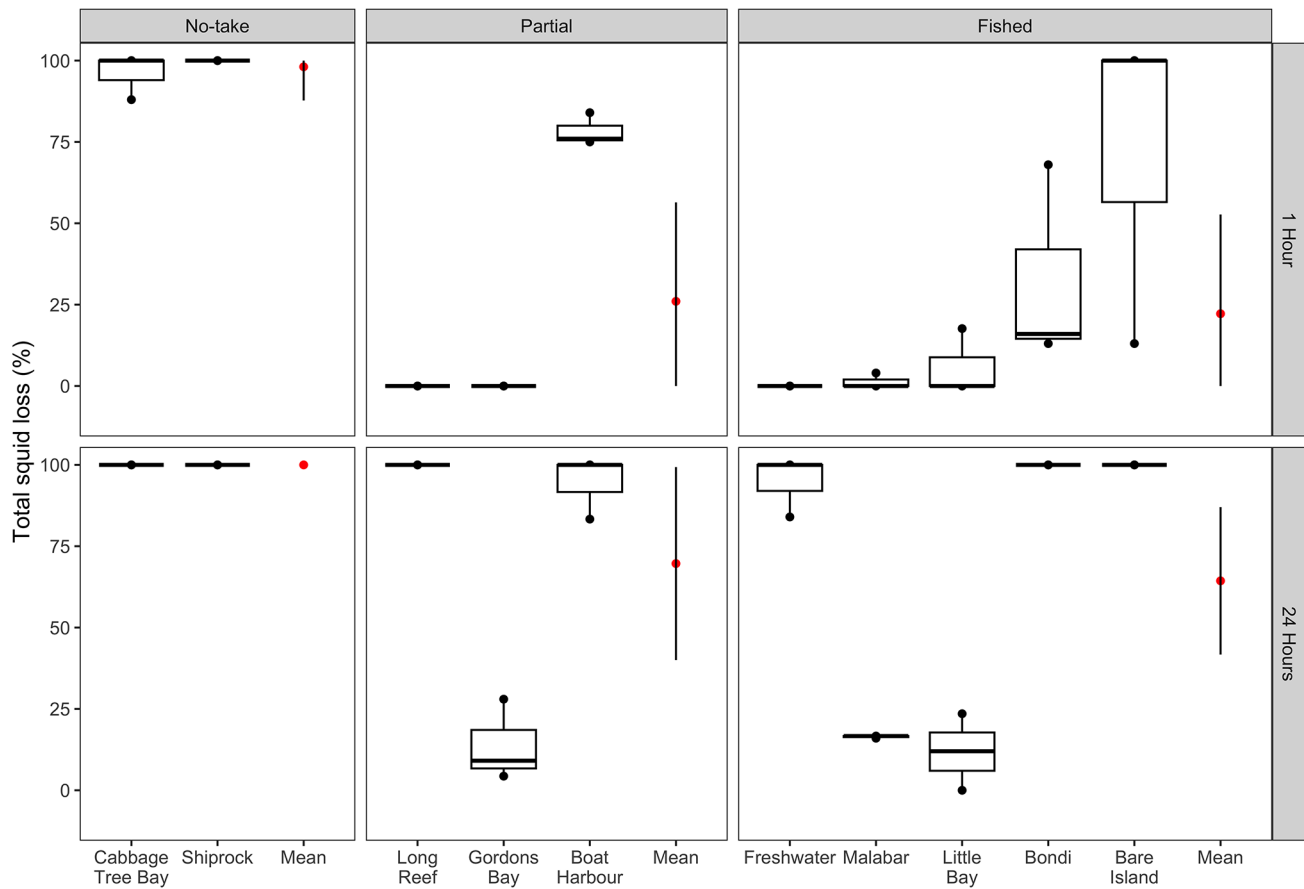


Fig. 2. Squidpop predation rates by fish (as a proportion of bait loss on each day of sampling; $n = 3$) across all sites after 1 h (top row) and after 24 h (bottom row) of deployment. From left to right: no-take MPA, partial MPA and fished study sites. Black dots: minimum and maximum points; lower whisker: data from minimum to Q1; upper whisker: data from Q3 to maximum; lower and upper boxes: Q1 and Q3, respectively; middle horizontal line: median. Group means are also presented in red, and bars around the mean represent values for the upper and lower 95% confidence intervals

$p = 0.013$), which were both higher in no-take MPAs when compared to either partially protected or fished sites, which were similar (Fig. S2, Table S4). No-take sites showed an increased mean summed MaxN of 73 [68, 215] when compared to partially protected sites and an increase of 61 [upper and lower CI; 83, 205] individuals when compared to fished sites. Mean species richness differed by 8 [1, 15] species and by 8 [2, 15] species for no-take sites compared partial and fished sites, respectively, corresponding to a mean richness of $11(\pm 3)$ species for no-take sites and $3(\pm 1)$ for both partial and fished sites (Fig. S2, Table S4).

Video footage showed that rates of herbivory by *G. tricuspidata* were affected by protection status (GLMM: $df = 2$, $\chi^2 = 7.375$, $p = 0.025$) and were higher in no-take MPAs compared to fished sites (Tukey's post hoc: $p = 0.035$) but not partially protected sites (Tukey's post hoc: $p = 0.514$), which were similar (Fig. 4, Table 2). Models showed an average of 2.8 [0.6, 5.0] more bites per day when comparing no-take to partial sites and

4.0 [1.8, 6.2] more bites per day when compared to fished sites. When surveyed using UVC, no difference in fish species composition was found based on protection status (MANOVA: $df = 2$, pseudo- $F = 1.074$, $p = 0.374$; Fig. S6, Table S5); however, when surveyed using video footage, protection status was a significant predictor of species composition, where no-take sites differed from partially protected (post hoc pairwise comparison: $p = 0.001$) and fished (post hoc pairwise comparison: $p = 0.030$) sites (Fig. S3, Table S5). For both UVC and video analysis, there was significant variation among sites (Figs. S3 & S6, Table S5).

3.3. Fish and benthic assemblages at protected and fished sites

A total of 101 fish species were recorded from the fish surveys (UVC; Table S2). There was no effect of protection status on overall fish abundance (GLMM:

Table 2. Analysis of deviance results from linear mixed models, post hoc comparisons and modelled group means for predation rates after 1 and 24 h, overall herbivory rates and herbivory by *Girella tricuspidata*. Significant p-values (<0.05) in **bold**

Source	df	Predation 1 h			Predation 24 h			Herbivory			<i>G. tricuspidata</i> herbivory		
		Dev	χ^2	p	Dev	χ^2	p	Dev	χ^2	p	Dev	χ^2	p
Protection	2	3348.5	7.684	0.021	99.89	3.626	0.163	253.84	2.330	0.312	171.83	7.375	0.025
Residuals		3340.8			96.23			256.17			179.20		
Post hoc comparisons				p			p			p			p
Partially protected vs. No-take				0.038			1.000			0.621			0.514
Fished vs. No-take				0.067			1.000			0.363			0.035
Fished vs. partially protected				0.580			1.000			0.918			0.192
Modelled group means		Mean	SE	95% CI	Mean	SE	95% CI	Mean	SE	95% CI	Mean	SE	95% CI
Fished		22.44	22.68	22.0, 66.9	64.37	0.16	41.7, 87.0	61.07	13.39	34.8, 87.3	2.03	5.15	0, 12.12
Partially protected		26.14	24.43	21.7, 74.0	69.67	0.15	40.0, 99.3	70.16	27.23	36.4, 100	22.77	46.71	0, 114.33
No-take		98.00	8.95	80.5, 100	100	<0.001	0.99, 100	95.43	21.10	54.06, 100	124.88	286.1	0, 685.53

df = 2, $\chi^2 = 0.621$, p = 0.733; Fig. S4, Table S6) or species richness (GLMM: $\chi^2 = 4.753$, p = 0.093). Large fish size (≥ 20 cm) (GLMM: $\chi^2 = 16.518$, p = 0.005) and total fish biomass differed based on the level of protection (GLMM: $\chi^2 = 10.763$, p = 0.005), where no-take sites showed over double the biomass of partially protected and fished sites (Table S6). No-take MPAs showed higher biomass overall (7.4 [0.7, 14.0] kg more biomass per site, Tukey's post hoc: p = 0.001) and bigger fish (an increase of 6.8 [3.9, 9.7] cm for fish already over 20 cm; Tukey's post hoc: p < 0.001) compared to partially protected sites. No-take sites also showed a higher biomass (by 7.3 [0.6, 13.9] kg more biomass per site; Tukey's post hoc: p < 0.001) and larger fish sizes (by 7.1 [4.4, 9.8] cm; Tukey's post hoc: p < 0.001) when also compared to fished sites. For species richness, there were more species (by 10 [1, 19] species) in no-take compared to fished sites only (Tukey's post hoc: p = 0.036; Fig. S4, Table S6). When divided into trophic groups, we recorded 5.2 [0.3, 10.8] kg more biomass for predatory fishes in no-take compared to partially protected sites (Tukey's post hoc: p = 0.006) and 5.5 [0.03, 11.0] kg more compared to fished sites (Tukey's post hoc: p < 0.001; Fig. S5a). The biomass of herbivorous fishes increased by 1.5 [0.6, 2.4] kg in no-take compared to partially protected (Tukey's post hoc: p < 0.001) and by 1.1 [0.2, 2.1] kg compared to fished sites (Tukey's post hoc: p < 0.001). We also observed a significantly higher biomass of herbivorous fishes at fished compared to partially protected sites (by 0.4 [0.2, 0.6] kg; Tukey's post hoc: p < 0.001; Fig. S5b). Omnivorous fish biomass was 1.0 [0.008, 2.0] kg higher in no-take compared to partially protected sites (Tukey's post hoc: p = 0.001) and 1.0 [0.03, 2.0] kg higher in no-take compared to fished sites (Tukey's post hoc: p < 0.001; Fig. S5c). The biomass of planktivores was similar across all sites (Fig. S4d).

Four urchin species were recorded (*Heliocidaris erythrogramma*, *Centrostephanus rodgersii*, *Phyllacanthus parvispinus* and *H. tuberculata*), with no evidence that total urchin densities (GLMM: df = 2, $\chi^2 = 1.1019$, p = 0.576) or habitat complexity (as measured by rugosity) (GLMM: df = 2, $\chi^2 = 1.981$, p = 0.371) varied among sites of varying protection status (Fig. S7, Tables S7 & S8).

We recorded 8 algal taxa to species and another 8 to genus level (Table S3). Total percent cover of algae did not differ based on protection status (GLMM: df = 2, $\chi^2 = 0.750$, p = 0.687; Fig. S8, Table S8). Protection status similarly did not have a significant effect on algal community composition, but we did detect among-site variation (Table S5).

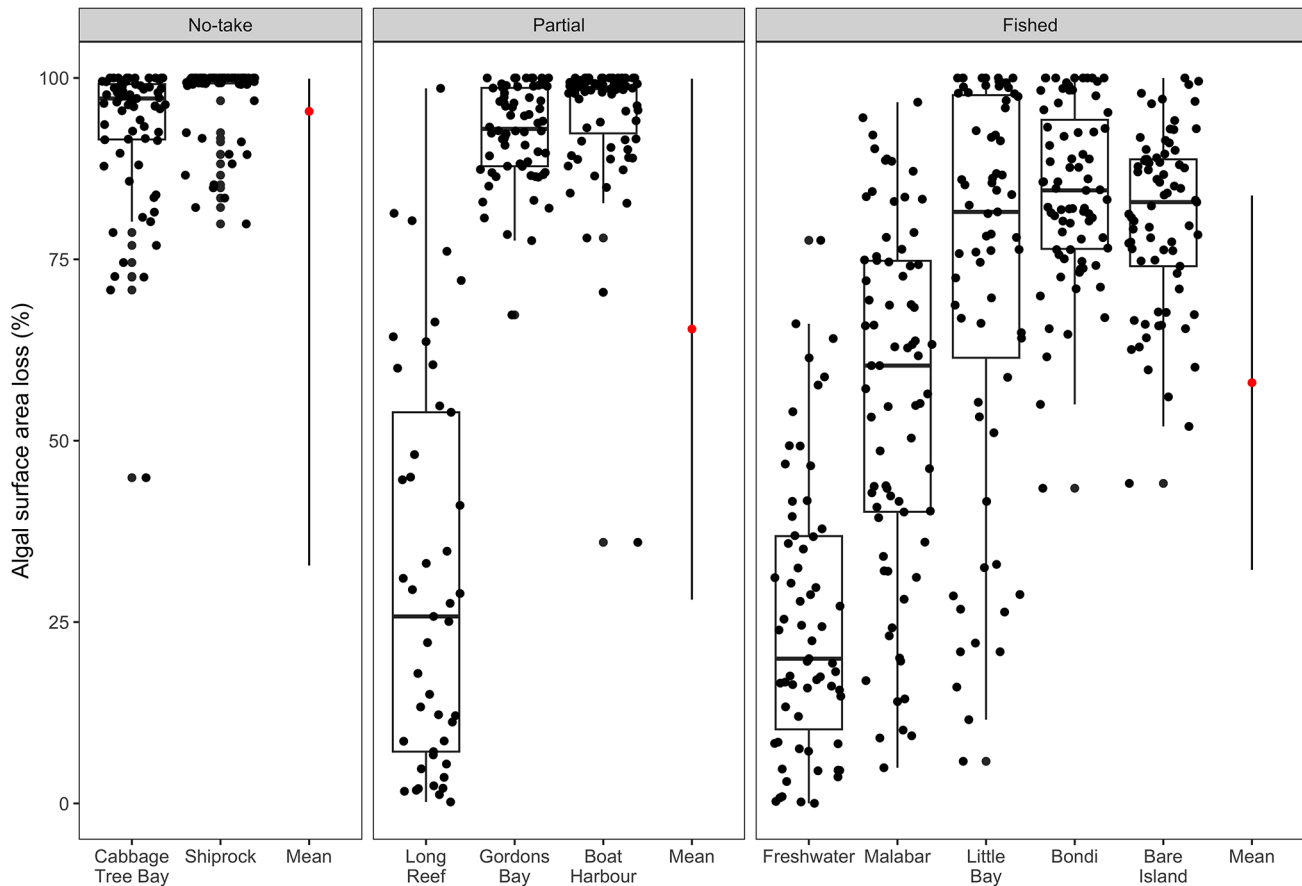


Fig. 3. Rates of fish herbivory (as algal surface area percentage loss) after 24 h, across all sites. From left to right: no-take MPA, partial MPA and fished study sites. Black dots represent individual *Ulvapop* data, and group means are also presented in red, with bars around the mean showing upper and lower 95% confidence intervals. Boxplot definitions: see Fig. 2

4. DISCUSSION

In this study, 2 lines of evidence show that fishing impacts both ecological processes and community composition of shallow reef fish communities in Sydney. Firstly, squidpop predation rates by fish were higher in no-take MPAs when compared to both partially protected MPAs and fished sites. Secondly, herbivory (total bites) by *Girella tricuspidata* was higher in no-take MPA sites in comparison to both partially protected and fished sites. Thirdly, total fish biomass and fish length (≥ 20 cm) were higher in no-take MPAs. In contrast, partially protected sites were indistinguishable from fished sites in terms of predation rates or fish community assemblages.

Measuring processes such as predation and herbivory inside and outside of MPAs is important, as it assesses the functioning of marine communities, and hence the effectiveness of protection. The 2 no-take MPA sites considered here showed higher predation rates after 1 h (88–100% bait loss) than either the

partially protected MPAs or fished sites. A Californian study found similar results, with 98% of squidpops being consumed in old no-take MPAs (>40 yr), a much higher predation rate than was observed at newly established, partially protected MPAs (approx. 8 yr) (Rhoades et al. 2019). Levels of predation recorded here were similar to predation rates estimated in tropical reefs also using standardised squidpop assays (~100% bait loss after 1 h), and higher than predation rates recorded in other macrophyte-dominated habitats like seagrass beds, mangrove forests or sand habitats of Central America (Duffy et al. 2015). Our results are similar to studies that test how protection status affects predation on other prey. Tethering experiments at various locations in the Mediterranean (Sala & Zabala 1996, Guidetti 2006, Vergés et al. 2012) and New Zealand (Shears & Babcock 2002) showed that predation rates on sea urchins were higher in no-take MPAs due to higher densities of urchin-eating predatory fish at these sites. Using a broader approach, Soler et al.

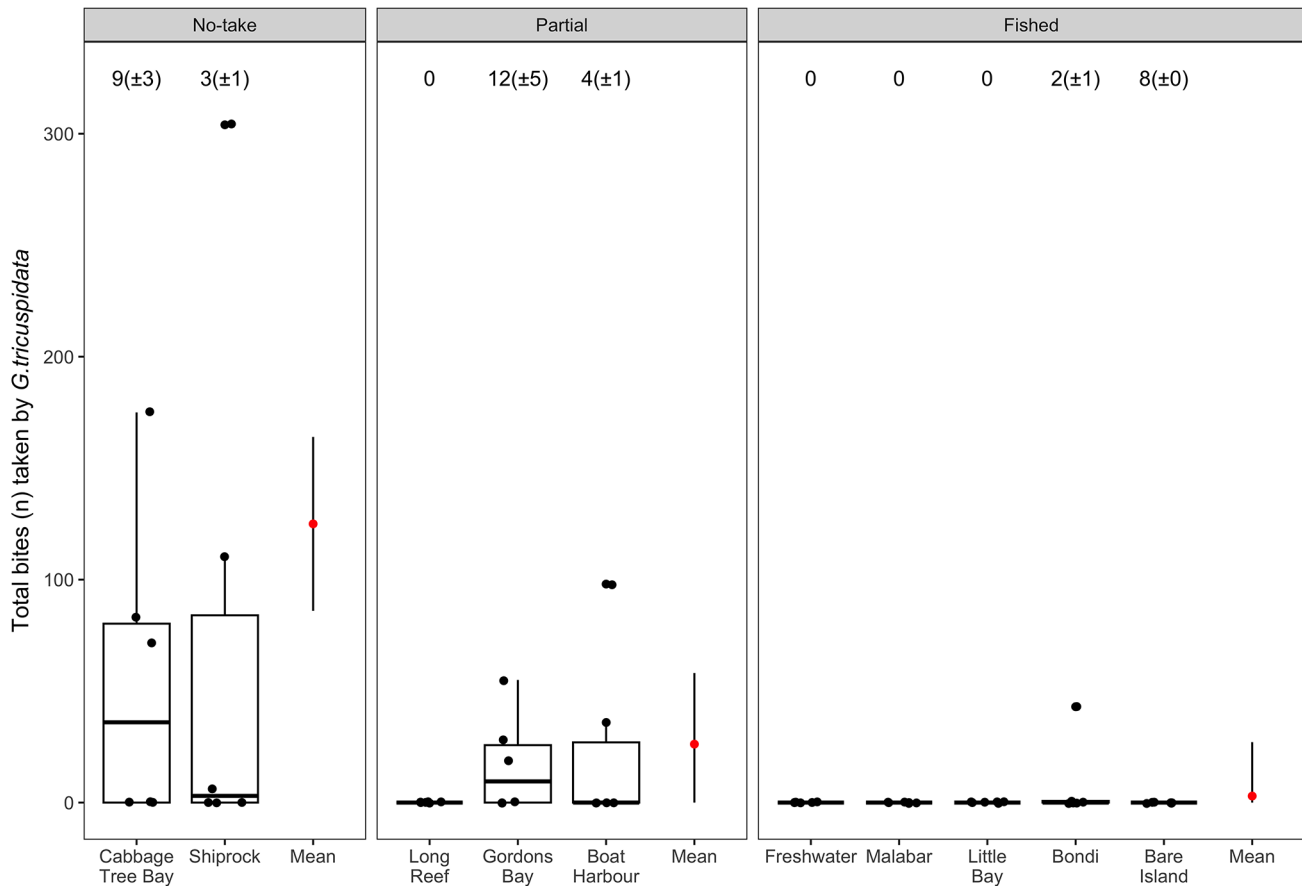


Fig. 4. Herbivory (mean total bites) by *Girella tricuspidata* from video footage of the initial hour of algal deployment. From left to right: no-take MPA, partial MPA and fished study sites. Black dots represent the number of bites per replicate (for each camera; $n = 3$, per day; $n = 3$), and group means are also presented in red, with bars around the mean showing the upper and lower 95% confidence intervals. Numbers above each boxplot represent the mean (\pm SE) MaxN for *G. tricuspidata* at each site across the 3 survey days. Boxplot definitions: see Fig. 2

(2018) also found that fish consumed 71% more prey biomass in no-take MPAs relative to nearby fished areas in southern Australia. It is important to note that the squidpop method measures the relative feeding intensity of generalist predators, with dried squid being palatable to a range of fishes including omnivores and attracting smaller predators due to its accessibility (Duffy et al. 2015). This is reflected in our study, where predation intensity was driven by the planktivore *Atypichthys strigatus* and high numbers of a mid-level species, rather than higher-level predators. Further studies are needed to measure absolute predation intensity where specific predators and specific prey can be identified.

Our conclusion that no-take MPAs harbour higher total fish biomass, abundance of large fish (≥ 20 cm) and more species than partially protected MPAs or fished sites is consistent with the findings of Turnbull et al. (2018) on Sydney reefs and with larger-scale

studies across multiple bioregions along the New South Wales coastline of eastern Australia (Coleman et al. 2013, 2015, Harasti et al. 2018, Malcolm et al. 2018, Knott et al. 2021). The results are also reflected in multiple global studies (Lester & Halpern 2008, Edgar 2011, Currie et al. 2012) that show the effectiveness of no-take MPAs on biomass and diversity metrics. Edgar et al. (2014) analysed MPAs across Australia and New Zealand, determined that 2 key factors in the conservation benefits of no-take MPAs was age (>10 yr old) and large effect size. As the 2 no-take MPAs considered in this study are similar in age and size, this was not analysed. Although we found no differences in abundance of all fish between MPA and fished sites, there was higher abundance of large fish and larger biomass indices in no-take MPA sites, which is an important finding for Sydney MPAs. This may relate to the findings of Rees et al. (2021) and Bosch et al. (2022), where the abun-

dance of adult fishes was negatively associated with high human population densities, suggesting fishing may be a driver of their distribution. Large female fish have disproportionately higher fecundity and reproductive energy output than a higher abundance of small fish would have (Hixon et al. 2014, Barneche et al. 2018). Large fish size and fish biomass can therefore be used to indicate likely reproductive output, which should be much higher under full no-take protection, where fish size is larger (Halpern 2003, Lester et al. 2009).

Full no-take protection provides much more effective conservation of marine communities than partial protection, facilitating, for example, long-term stability amongst fish communities (Pettersen et al. 2022). Sites within partially protected areas are usually similar to fished areas in terms of biomass, density, richness and individual size of organisms (Lester & Halpern 2008), especially for target species (Di Franco et al. 2009). In this study, partially protected MPAs were indistinguishable from fished sites for all response variables, mirrored in the same region (Turnbull et al. 2018) and surrounding bioregions (Knott et al. 2021). It is likely that the communities within Sydney's partially protected MPAs, where some forms of fishing are allowed, reflect the inadequacy of such protection where exploited fishery stocks are still targeted and are unable to recover (Edgar 2011, Currie et al. 2012).

Regulation and enforcement of permitted fishing activities within partially protected MPAs can impact reserve effectiveness, with moderate to high regulation generally performing better for biodiversity metrics (Zupan et al. 2018). There is limited information available for the actual fishing effort that takes place within the partially protected MPAs studied here, but regulations do differ between them (Table 1), and this was not accounted for. In contrast to our findings for Sydney's MPAs, there are examples of highly regulated, partially protected areas that do have positive effects on fish density and biomass (Curley et al. 2013, Sciberras et al. 2015, Giakoumi et al. 2017, Harasti et al. 2018, Zupan et al. 2018, Hall et al. 2022). Additionally, it is difficult to disentangle potential cascading effects of intertidal protection regulations on subtidal fish communities, for example as may be the case for the Malabar (fished) site studied here, and this warrants further investigation. In the long-term, evidence so far would suggest that no-take MPAs are indeed the most effective and that in comparison, partially protected MPAs intrinsically do not provide the same long-term retention of targeted fish species (Pettersen et al. 2022), preventing

them from reaching the same level of functional or trophic diversity (Coleman et al. 2015). While these results suggest that conservation resources are best allocated towards the management of no-take zones, in ecosystems where partially protected areas may be deemed appropriate, ecological targets must be clearly defined. Regulations must then be set accordingly so that there is some level of biological enhancement that is distinguishable from areas that fall under general use regulations.

The effect of protection status on herbivory was less clear than for predation. Although herbivorous fish biomass was higher inside fully protected sites, overall, herbivory rates did not differ between MPA and fished sites. However, there are some key results that warrant further investigation. Video footage revealed that luderick *G. tricuspidata*, which was nearly exclusively responsible for all herbivory in the first hour, consumed *Ulva* spp. at higher rates in MPA sites (regardless of protection level) than in fished sites, with particularly higher rates in no-take MPAs. Ferguson et al. (2016) made similar observations for sites ~200 km south of Sydney, in that there too was a general, albeit inconclusive, trend for grazing by *G. tricuspidata* to be higher within MPA sites. Ferguson et al. (2016) also found that *G. tricuspidata* was larger and more abundant inside MPAs, and previous research has shown that this species exhibits strong site fidelity on shallow reefs (Ferguson et al. 2013). In combination, this suggests that the effect of fishing on *G. tricuspidata* is significant and that marine protected areas can reduce this impact (Ferguson et al. 2017). Beyond these findings relating to *G. tricuspidata*, the overall lack of relationship between herbivory and protection is consistent with results from other parts of the world. For example, Vergés et al. (2012) found no effect of protection on fish herbivory rates within the Mediterranean. Similarly, Ferguson et al. (2017) also found no relationship between herbivory and protection status. These differences are likely due to *G. tricuspidata* being a species highly targeted by fishers in eastern Australia, whereas the analogous species in Western Australia (*Kyphosus cornelii*, *K. sydneyanus* and *K. gladius*) are not targeted at all. In any case, it is worth noting that the bait used in these bioassays (*Ulva* spp.) is a highly palatable alga that is preferred by many fish species (Barrientos et al. 2021), and the herbivory patterns observed may not reflect fish consumption patterns on dominant habitat-forming algae such as the kelp *Ecklonia radiata*. Ongoing monitoring of the influence of MPAs on herbivory is recommended, given high variation within the data

presented here and also because changes to herbivory regimes are expected in this region with ongoing range expansions of tropical herbivorous fishes (Vergés et al. 2014, 2019).

We acknowledge here that measures of bait loss described above likely represent a range of feeding behaviours not strictly limited to piscivory and herbivory. For example, the use of dried inanimate baits may attract scavenging species as well as active/aggressive foragers, and tethering of different bait types can attract different predator functional groups (Yarnall & Fodrie 2020). Similarly, algal tethers not only attract herbivores but also invertivores (Ritter et al. 2021), and given that *Ulva* is largely an intertidal genus in the region, it is possible that consumption of this species represents a biased metric of herbivory for subtidal species. While all baits introduce some element of bias, they are nevertheless considered appropriate for spatial comparisons of relative rates of bait consumption, which is what squidpop assays are designed for (Duffy et al. 2015).

Variation in consumer pressure, from predatory and herbivorous fish to sea urchins within marine communities, can have cascading impacts on habitat-forming seaweed species (Sala & Zabala 1996, Shears & Babcock 2002, Shurin et al. 2006). In this study, however, urchin densities and algal cover were generally not related to the protection status of sites. This could be attributed to abundances of known urchin predators being too low to significantly impact urchin densities within these small MPAs, as hypothesised by Turnbull et al. (2018). Similarly, Guidetti et al. (2005) found that despite a positive influence of protection status on urchin predators, there was no relationship between predator abundance and urchin density within urbanised Mediterranean MPAs. It is possible that large foraging distances shown by predatory species may result in urchin predation that is not localised to within MPA boundaries. Alternatively, urchin predators may have alternate prey sources, particularly if the biomass of fishes from lower trophic groups has also increased. In a contrasting example from Japan, the implementation of a small MPA containing an artificial reef structure did increase urchin predator numbers, leading to a positive impact for macroalgae cover, but this was demonstrated under a complex set of size-dependent predatory interactions (Kawamata & Taino 2021). For Sydney's MPAs, any cascading benefits from an increased biomass of higher-order fishes, for example via regulation of herbivore abundances resulting in increased macroalgal cover, will require further testing.

The findings from this study support research from other regions that conclude that well-enforced, no-take MPAs are the only level of protection which significantly impacts marine communities, whereas partially protected MPAs produce no significant impacts (Di Franco et al. 2009, Edgar 2011, Currie et al. 2012, Edgar et al. 2014). Our standardised bioassays suggest that protection status is impacting energy flows within ecosystems, not only fish abundance. Predation rates were higher in Sydney's no-take MPA sites when compared to all other sites (both partially protected MPAs and fished areas), although herbivory rates were not significantly influenced. No-take MPAs harboured a greater abundance of large fish and higher species richness and biomass in comparison to all other sites. In contrast, both partially protected MPAs and fished sites did not indicate any conservation benefits for ecological traits. To protect Sydney's marine communities effectively from fishing, the extension of full no-take MPAs is recommended as a more impactful management action than partially protected areas (Turnbull et al. 2018, 2021, Knott et al. 2021).

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