Baited video, but not diver video, detects a greater contrast in the abundance of two legal-size target species between no-take and fished zones

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Abstract
Inherent differences between baited remote video versus diver-operated video survey methodologies may influence their ability to detect effects of fishing. Here, the ability of no-take zones (NTZs) to provide protection for legal-sized fish from targeted species within the Ningaloo Marine Park (NMP) was assessed using both baited remote underwater stereo-video (stereo-BRUV) and diver-operated stereo-video (stereo-DOV). The relative abundance of legal-sized individuals of three recreationally targeted fish species, spangled emperor *Lethrinus nebulosus*, chinaman cod *Epinephelus rivulatus* and goldspotted trevally *Carangoides fulvoguttatus*, were examined using both methodologies inside and outside six NTZs across the NMP. Stereo-BRUVs found positive effects of protection on the relative abundance of legal-size *C. fulvoguttatus* and *L. nebulosus* in NTZs. Stereo-DOVs, however, did not detect any differences in relative abundances and sizes of these species between areas opened and closed to fishing. These contrasting results suggest that choice of sampling methodology can influence interpretations of the ability of NTZs to provide adequate levels of protection for target species. Our results suggest that stereo-BRUVs are a superior technique to stereo-DOVs for assessing the effectiveness of no-take zones for protection of fishery target species, reflecting bait attraction and an absence of diver influence on fish behaviour.

Keywords Fishing effects · Long-term monitoring · No-take zones · Stereo-BRUVs · Stereo-DOVs · Target species

Introduction

No-take zones (NTZs), where fishing activities are prohibited, are used worldwide as a spatial management tool for biodiversity conservation (Edgar et al. 2014; Malcolm et al. 2016; Sciberras et al. 2015). Many studies have shown that NTZs are useful to investigate the effects of extractive fishing on fish assemblages when contrasted with comparable unprotected areas (Halpern et al. 2010; Malcolm et al. 2016; Watson and Harvey 2007). Increases in fish species richness (Edgar and Barrett 1999; Rife et al. 2013), abundance (Malcolm et al. 2015; Pande et al. 2008) and size (Bornt et al. 2015; Harasti et al. 2018; Malcolm et al. 2018) have been observed within NTZs. Additionally, NTZs may act as an insurance measure against wider fisheries’ stock depletion, particularly where NTZs result in higher fish abundance in surrounding areas (Kerwath et al. 2013; Russ et al. 2008; Sackett et al. 2017).

Given the biodiversity conservation objectives of NTZs, assessments of their effectiveness require the use of non-destructive methods that sample fish assemblages with a minimum of bias and selectivity (Davis et al. 2018). Commonly used non-destructive methods include underwater and surface visual census (UVC/SVC; Babcock et al. 2008; Wilson et al. 2012), baited remote underwater stereo-video (stereo-BRUV; Langlois et al. 2010; McLean et al. 2016; Malcolm et al. 2018), baited remote underwater video (single camera) (BRUV; Kiggins et al. 2020) and diver-operated
stereo-video (stereo-DOV; Goetze et al. 2019; Shedrawi et al. 2014). Over the past decade, stereo-video methodologies (such as stereo-BRUV and stereo-DOV) have been adopted more regularly due to the decreasing cost of technology, the benefits of maintaining a permanent record that can be revisited if required, and the ability to obtain precise length measurements (Goetze et al. 2015; Holmes et al. 2013; Watson et al. 2010). While there are several advantages associated with each technique, both stereo-BRUV and stereo-DOV methods have limitations and can introduce sources of bias which may influence the fish communities recorded (Goetze et al. 2015; Holmes et al. 2013; Langlois et al. 2015; Watson et al. 2010). The presence of SCUBA divers during stereo-DOV sampling may bias fish behaviour (Goetze et al. 2017; Lowry et al. 2012). Fish may avoid or be attracted to divers depending on a myriad of factors, including learned avoidance responses due to fishing activity or attraction due to regular feeding (Gotanda et al. 2009; Januchowski-Hartley et al. 2012). In the case of stereo-BRUVs, the repeated use of bait can alter fish behaviour, potentially resulting in abundance and size measures being obtained that are not truly reflective of assemblage structure in an area (Birt et al. 2012). However, several studies have suggested that a representative sample of a fish assemblage can still be observed with baited video methods (Cappo et al. 2006; Coghlan et al. 2017; Harvey et al. 2007), with larger and typically rarer predators being more effectively sampled than with diver-based techniques (Goetze et al. 2015; Langlois et al. 2010; Watson et al. 2005). Comparative studies of diver and remote stereo-video methods for sampling fish assemblages have typically recommended that both methods can be useful for different portions of the fish assemblage (e.g. Goetze et al. 2015; Langlois et al. 2010; Watson et al. 2005, 2010). Goetze et al. (2015) undertook similar research for periodically closed areas in Fiji concluding that stereo-DOVs were most suitable for monitoring herbivorous species in periodically harvested closures, while stereo-BRUVs were recommended for sampling carnivorous species or those wary of divers. Comparisons of these two survey methods have not occurred inside and outside of permanently closed NTZs.

Fish abundance and size structure are considered sensitive indicators of fishing and, therefore, the comparison of these metrics inside and outside NTZs should provide an approach to investigate the existence of methodological biases between diver and remote stereo-video methods. A recent meta-analysis of targeted fish abundances recorded during discrete surveys inside and outside of a network of no-take zones within the Ningaloo Marine Park (NMP) over a 30-year period, found mixed patterns amongst fish groups and sampling methods, suggesting stereo-BRUV had more consistently detected greater abundance of targeted species within no-take zones in comparison with DOVs and UVC (Cresswell et al. 2019). Such studies highlight the need to understand how the choice of sampling methods can impact the findings of long-term monitoring programmes that aim to assess the effectiveness of spatial zoning. Here, we contrasted stereo-BRUV and stereo-DOV methodologies to assess the abundance and size of recreationally targeted fish species inside and outside NTZs within the NMP. It was hypothesised that the abundance of legal-sized individuals and the length of targeted species would be greater in the NTZs than in areas open to fishing. Further, it was hypothesised that stereo-BRUVs would more consistently detect differences inside and outside NTZs than stereo-DOVs.

Materials and methods

Study site

The Ningaloo Marine Park (NMP) is located adjacent to the North West Cape of Western Australia and covers a total area of 2633.43 km². It stretches along approximately 300 km of coastline from 23°48′S to 21°48′S (Fig. 1) and covers the majority of Ningaloo Reef (a World Heritage site). The NMP
was first established in 1987 and was revised and extended in 2004 to incorporate the full length of the fringing coral reef (MPRA and CALM 2005). The NMP covers a total area of 263,343 ha, and includes 18 separate NTZs with a total area of 88,565 ha. The 18 NTZs vary greatly in size, ranging between 8 and 44,752 ha.

The focus of this research project was on the shallow lagoonal waters (depth ~ 0.5–8 m), inside and outside of six NTZs, in the area between Tantabiddi and Pelican Point (Fig. 1). Surveyed sites are from the Department of Biodiversity, Conservation and Attractions (DBCA) Ningaloo Marine Park long-term monitoring programme and have been chosen to be interspersed to avoid any confounding impacts of medium-scale variation in habitat or human access. The six surveyed NTZs were: Mangrove Bay (11.35 km²), Mandu (13.49 km²), Osprey (95.13 km²), Winderabandi (55.26 km²), Cloates (447.52 km²) and Pelican (108.64 km²; Fig. 1). All surveyed NTZs were in place by 1987 under an earlier spatial zoning scheme (MPRA and CALM 2005; Cresswell et al. 2019). Although any boat-based extractive uses are prohibited in the NTZs surveyed here, shore-based recreational line fishing is permitted adjacent to the landward borders of NTZs in some locations within the Osprey, Winderabandi, Cloates and Pelican NTZs (MPRA and CALM 2005). There have not been any major commercial fishing activities within the NMP since the 1970s.

**Experimental design**

The current study used stereo-DOV surveys collected as part of the existing long-term monitoring programme (LTMP) of fish assemblages within the NMP conducted by the DBCA. The survey areas are known to support relatively high fish species richness and to encompass a range of site attached and mobile species, including recreationally targeted species (Cassata and Collins 2008; MPRA and CALM 2005).

Stereo-BRUV surveys were performed over a ten-day period in August 2015 with a total of 89 deployments conducted (55 within NTZs and 34 outside) while 102 stereo-DOV transects were completed (66 within NTZs and 36 outside) in August 2014. These replicates were summed into a total of 17 sites, which comprised 3–5 independent replicate stereo-BRUV deployments or six replicate stereo-DOV belt transects (Fig. 1).

Sampling was stratified for a consistent depth (2–8 m) and habitat, characterised by contiguous reef structure or broken up coral or rubble bordering the lagoon. Stereo-BRUV surveys were conducted at the same sites in comparable habitat as stereo-DOV surveys. The one exception to this occurred within the Osprey NTZ, where stereo-BRUV deployments were slightly offset from the stereo-DOV survey site due to restrictions of the use of baited cameras in areas popular for snorkelling/swimming. The stereo-BRUV site at Osprey was offset approximately 1800 m from the stereo-DOV site, to avoid the designated swimming area. Regardless of this offset, great care was taken to ensure that the benthic composition and habitat of the sites both inside and outside each NTZ and of the individual deployment locations for each method were as comparable as possible. In addition to the lack of temporal interspersion of the two sampling methods, it was also recognised that the sampling units for stereo-DOV and stereo-BRUV are very different and so formal statistical comparison between the two sampling methods was restricted to comparison of mean length metrics, whereas no comparison of abundance metrics was made. Instead, simultaneous analyses of the effect of NTZs and habitat covariates for both sampling methods were conducted. The design of the LTMP for the NMP is established to provide information at the level of the marine park and is lacking adequate replication to investigate the generality of any patterns in the targeted fish assemblage for each NTZ surveyed.

**Sampling methods**

**Baited remote underwater stereo-video (stereo-BRUV)**

This study used a stereo-BRUV system consisting of two paired GoPro HERO3+ cameras (see Langlois et al. 2010 for design). Cameras were installed on a steel frame separated by 0.7 m, facing 8° inwards to achieve an optimised field of view for precise fish length measurements (see Harvey and Shortis 1995; Langlois et al. 2010; Watson et al. 2010). To achieve accurate length measurements, the cameras were calibrated prior to field work using the software CAL (SeaGIS Pty Ltd 2014; Shortis and Harvey 1998). A 1.2 m long plastic rod with a plastic-coated, wire mesh bait basket and a synchronising diode was extended from the centre of the steel frame (Watson et al. 2010; Watson and Harvey 2007). Approximately 1 kg of crushed pilchards (Sardinops spp.) were used as bait, with crushing done to maximise the amount of fish oil and flesh released. The stereo-BRUV system was deployed on the seafloor by boat and set to film for a period of 60 min. The minimum distance of ~250 m was maintained between concurrent deployments to minimise the likelihood of fish travelling between neighbouring deployments within the 60-min deployment duration (see Cappo et al. 2004).

**Diver-operated stereo-video (stereo-DOV)**

The stereo-DOV system consisted of two paired Canon Legria HF G25 cameras, following the same design as the stereo-BRUV system (see Langlois et al. 2010 for design). Additionally, a synchronising diode was attached to the
stereo-DOV system and floats were fixed to the base bar to make the system neutrally buoyant. Six replicate belt transects (50 m × 5 m) were conducted at each site with a minimum distance of 10 m separating each replicate transect. SCUBA divers swam at an approximate speed of 0.33 ms\(^{-1}\) staying circa 0.5–0.7 m above the substrate. Methods followed Goetze et al. 2019, with the system swum at a slight downwards facing angle to keep the horizon line (where the ocean floor meets the water) in the upper third of the video frame.

### Video analysis

EventMeasure Stereo\(^{TM}\) was then used to identify, count and measure fish (SeaGIS Pty Ltd 2014). All fish were identified to the lowest taxonomic level possible. An exception identified during this process were the various mackerel species, *Scomberomorus* spp., which could not be reliably distinguished from video imagery, these are herein referred to as *Scomberomorus* spp. To standardise the sampling areas, only fish within the 7 m survey boundary, for both survey methods, and within 2.5 m to either side of the centre transect point for stereo-DOV surveys were included. For stereo-BRUVs, MaxN was used as the relative abundance of a species, defined as the maximum number of individuals from the same species present at any one time within the 60-min sample duration (Priede et al. 1994). For stereo-DOVs, the total number of individuals of all species observed in a stereo-DOV transect was used as the abundance.

After species identification was completed, all recorded fish were assigned to either targeted or non-targeted species, with targeted species being defined as those species most commonly retained (landed and kept) by recreational fishers within the shallow water lagoon of the NMP (STable 1; Ryan 2013; Ryan et al. 2015). *Caranxoides fulvoguttatus* was also included as a target species due to observations from unpublished local boat ramp surveys, while *Epinephelus fasciatus* was also included due to its similarity to the more commonly retained *E. rivulatus*. Lengths (snout to tail fork = fork length; FL) were measured of all fish at the time of MaxN for stereo-BRUVs and for all individuals encountered on a stereo-DOV transect. Length data obtained were then used to identify which individuals of the targeted species were either equal to or greater than the minimum legal length (MLL), hereafter referred to as ‘legal-sized’ (see STable 1) for subsequent analysis. The total number of individuals, species and families, as well as the five most ubiquitous and abundant families and species recorded with each method are provided in the appendix (STable 2).

Habitat types and percentage cover were assessed using TransectMeasure\(^{TM}\) (SeaGIS Pty Ltd 2014). Following methods given in Langlois et al. (2020) and detailed here https://benthic-bruvs-field-manual.github.io/, a freeze-frame of each stereo-BRUV and five separate freeze-frames (evenly spaced) from each stereo-DOV transect, were overlaid with a 5 × 4 grid and the major habitat type of each grid was classified following a modified CATAMI classification scheme (Althaus et al. 2015). This resulted in the description of six broad habitat types: stony corals, black octocoral, sponges, macroalgae, rubble and sand. An additional habitat variable, reef, was composed of the three reef associated broad habitat types, including rubble, macroalgae and black octocoral. The percentage cover of each habitat type per sample was calculated, with grids classified as open water excluded from this calculation. Additional to the habitat composition, habitat complexity was classified on a scale from flat (0) to high structural complexity (5) within each grid cell. The mean and standard deviation (SD) of relief was calculated for each sample. The methods to estimate mean and SD of relief have been independently established for each method following complementary approaches and as such should be relatively comparable but will not be the same between each sampling method (i.e. DOV vs BRUV) given the different sampling unit areas (Collins et al. 2017).

### Statistical analysis

Analysis of the relative abundance of legal-sized individuals from each target species was conducted separately for each method. The analysis followed a two-factor sampling design with Status (fixed, two levels: NTZs, fished areas) and Site (random, nested within Status). Univariate analyses were used to compare the mean length for each species using permutational multivariate analyses of variance (PERMANOVA; Anderson 2001; Anderson et al. 2008) in the PRIMER v6 software package (Clarke and Warwick 2001). The analyses were performed using the Euclidean distance dissimilarity measure on raw length data (no zeros present). To create a statistical test for mean length, a four-factor design was used which included an additional factor, Replicate (random; nested in Method, Status and Site). ‘Replicate’ was added because the number of individuals measured varied between deployments. It also accounted for nonindependence (Bornt et al. 2015).

Highly correlated (\(R^2 > 0.9\)) environmental variables were excluded, and their distributions examined for uniformity and transformations were performed where necessary (Zuur et al. 2010). This resulted in only five environmental variables being examined: mean relief, SD relief and the % coverage of sand, stony coral and reef with a log transformation. Additional variables that document human access gradients were considered, but a lack of consistent human use data across the study area precluded their use here.

Generalised additive mixed models (GAMMs) with full-subset model selection (FSSgam, Fisher et al. 2018) was used to determine if Status or any measured environmental
or interactions between these predictors best explained variance in the abundance distribution for the species of interest. Models containing variable combinations with correlations > 0.28 were excluded to eliminate potential problems with collinearity and overfitting (Graham 2003). Abundance data was modelled using a tweedie distribution, implemented via a call to gam() (mgcv, Wood 2011). Model sizes were limited to only three terms (size = 3) and k in the GAMMs was limited to 5. Model selection was based on Akaike’s Information Criterion (AIC, Akaike 1973) optimised for small sample sizes (AICc, Hurvich and Tsai 1989) and the most parsimonious model chosen was that with the fewest variables but within two units of the lowest AIC. Importance scores of each variable were obtained by summing the AICc weights of each model that each variable occurred within (Guthery et al. 2003) and these scores were then plotted to identify the relative importance of predictor variables across all possible models. The R language for statistical computing (R Development Core Team 2013) was used for all data manipulation (dplyr, Wickham et al. 2022), analysis (mgcv, Wood 2011) and graphing (ggplot2, Wickham 2016).

Results

In total, 13 species targeted by recreational fishing effort were recorded from the 89 stereo-BRUV deployments and 102 stereo-DOV transects but only seven species were recorded on more than four occasions (Table 1). These species differ in the degree they are retained by recreational fishers from commonly caught Lethrinus nebulosus (spangled emperor) and Epinephelus rivulatus (chinaman rockcod), to moderately caught L. laticaudis (grass emperor), to less often caught C. fulvoguttatus (goldspotted trevally), and the less often recorded species E. coioides and G. grandoculis (golden trevally; Ryan et al. 2015). Stereo-BRUVs recorded 12 targeted species, while only eight species were recorded by stereo-DOVs. The targeted species Lethrinus laticaudis was unique to stereo-DOVs, while five species were only recorded on stereo-BRUVs (Gymnocephalus grandoculis (Robinson’s seabream), Scomberomorus spp (mackerel), Cephalopholis sonnerati (tomato rockcod), Epinephelus coioides (estuary cod) and Variola louti (yellow-edged coronation trout). Of the 13 targeted species, 10 were smaller than the minimum legal-size for retention and/or the sample size was too small to allow for analysis. Legal-sized individuals from C. fulvoguttatus, E. rivulatus and L. nebulosus were recorded in sufficient numbers by one or both methods to allow analysis (Table 1). However, although C. fulvoguttatus and E. rivulatus were sampled successfully by stereo-BRUV, their occurrence was too rare on stereo-DOV transects (<10% of the transects) to allow for statistical analysis.

The two methods recorded contrasting numbers of the highly targeted and retained species L. nebulosus, with 109 individuals recorded by stereo-BRUVs and 429 individuals recorded on stereo-DOVs (STable 1). However, ~35% of the measured individuals recorded on stereo-BRUVs were of legal size, opposed to only ~5.5% on stereo-DOVs (STable 1).

### Table 1

| Method   | Species               | Best models                                      | ΔAICc | ωAICc | R²  | EDF |
|----------|-----------------------|--------------------------------------------------|-------|-------|-----|-----|
| stereo-BRUV | Lethrinus nebulosus | Mean Relief×Status, SD Relief×Status             | 0     | 1.00  | 0.45| 18.83|
|          | Carangoides fulvoguttatus | Mean Relief+ Status                             | 0     | 0.34  | 0.39| 12.84|
|          | Epinephelus rivulatus  | Mean Relief+ SD Relief                           | 0.34  | 0.28  | 0.38| 12.53|
|          |                       | Mean Relief+ SD Relief+ Status                   | 0.58  | 0.51  | 17.43|
| stereo-DOV | Lethrinus nebulosus | Reef                                             | 0.97  | 0.36  | 0.51| 17.80|

Difference between lowest reported corrected Akaike Information Criterion (ΔAICc), AICc weights (ωAICc), variance explained (R²) and effective degrees of freedom (EDF) are reported for model comparison. Model selection was based on the most parsimonious model (fewest variables) within two units of the lowest AICc. Best models are ordered by parsimony.

Variables influencing the distribution of legal-sized target species

The most parsimonious model for the abundance of legal-size L. nebulosus in the stereo-BRUV data included an interaction between status and mean relief and between status and SD of relief, which together explained 45% of the variation in its distribution (Table 1). Both of these interactions indicated that the abundance of L. nebulosus was higher in no-take zones (NTZs); however with increased levels of mean relief, the abundance in protected areas decreased, while increased levels of the SD of relief (i.e. increased variability of relief) in protected areas correlated with a higher abundance of L. nebulosus (Figs. 2, 3). Due to the very low number of greater than legal-size L. nebulosus within the fished sites, modelled relationships...
Differences in length distribution

Considering all *L. nebulosus* observed (109 on stereo-BRUVs, 429 on stereo-DOVs), stereo-DOVs yielded length measurements of a higher proportion (78%, *n* = 307) than stereo-BRUVs (58%, *n* = 63). Considering only legal-sized *L. nebulosus*, however, stereo-BRUVs facilitated the measurement of 22 individuals compared to 17 by stereo-DOVs. Of the 47 *L. nebulosus* measured from stereo-BRUVs in NTZs, 21 were larger than the minimum legal-size of 410 mm as opposed to only 1 individual in fished areas. While 13 of the 287 individuals measured on stereo-DOVs in NTZs were larger than the minimum legal size and only 4 individuals in fished areas.

Analysis of variance of the mean length of *L. nebulosus* found a significant interaction of sampling method and status (Table 2, Fig. 4). Pairwise comparisons indicated this was driven by significantly larger *L. nebulosus* observed within the NTZs when sampled by stereo-BRUV (*t* = 2.96, *p* < 0.01) whereas no difference was observed in the stereo-DOV data. No significant difference in mean length was found in either *C. fulvoguttatus* or *E. rivulatus* inside and outside the NTZs when sampled with stereo-BRUV, and insufficient length measures were obtained for these species to analyse the patterns observed using the stereo-DOV method.

Discussion

Baited remote underwater stereo-video (stereo-BRUV) found consistently greater abundance of two commonly targeted fish species (*Lethrinus nebulosus* and *Carangoides fulvoguttatus*) and a greater length distribution of *L. nebulosus* within no-take zones (NTZ) compared to fished locations within the Ningaloo Marine Park (NMP). In contrast, diver-operated stereo-video (stereo-DOV) did not. In addition, for the most frequently retained target species (*L. nebulosus*), stereo-BRUVs surveyed larger individuals in NTZs compared to areas open to fishing. In contrast, for target species sampled using the stereo-DOV method, the influence of NTZ status was either minor or could not be tested due to the low number of legal-sized individuals sampled, and there was no difference in the mean length of *L. nebulosus* inside and outside NTZs. These results suggest that stereo-BRUVs are a more suitable method to investigate the influence of fishing on the abundance and size of targeted species in shallow (< 8 m) lagoon areas at this location. It remains unclear whether the differences between survey methods would persist if much greater numbers of individual fish were recorded through increased sampling effort using the stereo-DOV method (i.e. further length measures obtained for legal-sized individuals) (see Weerarathne et al. 2021).

However, given that the current design is likely at the limits
of realistic ongoing resourcing in such a remote location, this suggests that stereo-DOV may not be optimal for sampling the legal-sized target species at this location.

An understanding of potential methodological biases of available sampling methods is essential to design ecological assessment programmes, and the interpretation of data that comes from them (Holmes et al. 2013). Consideration should be given to both the direct limitations of the methodologies themselves (e.g. performance in low water visibility, observer bias, depth restrictions of divers) as well as their relative performance to detect differences in indicators of interest (e.g. habitat composition, fish abundance and size). In the current study, we found that the remote stereo-BRUV method detected a larger mean size of the primary target species, \textit{L. nebulosus}, than the diver-based method (stereo-DOV). Similar results have been obtained inside NTZs comparing stereo-DOV and stereo-BRUV methodologies in the past (Watson et al. 2010). However, no previous research has examined how methods compare when surveying fish assemblages inside and outside NTZs for carnivorous target

Table 2 Results of permutational analysis of variance (PERMANOVA) for mean length of targeted species recorded on stereo-BRUVs and stereo-DOVs, inside and outside the no-take areas across the Ningaloo Marine Park

| Species                  | Source          | df  | MS     | F      | p  |
|--------------------------|-----------------|-----|--------|--------|----|
| \textit{Lethrinus nebulosus} | Method          | 1   | 8466.4 | 0.75   | 0.402 |
|                          | Status          | 1   | 4722.6 | 0.42   | 0.51  |
|                          | Method × Status | 1   | 1.67E+05 | 14.8  | 0.003 |
| \textit{Carangoides fulvoguttatus} | Status     | 1   | 9238.8 | 0.18   | 0.68  |
| \textit{Epinephelus rivulatus}  | Status         | 1   | 4698.5 | 1.38   | 0.254 |

The interaction of Method (stereo-BRUV vs stereo-DOV) and Status (inside and outside the no-take areas) was only investigated for \textit{Lethrinus nebulosus} due to the limited number of length measures for the other species. Significant results ($p<0.05$) are shown in bold. All unique permutations $>9999$
species. Although Goetze et al. (2015) found that stereo-DOV was adequate for characterising populations of fished herbivorous species inside and outside Periodic Harvesting Closures, the current study suggests that stereo-BRUV may be more appropriate to characterise populations of fished carnivorous species (e.g. Lethrinid, Carangids) inside and outside permanent No-take Zones.

There is a growing body of research suggesting that fishing has an influence on fish behaviour, increasing their overall ‘wariness’ when visually sampled by divers (Goetze et al. 2017; Januchowski-Hartley et al. 2011; Kulbicki 1998). This effect may be amplified in larger and older fish that are generally targeted more frequently by fishing activity and have had a longer period of time to build up acquired behaviours (Gotanda et al. 2009). As *L. nebulosus* is a relatively mobile species that has the capacity to move across NTZ boundaries over longer periods (e.g. months to years) within the NMP (Pillans et al. 2014), larger individuals that have moved into NTZs may not be detected by the diver-based stereo-DOV method because these fish have acquired wariness behaviours and are diver avoidant. As spearfishing is permitted in all fished areas to the south of the Winderabandi sanctuary zone, this may well have been a contributing factor towards wariness in the current study. As such, the remote stereo-BRUV method may provide a more representative estimate of the size range for mobile fish species inside and outside the NTZs found within the NMP.

While avoidance behaviour is likely to have played a role in the results observed, it is possible that stereo-BRUV method may also overestimate the abundance of larger individuals. The area sampled by stereo-BRUVs is unknown and can be inconsistent within a study based on variations in current strength between sites (Taylor et al. 2013) and the burley effect due to other fish feeding on the bait (Langlois et al. 2015). Similarly, as larger *L. nebulosus* individuals are more mobile than smaller conspecifics (Pillans et al. 2014), the use of bait may sample these size classes from a larger area, effectively over-sampling larger bodied fish. However, in the current study, stereo-BRUV only observed a greater abundance of larger bodied individuals within the NTZ, suggesting the pattern observed is due to stereo-BRUVs’ more accurately detecting the influence of fishing pressure. Here, the low proportion of length estimates obtained by the stereo-BRUV method in comparison to the stereo-DOV (58% and 72%, respectively) is likely due to high habitat complexity across the study sites, with the static nature and close proximity of the stereo-BRUV units to the benthos meaning that fishes further from the camera were frequently partially obscured, making accurate length estimates impossible. As such, any differences in habitat complexity (measured as mean and SD relief) between study sites have the potential to correlate with variation in the size structure being sampled, particularly if behavioural factors mean that sizes are not evenly distributed with increasing range from the diver-based or remote stereo-cameras. However, recent careful analysis of fish behaviour and abundance measures obtained from stereo-BRUV deployments have revealed that the presence of larger bodied fish during deployments had no influence on the size distribution of conspecifics sampled, suggesting that larger fish do not displace smaller ones across the 60-min sampling duration with stereo-BRUVs (Coghlan et al. 2017).

*Lethrinus nebulosus* is the primary target species within NMP (Holmes et al. 2017), and as such any NTZ effects are likely to be most apparent in this species. In this study NTZ effects were less obvious in other target groups/species (i.e. *Carangoides fulvoguttatus* and *Epinephelus rivulatus* using stereo-BRUV), with the stereo-DOV method failing to record high enough abundances of any target species other than *L. nebulosus* to facilitate statistical analysis. This is likely due to a combination of detectability issues using the selected methodologies (i.e. stereo-DOV can be poor at detecting cryptic and pelagic species; Holmes et al. 2013), sub-optimal habitat at study sites for the species in question.
(e.g. *E. rivulatus* is primarily found in macroalgal dominated habitats; Ayling and Ayling 1987; Mackie and Black 1996) and lower relative fishing effort on other target species (Ryan et al. 2015). *C. fulvoguttatus* is the only other species to display a positive NTZ effect, detected using stereo-BRUV. While NTZs are generally considered to be less effective for benthic-pelagic mobile species (Grüss et al. 2011; Le Quene and Codling 2009; Walters et al. 2007), some studies suggest that such benthic-pelagic species can be site attached (including *C. fulvoguttatus*) and therefore more likely to be protected with the relatively small NTZs within the NMP (Pillans et al. 2011). Bearing in mind that this species is easily capable of swimming between adjacent stereo-BRUV deployments (~250 m) during the 60-min videos, this result should be considered with caution. However, there were no consistent patterns of schools of this species between adjacent stereo-BRUV deployments, suggesting that NTZs within the NMP may actually provide a degree of protection for this highly mobile species.

The results of prior studies examining NTZ effectiveness at this location have been mixed, with variation in methodologies over the years and between studies making it difficult to draw clear conclusions (Wilson et al. 2012; Fitzpatrick et al. 2015). A recent meta-analysis of NTZ assessments within NMP reached a similar conclusion, finding conflicting results and effect sizes amongst fish species, methods and studies (Cresswell et al. 2019). While they found higher abundance of *L. nebulosus* overall inside NTZs, there was no difference in the abundance of *E. rivulatus*. Fitzpatrick et al. (2015) found higher abundance and larger size of both *L. nebulosus* and *E. rivulatus* inside NTZs, when sampling across multiple habitat types (including shallow water algal habitat where *E. rivulatus* is more abundant), using a stereo-BRUV method. Alternately, Wilson et al. (2012) found little evidence to suggest higher abundance or biomass of targeted species inside NTZ using a diver-based UVC method, instead finding habitat complexity to play a more important role in structuring targeted fish communities. Our study also highlighted the important role that habitat complexity plays in structuring the abundance patterns of targeted fish species at this location, with habitat complexity attributes consistently being found to be important for predicting the distribution of *L. nebulosus* and being the primary factor explaining variation in abundance for both *C. fulvoguttatus* and *E. rivulatus*. Here, sites inside and outside the NTZs were chosen to have as comparable habitat characteristics as possible (i.e. shallow water lagoon, back-reef, mid/low coral cover, medium complexity). Habitat factors (including an awareness of optimal habitat for species being examined) should also be considered as a key component of sampling design.

This study highlights the importance of considering which method should be used to sample fish assemblages, especially for long-term monitoring. The objectives of the long-term monitoring programmes need to be considered, e.g. if the entire fish community should be assessed or only specific species, families or feeding guilds. Further, it needs to be considered if differences between fished and NTZs or across gradients in fishing pressure are an essential component of the assessment. Stereo-DOVs might be more suitable for monitoring an entire assemblage and investigating the influence of habitat change, but we have found that this method underrepresents fisheries target species. If the primary objective is to examine the effectiveness of spatial closures on targeted carnivorous fish species or across known fishing pressure gradients, stereo-BRUVs appear to be a more suitable sampling methodology, and likely to be just as sensitive to the influence of habitat change as stereo-DOVs.

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Author contributions AJH, TL, DM and THH conceived the ideas and designed methodology; AJH and TL analysed the data; All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics statement Sampling was conducted in waters of north-west Australia and was covered by The University of Western Australia Animal Ethics Approval # RA/3/100/1317.

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