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10. Fish and shark assemblage dynamics

10.1 Ontogenetic shifts in commercially important *Lethrinus punctulatus* a short-lived endemic species of the Pilbara, Western Australia

Authors: Taylor MD, McLean D, Candland L, Piggott C, Wakefield C, Langlois T.

ABSTRACT

The Dampier Archipelago in north-west Australia, is home to high marine diversity as well as one of Australia's busiest ports and a suite of demersal fisheries. The present study aims to build on the limited knowledge of the endemic blue spotted emperor, *Lethrinus punctulatus*, a short-lived, commercially important indicator species of the Pilbara Demersal Scalefish Fishery. To achieve this, we examine the distribution of *L. punctulatus* across a continuous depth gradient and its association with a variety of environmental variables. Baited remote underwater stereo-video systems were deployed across this continuous depth gradient, and a variety of substrata and habitat types, along the outer edge of the Dampier Archipelago and out into the open ocean to 60 m depth (50 km offshore). Biomass increased with increasing depth reflecting the exclusive presence of juveniles in depths <10 m and the tendency for larger mature individuals to be found in depths >40 m. Juveniles of this species disassociated with complex reef habitat, where predatory fish are often abundant, and were associated with shallow macroalgal habitat. This study identifies important shallow macroalgae habitats for a commercially important endemic emperor species. Protection of these habitats is essential to support sustainable fishing of adults in offshore deeper waters. The use of stereo-video for sampling a fish species across its range and growth is an example of a non-extractive approach to investigating abundance, life history, and ontogenetic changes. This approach may be appropriate for sampling other targeted species and identifying areas of importance in terms of protection and fishing effort.

10.1.1 INTRODUCTION

Broad scale environmental variables such as depth, temperature, and oceanographic conditions, have significant effects on the distribution of demersal fish species (Travers et al. 2006; Dulvy et al. 2008). Finer scale environmental variables, such as relief and habitat composition, can greatly influence the distribution of individual species as well as the distribution of communities within an ecosystem (Shepherd and Brook 2007; McLean et al. 2016). By looking at a single species and tracking its size distribution in relation to both fine and broad scale variables we can gain an understanding of how these relations change across the life-history of a species. These shifts occur as patterns of resource use vary with increased size and age (Werner and Gilliam 1984), and are driven by metabolic requirements to maximise growth rates while minimising the threat of predation (Schoener 1974). Such ontogenetic shifts have been investigated across both terrestrial and marine organisms, and can create spatially partitioned populations, represented by different age classes (Dahlgren and Eggleston 2000; Travers et al. 2006). In the marine environment spatially distinct size-structured populations are common and are seen in many commercially important fish species as they make ontogenetic niche shifts throughout their development from larvae to mature adults (Chittaro et al. 2005; Nakazawa 2014). A significant proportion of spatial variability observed in commercial fish species can be attributed to changes in depth (e.g. Bell 1983; Donaldson 2002); with adults often found across a greater range of depths and habitats, while juveniles are often limited to shallow, sheltered coastal habitats (Dahlgren and Eggleston 2000; Shepherd and Brook 2007; Faunce and Serafy 2007). Understanding this connectivity between juvenile habitats and those that support adult populations is important for understanding species life history and ensuring sustainable management of fisheries stock.

The Lethrinidae (emperors) are one of the most important families for commercial fisheries in tropical Australia (Fletcher and Santoro 2015). A number of species within this family are considered to be indicators for multi-species fisheries in Western Australia (DoF 2011). In the Pilbara Demersal Scalefish Fisheries of north-west Australia the endemic species *Lethrinus punctulatus*, blue spotted emperor, is considered as an indicator for short-lived commercial species by the Department of Fisheries (DoF 2011). Globally *L. punctulatus* is not considered as a separate species, but as a synonym for *Lethrinus lentjan*, pink ear emperor. For the case of this study we will use the name *L. punctulatus* and consider this as a separate endemic species based on their consideration as such by the Department of Fisheries. Whilst studies of *L. punctulatus* are limited, many Lethrinids have been recorded showing significant changes in cross shelf abundance with adult abundance lower in shallower depths (Newman 1997; Newman and Williams 2001). In north west Australia, juvenile Lethrinids are often found in macroalgal dominated sites (Wilson et al. 2012; Evans et al. 2014), while other studies have also found juvenile associations with mangrove and seagrass habitats before relocation to diverse reef systems once matured (Kimirei et al. 2011). Shallow habitats are highly productive; providing both food, and shelter from predators. While reef habitats, despite being productive, are likely to have an abundance of species that predate juvenile Lethrinids (Heinlein et al. 2010; Evans et al. 2014).

The Pilbara Demersal Scalefish Fisheries predominantly target Lethrinids, Lutjanids (snappers), and Epinephelids (cods), and is active in the waters adjacent to our study area around the Dampier Archipelago (Newman et al. 2015). Across the region three fisheries, the Pilbara Trap, Trawl, and Line Fisheries combine to make up the Pilbara Demersal Scalefish Fishery and have an estimated value of AUS$ 12 million (Newman et al. 2015). The Pilbara Line Fishery tends to operate ate depths >140 m and almost exclusively target *Pristipomoides multidens* (goldband snapper) and *Etilis carbunculus* (ruby snapper) (Newman et al. 2015). Both the Pilbara Fish Trawl Fishery and the Pilbara Trap Fishery extract significant amounts of lethrinids with *L. punctulatus* making up 93 t (8.5%) and 49 t (18.3%) of each fisheries catch (Newman et al. 2015). The Pilbara Fish Trawl Fishery operates between the 50 m and 200 m isobath and is responsible for the largest component of the Pilbara

Demersal Scalefish Fisheries at 1,105 t in 2014-15 (Newman et al. 2015). The Pilbara Trap Fishery was only responsible for 268 t in 2014, and is limited to water deeper than 30 m. Full assessment and review of the catch range for the Trawl Fishery is underway, as such any further knowledge of the spatial distribution of commercially important indicator species in the region could support legislative decisions affecting the future of this fishery.

Indicator species for these fisheries are assigned by the Department of Fisheries based on criteria set out in Lenanton et al. (2006). Identification of indicator species allows for efficient monitoring and assessment of the fishery as a whole. *L. punctulatus* is one of five indicator species for the Pilbara Demersal Scalefish Fisheries alongside red emperor (*Lutjanus sebae*), *P. multidens*, brown-stripe snapper (*Lutjanus vitta*) and rankin cod (*Epinephulus multinotatus*) (DoF 2011). Due to its limited geographical range and historical taxonomic discrepancies there has been little research into *L. punctulatus* (Hutchins 2004; Travers et al. 2006). Current research and preliminary observation by the Department of Fisheries suggests that juvenile *punctulatus* of less than 200 mm in length are limited to shallow depths and are predominantly found in macroalgal dominated habitats, but rarely in areas containing sandy, coralline or sponge habitats (Wakefield pers. comms.). Other lethrinid species are known to associate with low relief soft bottom habitats including macroalgal and seagrass beds (Evans et al. 2014). Macroalgal habitats have also been indicated to be important nursery habitats in the north west of Australia, with lethrinids particularly positively correlated with macroalgal habitat (Evans et al. 2014).

The present study aims to investigate ontogenetic shifts in the short-lived commercially important *L. punctulatus* by assessing its inshore to offshore changes in size distribution as it relates to depth and habitat. By conducting a continuous study across a large depth and habitat range, using stereo-baited remote underwater video systems to obtain detailed size information on the population of this species, it is possible to identify relationships between size and environmental variables. We expect to see depth related ontogenetic niche partitioning and evidence of a spatially distinct size-structured population; with individuals of greater size found at greater depth and smaller juveniles limited to shallower depths. In terms of habitat associations we expect to see associations with macroalgae dominated habitat in the smallest individuals of both species, while larger individuals likely to be correlated with low relief deep reefs.

10.1.2 METHODS

Study Site

The present study was conducted offshore of the Dampier Archipelago in the Pilbara region of Western Australia (Figure 10.1.1). Considered as one of the most biodiverse regions of Western Australia, this tropical archipelago has a diverse range of habitats ranging from sheltered mangroves to exposed coral reefs. It is home to approximately 800 fish species with greatest diversity reported in the outer islands of the archipelago (Hutchins 2004; Fox and Beckley 2005). Situated to the north west of the busy natural resource hub of Dampier, this region is well known for its fishing and snorkelling, as well as for shipping associated with resource extraction on the North West Shelf.

The islands of the Dampier Archipelago (20.4846° S, 116.5905° E) are protected and managed by the Department of Biodiversity, Conservation and Attractions (DBCA) however marine protection is limited with recreational fishing permitted in the majority of the region. Commercial fishing is limited to waters over 30 m deep for the Pilbara Trap Fishery, and greater than 50 m in depth for the Pilbara Trawl Fishery. The pressure of commercial fishing is however low in this region, comparative to other regions in Australia, due to the large spatial extent of the fishery, limited quotas and low fishing effort (Newman et al. 2015).

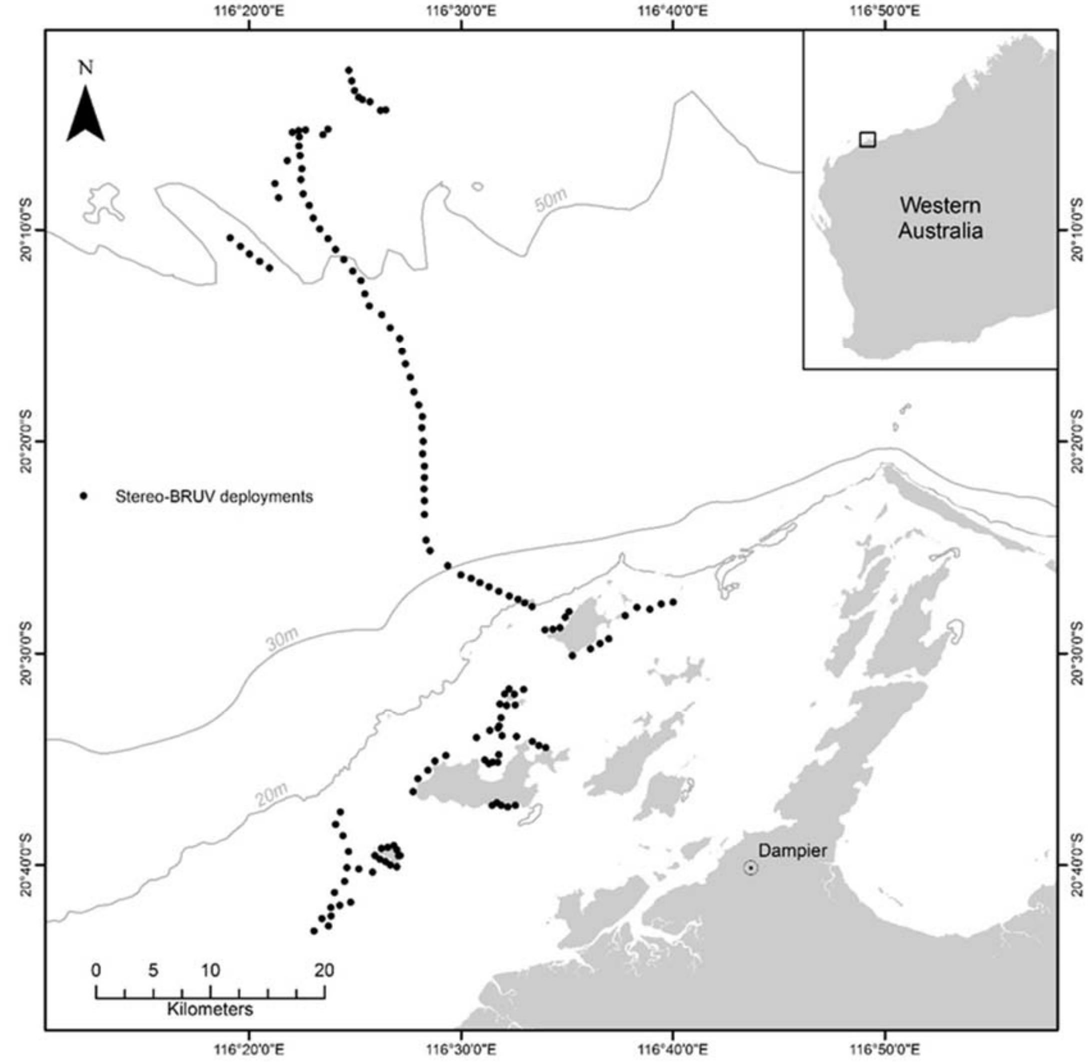

Figure 10.1.1 Location of 139 stereo-BRUV deployments conducted in the Dampier Archipelago and offshore onto the continental shelf, Pilbara region of north-western Australia.

Sampling Protocol and Equipment

Sampling was conducted between 10th and 13th of September 2015 using baited remote underwater stereo-video systems (stereo-BRUVs) to survey fish assemblages (Figure 10.1.2). A continuous transect using a total of 148 stereo-BRUV deployments, 139 usable deployments, was collected from the waters along the northern edge of the Dampier Archipelago and offshore into deeper waters to the north (Figure 10.1.1). Sampling was conducted from shallow waters (1.1 m) within the Dampier Archipelago to deep offshore waters (56.6 m; mean depth 25 m).

The sampled transect extended approximately ~50 km to the north of Rosemary Island and was continuously sampled across a depth gradient. Stereo-BRUV deployments were stratified for complex structured seafloor, for example reef, rocky, macroalgal, sponges, rubble, etc. Deployments were located ~1000 m apart in order to maintain independence of deployments (Cappo et al. 2004) and to maximise the spatial distribution to cover a greater range of depths. Favourable structure was located using a ship-borne digital sounder operated by the boat pilot, and visual searches in shallow waters. As a result, sand dominated habitats are likely to be underrepresented in this study, especially in shallower waters where avoidance is easier. In order to reduce variability associated with crepuscular and nocturnal fish assemblage changes all sampling commenced two hours after dawn and conclude two hours before sunset.

Ten stereo-BRUVs were deployed concurrently in order to maximise sampling efficiency, with their design based on that described in Langlois et al. (2010; 2015). Each stereo-BRUV consisted of a pair of video cameras (GoPro Hero 3+ Silver or Canon Legeria HFG25) mounted 0.7 m apart on a steel frame in underwater housings. A plastic coated wire mesh bait bag was filled with approximately 1 kg of crushed pilchards (*Sardinops* spp.) (Harvey et al. 2007) . This is the same quantity and species used as baits in the fish traps of the Pilbara Fish Trap fishery, they are crushed in order to promote dispersal of flesh and fish oil as a bait plume (Willis and Babcock 2000). Each stereo-BRUV was deployed from a boat and left to film for at least 60 minutes on the seafloor before retrieval and redeployment. Details regarding the stereo calibration process can be found in the work of Harvey and Shortis (1996) and Shortis and Harvey (1998).

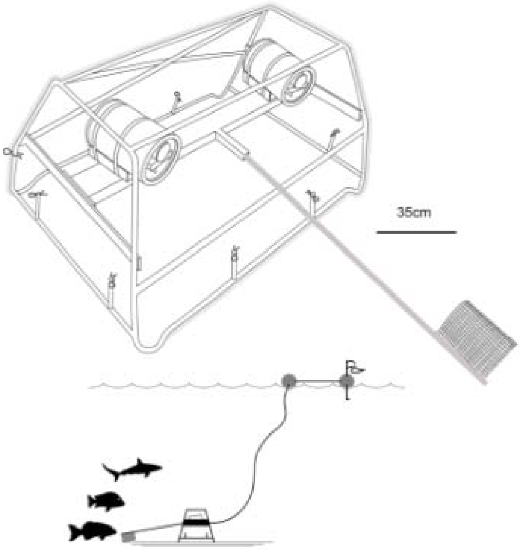

Figure 10.1.2 stereo-BRUV schematic "drawing by T. Simmonds (AIMS)"

Table 10.1.1 Top model outputs for predicting the abundance and biomass of *Lethrinus punctulatus* from full-subset generalised additive models (GAMs). Model selection was based on the most parsimonious model within two units of the lowest Akaike Information Criterion (AIC) value, which have the fewest variables. The effective degrees of freedom (edf), variance explained (R^2), Bayesian Information Criterion (BIC) and AIC weights (wAIC) are also reported for model comparison

DEPENDENT VARIABLE	MODEL	EDF	R2	AIC	BIC	WAIC	BEST MODEL
Abundance		5.08	0.24	756.63	0.44	0.33	Relief (mean)/Black and Octocorals (log)
Biomass	(1)	2	0.08	310.88	322.32	0.14	Relief (log sd)
	(2)	2	0.08	311.26	322.7	0.12	Depth

Video Analysis

Videos were analysed using EventMeasure™ (stereo) (http://www.seagis.com.au/). This software was used in order to obtain relative abundance counts as the maximum number of individuals (MaxN) for *L. punctulatus* within the field of view of a single video frame (Priede et al. 1994). The use of MaxN is considered to be a conservative estimate of the number of individuals of any one species observed during a BRUV deployment (Cappo et al. 2003). Individual length measures (snout to fork; fork length) were obtained using EventMeasure™ as well as the distance of the fish from the camera (range). Any individual found to be further than 7 m from the cameras was discounted in order to ensure good measurement accuracy, as well as a standardised sampling unit. Length measures were not possible when an individual was only visible on a single camera, however 3D position of the individual was still recorded by placing a point on an object of a similar distance from the cameras. This enables the determination of whether this fish was within our sample boundary (7 m) and any subsequent adjustment of the MaxN. In cases where one of the two cameras was either obscured or where one of the cameras had recording problems, measurements were not possible. This resulted in eight deployments being excluded resulting in 140 deployments being analysed. Data checking and formatting of EventMeasure™ outputs was completed using the R language for statistical computing (R Core Team 2015) using scripts provided by Langlois et al. (2015) and the packages tidyr (Wickham 2016) and dplyr (Wickham and Francois 2016). For more information, examples and R scripts for data tidying see http://github.com/TimLanglois/Stereo-or-mono-video-annotation-workflows.

Table 10.1.2 Abundance, mean abundance, depth range, mean depth, and unbiquity of each size class of *Lethrinus punctulatus*.

SIZE CLASS (MM)	ABUNDANCE (MEASURED)	AV. ABUNDANCE (WHEN PRESENT)	SE+/-	DEPTH RANGE (M)	AV. DEPTH (M)	SE+/-	DROPS PRESENT (%)
All	1373	19.34	1.23	1.5-56.6	20.27	1.878	50.71
50-125	308	10.62	2.39	1.5-10.4	4.38	0.38	20.71
125-200	454	13.35	3.12	1.5-10.4	4.71	0.35	24.29
200-275	326	8.56	2.23	3.7-56.6	29.87	3.60	27.14
275-350	285	8.64	1.96	4.4-56.6	42.12	3.03	23.57

Dominant habitat type and vertical relief of each deployment was characterised from stereo-video imagery using the software program TransectMeasure™ (http://www.seagis.com.au/) after methods described in McLean et al. (2016). This method superimposes a 5 x 4 grid over a high definition image obtained from each stereo-BRUV deployment. Within each grid rectangle, the dominant habitat cover was characterised by applying the CATAMI classification scheme (Althaus et al. 2013). Here habitat was selected from seven broad habitat types: unconsolidated (sand/rubble), consolidated (rocky bottom), hard corals, black and octocorals, sponges, hydroids, and macroalgae. A further habitat variable, reef, was created by combining consolidated, hard corals, soft octocorals, and macroalgae. For each deployment, a list of all habitat types and the number of rectangles in which they were dominant was recorded. We refer to this data as 'percentage cover' for simplicity but it is in effect how often each habitat type was encountered as the dominant habitat. Grid rectangles orientated towards open water were categorised as 'no biota' and excluded from the overall percent cover and from final analyses. Where biota was present, an estimate of relief was also made and categorised from 0-5 with an average and standard deviation calculated for each deployment (Wilson et al. 2012). These measures of relief alongside samples of depth and the eight habitat variables were examined with predictors removed if too rare or highly correlated with other variables. The variables utilised were depth, mean relief, standard deviation of relief (SD relief), macroalgae, black and octocorals, and the combined habitat variable of reef; and were transformed where necessary to reduce the influence of outliers. Data checking and formatting of the TransectMeasure™ outputs was completed using the R language for statistical computing (R Core Team 2015) using scripts provided in Langlois et al. (2015) and using the packages tidyr (Wickham 2016) and dplyr (Wickham and Francois 2016). For more information, examples and R scripts for data tidying see http://github.com/TimLanglois/HabitatAnnotation.

Statistical Analysis

Body-size distribution data: body-size distribution of *Lethrinus punctulatus* was analysed as a multivariate data set with the size classes as the dependent variable. An established direct plug-in methodology was used to select appropriate size class width (Wand 2012) and samples were standardized by total abundance to remove variation due to abundance. Size classes were calculated with bins of 75 mm starting from 50 mm. This resulted in classes of 50-125 mm, 125-200 mm, 200-275 mm, and 275-350 mm. Individuals under 200 mm in length can be considered as juveniles based on observations from the Department of Fisheries (Wakefield pers. comm.).

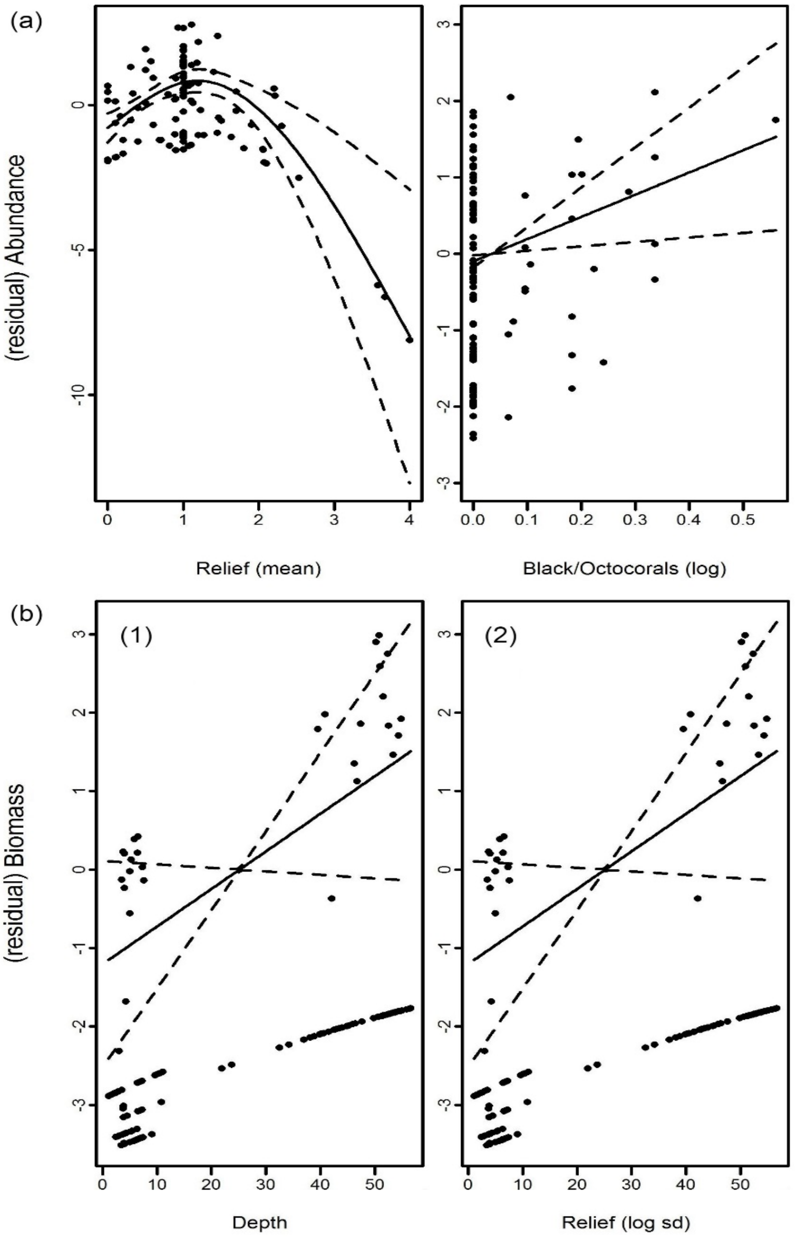

Figure 10.1.3. The total abundance (a) and Biomass (b) of *Lethrinus punctulatus* relative to the most important explanatory variables (Table 10.1.2). Two models of similar importance were plotted for biomass. Models were fitted using GAMs. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 x SE of the estimate.

Multivariate size class analysis*:* Prior to multivariate size class analyses, size class frequencies were cumulated and a dissimilarity matrix calculated using Manhattan distance (Bornt et al. 2015).

Patterns in the distribution of size classes were correlated with small and broad scale environmental explanatory variables via a distance-based linear model (DISTLM; Legendre and Anderson 1999), fitted using stepwise selection procedures to choose the most parsimonious model (via a multivariate analogue of the Akaike information criterion AICc; see Anderson et al. 2008). Using the vegan (Oksanen et al. 2016), ggvegan (Simpson 2015), and ggplot2 (Wickham 2009) packages in R a Distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999), a form of ordination, was used to visualize the chosen model with vectors overlaid for each size class and correlated environmental variables.

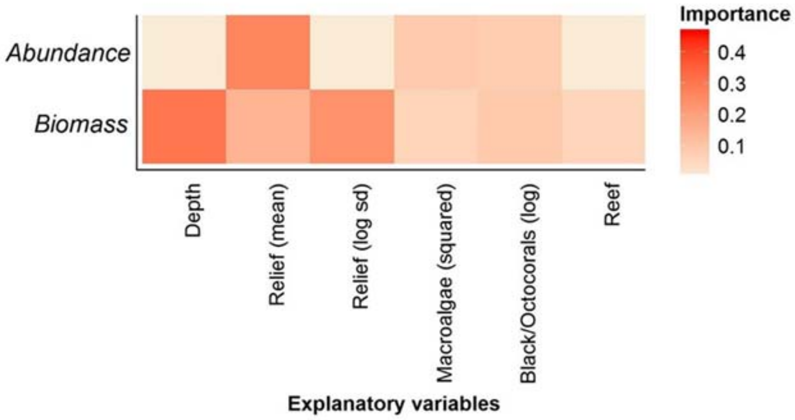

Figure 10.1.4 Relative importance of each explanatory variable in predicting abundance and biomass of *Lethrinus punctulatus*. Each value shows the relative importance of each predictor relative to the variance explained by the top model for the response variable.

Univariate analysis: The influence of small and broad scale environmental explanatory variables on the separate size class frequencies of *L. punctulatus* was investigated using generalised additive models (GAMs; Hastie and Tibshirani 1986). GAMs use a sum of smooth functions to model covariate effects. This allows for more flexible functional dependence of the response variable on the covariates, making GAMs useful for capturing the shape of a relationship without making prior assumptions about its parametric form.

Table 10.1.3 Results of the multivariate distance-based linear models (DistLM) relating the size-class composition for *Lethrinus punctulatus* with environmental variables in a step-wise selection procedure. Based on Manhattan dissimilarities of cumulated and standardised size-class bins. Prop., proportion of explained variance; Cumul., cumulative proportion of explained variance.

EXPLANATORY VARIABLE	*F*	*P*	PROP.	CUMUL.
+Depth	199.15	0.001	0.74268	0.74268
+Macroalgae	4.3634	0.037	1.55E-02	0.7582
+Reef	2.5251	0.096	8.78E-03	0.76698

Model selection was based on Akaike Information Criterion (AIC; Akaike 1973) and AIC weights (wAIC; Burnham and Anderson 2002). A full subsets method was used to fit models of all possible combinations up to a maximum of three variables – to prevent overfitting. Any variables with correlations > 0.9 were excluded entirely from the analysis, and models containing combinations of variables with correlations >0.28 were excluded to eliminate strong colinearity, which can cause problems with over-fitting and make interpretation of statistical results difficult (Graham 2003).

Models with AIC values that differ by less than two units show weak evidence for favouring one over the other (Raftery 1995; Burnham and Anderson 2002). The best model is therefore the one with the fewest variables (most parsimonious) and within two AIC units of the lowest AIC value. The wAIC, which represents probabilities or weights of evidence for each model, was used to facilitate interpretation of the best models. Relative support for each predictor variable was obtained by calculating the summed wAIC across all subsets of models containing that variable to obtain its relative importance (Burnham and Anderson 2002).

Since GAMs can account for data that are not normally distributed, models were fitted to untransformed abundance data using a Tweedie error distribution (Tweedie 1984). A Tweedie model is an extension of compound Poisson model derived from the stochastic process where a gamma distribution is used for the counted or measured objects (i.e., number or mass of fish) and has an advantage over delta-type two-step models by handling the zero data in a unified way. All analyses was performed using the R language for statistical computing (R Core Team 2015) with the package mgcv (Wood 2011).

10.1.3 RESULTS

The 140 stereo-BRUV deployments analysed from the Dampier Archipelago yielded 1580 *Lethrinus punctulatus* with accurate measurements possible for 87% (1373) of individuals.

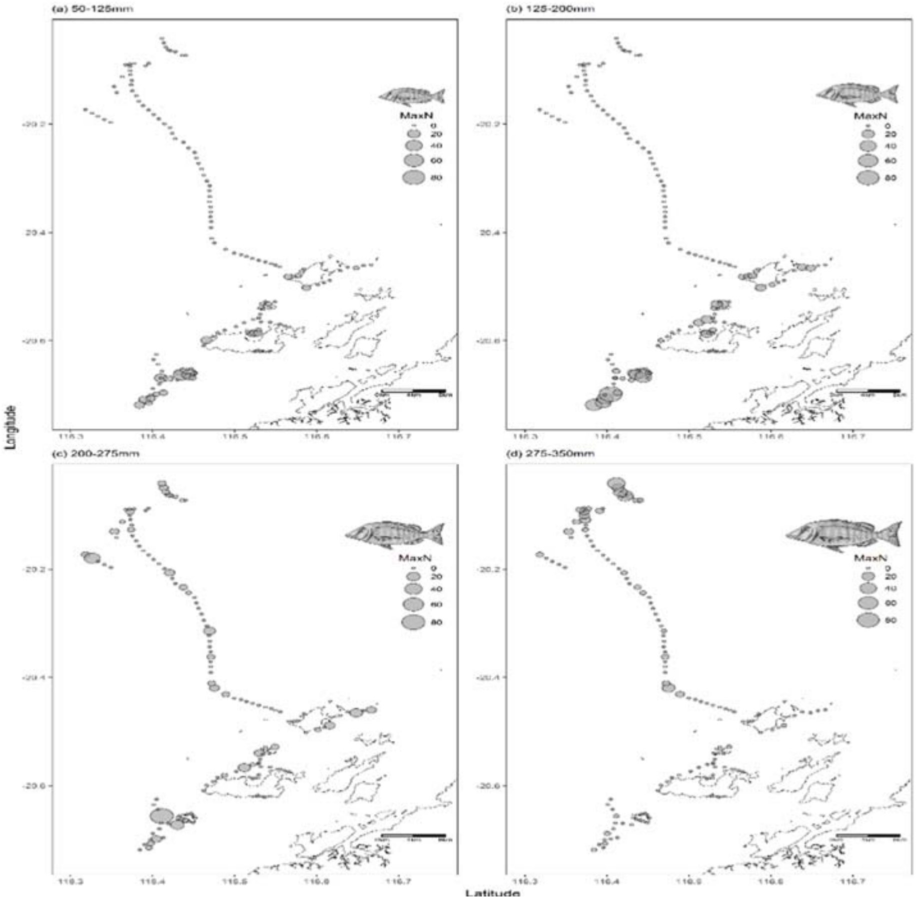

Figure 10.1.5 Spatial distribution of four size classes ((a) 50-125, (b) 125-200, (c) 200-275, (d) 275-350 mm) of *Lethrinus punctulatus.*

Abundance and Biomass

The most parsimonious model for abundance of *L. punctulatus,* mean relief and octocorals, explained 24% of variation in their distribution (Table 10.1.1) and showed a negative relationship with mean relief and a slight positive relationship of increasing abundance with increasing percent cover of octocorals (Figure 10.1.3a). In addition, an importance plot indicated that, despite not appearing in the top models, percentage cover of macroalgae and presence of black and octocorals were also important variables across all possible models (Figure 10.1.4).

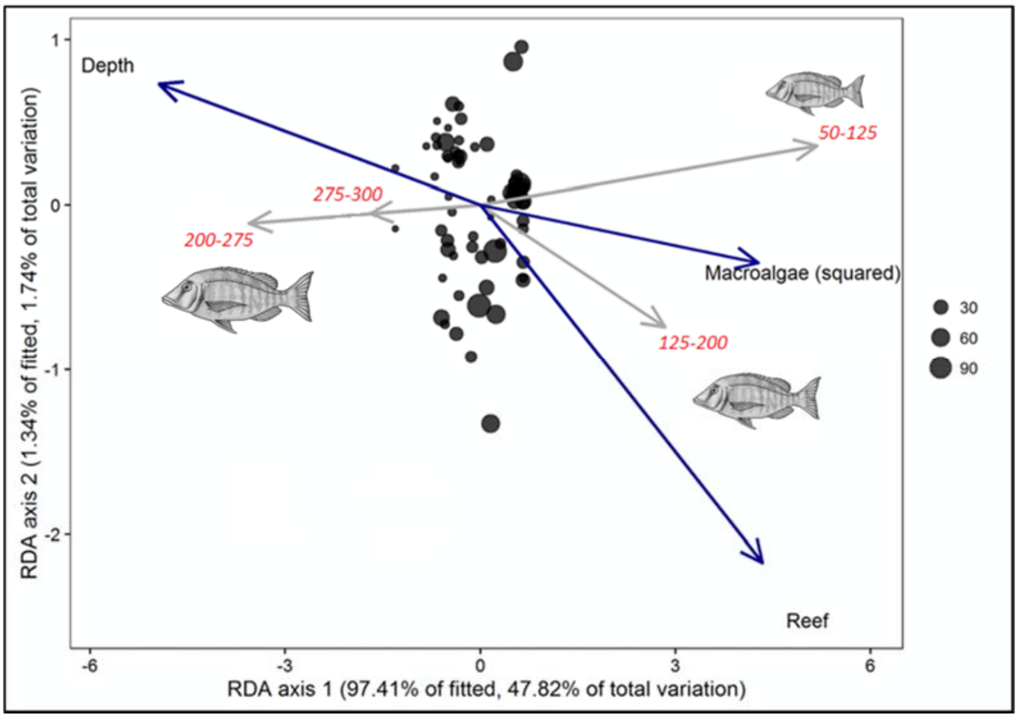

Figure 10.1.6 Distance-based redundancy (dbRDA) bubble plot illustrating the DISTLM model based on individual *Lethrinus punctulatus* size classes and the fitted environmental variables with their vector. The length and direction of vectors indicates the direction and strength of these relationships, respectively. Relative abundance of each species is shown by the size of bubbles.

Size size class composition

There were two top models for the biomass of *L. punctulatus* with both standard deviation of relief and depth each explaining 12% of variance in biomass (Table 10.1.4). Importance plotting indicated that across all models, mean relief and the percent cover of black and octocorals were the next two most important variables (Figure 10.1.4). Biomass of *L. punctulatus* showed strong positive correlation with increased depth and standard deviation of relief (Figure 10.1.3b(1), d(2)).

When split into individual size classes the number of measured individuals of each size of *L. punctulatus* was fairly uniform (Table 10.1.2) with all size classes containing over 20% of the overall population. The 125-200 mm size class contained the highest number of individuals and over 55% of measured *L. punctulatus* were found to be below the juvenile cut off. No individuals under 200 mm in length were recorded at a greater depth than 10.4 m., with average depth increasing with increasing size of *L. punctulatus.* When the physical distribution of each size class was plotted (Figure 10.1.5) it was apparent that those individuals of below 200 mm in length were located in the waters surrounding the Dampier Archipelago, while larger individuals tended to be located outside the archipelago farther from shore.

Table 10.1.4 Top model outputs for predicting the abundance of *Lethrinus punctulatus* in different size classes from full-subset generalised additive models (GAMs). Model selection was based on the most parsimonious model within two units of the lowest Akaike Information Criterion (AIC) value, which have the fewest variables.

SIZE CLASS (MM)	EDF	R^2	AIC	BIC	wAIC	MODEL
50-125	4.08	0.57	291.75	304.76	0.64	Depth/Black and Octocorals (log)
	5.78	0.57	293.71	309.44	0.24	Reef/Black and Octocorals (log)
125-200	4.03	0.45	296.66	309.63	0.66	Depth
200-275	3.35	0.32	324.27	335.97	0.33	Depth
	2.34	0.29	324.33	333.91	0.32	Macroalgae (sqrd)
	4.48	0.33	325.79	339.53	0.15	Depth/Relief (mean)
275-350	5.72	0.67	184.85	201.47	0.82	Depth/Relief (mean)

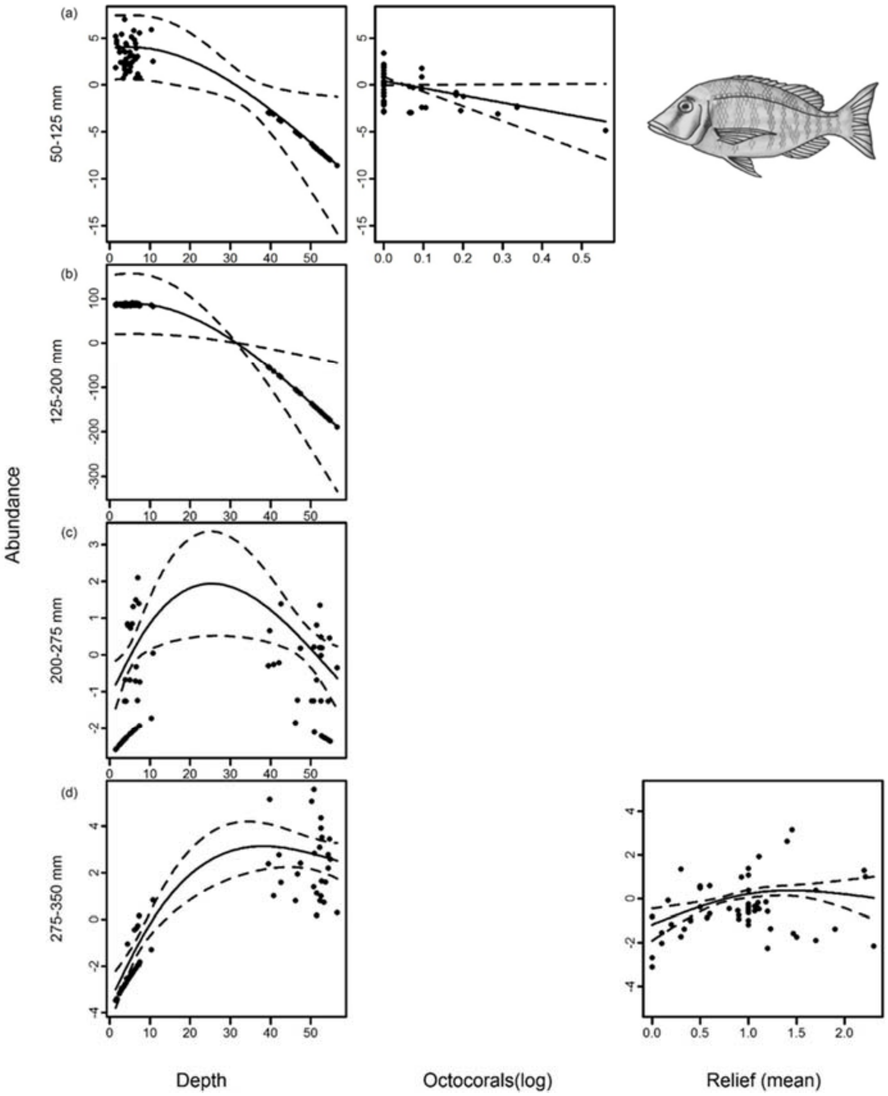

Figure 10.1.7 The total abundance of four size classes (a-d) of the indicator species *Lethrinus punctulatus* relative to the most important explanatory variables for each class (Table 10.1.4). Models were fitted using GAMs. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 x SE of the estimate.

Multivariate analysis found that percent cover of macroalgae, reef habitat and depth were the best predictors of the size-class composition for *L. punctulatus* (Table 10.1.3); explaining 49.56% of total variation and 98.79% of total variation. The ordination indicated a strong correlation of the smallest *L. punctulatus* (50-125 mm) with macroalgal habitat, the second smallest (125-200 mm) with macroalgal and reef habitat whereas the largest size classes (>200 mm) were correlated with greater depth and away from the reef and macroalgal habitat variables (Figure 10.1.6).

Full-subset modeling of size classes

Each independent full-subset model conducted for individual size classes of *L. punctulatus* found depth to be in the top model (Table 4), however the relationship with depth was different between the size classes with the smaller two size classes (50-125 mm, 125-200 mm), being most abundant at shallower depth. While the largest size class (275-375 mm), was more abundant at greater depth (Figure 10.1.7). The 200-275 mm size class showed some influence with depth, but this was not linear and they were abundant in both shallow and deep water. The smallest *L. punctulatus* showed a negative relationship between the percentage cover of octocorals and abundance. A generally positive relationship between the abundance of the largest size class (275-350 mm) and mean relief was also found (Table 10.1.4, Figure 10.1.7). Importance plotting and best models did not suggest that any other predictor variables contributed appreciably to the full-subset of models, except some importance of percentage cover of macroalgae to the 200-275 mm size class where macroalgae showed some importance ($r^2 = 0.29$) and a slight negative correlation with abundance (Table 10.1.4, Figure 10.1.8).

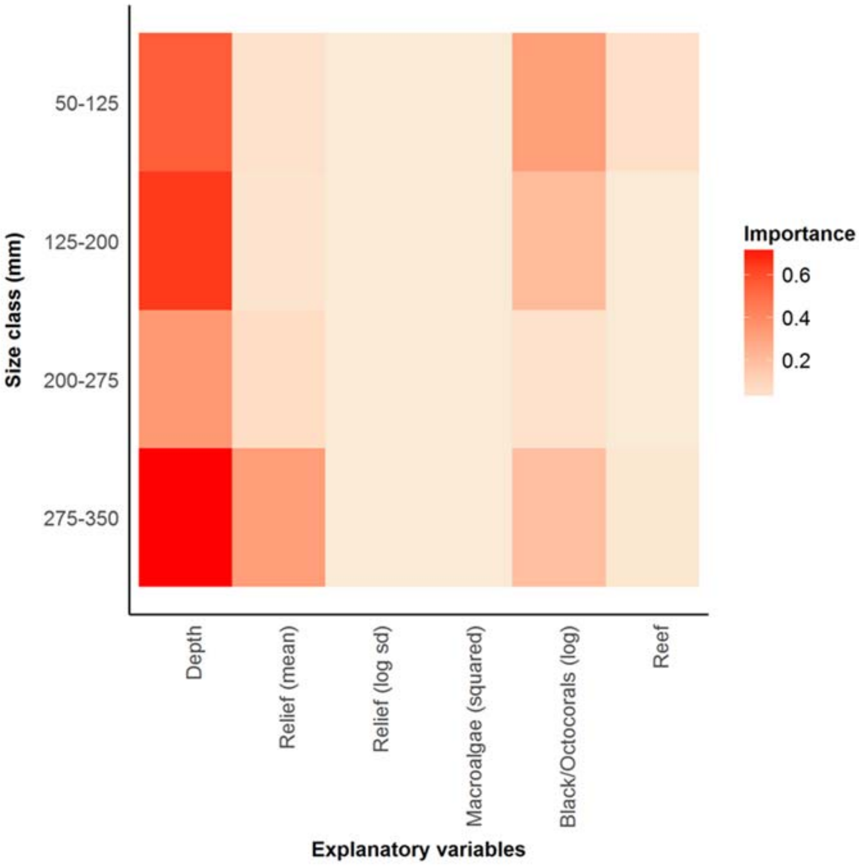

Figure 10.1.8 Relative importance of each explanatory variable in predicting the abundance of different size classes of *Lethrinus punctulatus* (Table 10.1.4). Each value shows the relative importance of each predictor explained by R^2, this is shown by the strength of the colour and signifies the power of this variable as a predictor.

10.1.4 DISCUSSION

A strong pattern of increasing body-size with increasing depth was found in *Lethrinus punctulatus* supporting the hypothesis of depth related ontogenetic niche partitioning in this species. Juvenile individuals of *L. punctulatus,* under 200 mm in length, were shown to be strongly associated with shallow depths with no individuals found in water of 10 m or greater depth. Individuals of 200-275 mm in length showed dispersal across all depths while larger individuals were strongly associated with greater depths. Information based solely on abundance or biomass estimates, as typically provided by studies using stereo-BRUV, did not provide clear evidence of ontogenetic shifts with abundance not influenced by depth, however greater biomass was seen in deep waters suggesting that larger individuals had been recorded.

Smaller individuals (<200 mm) were associated with shallower depths and the more protected waters surrounding the Dampier Archipelago. This suggests that juvenile *L. punctulatus* recruit to, or develop in, shallow-water habitats. Those habitats are likely to provide shelter from predators and food in productive macroalgal, seagrass, and mangrove beds (Steele 1999; Evans et al. 2014). This is the first time associations have been reported between small *L. punctulatus* and shallow-water habitats, however this association has been recorded in other Lethrinid species (Kimirei et al. 2011), and small *L. punctulatus* have been observed in shallow-water habitats in Department of Fisheries trap sampling (Wakefield pers. comm.). Juvenile *L. punctulatus* were correlated with the very shallowest waters in the outer Dampier Archipelago whilst progressively larger size class were found at progressively greater depths, suggesting a distinct size-structured population related to a depth gradient. A slight positive correlation was found between the abundance of juveniles and macroalgal dominated habitats, but a negative correlation with epibiotic habitats was of greater importance. Findings suggest that juveniles are found in macroalgal dominated habitats due in a large part to showing a strong disassociation with other reef building and open habitats. This is supported by pilot trapping studies conducted by the DPIRD which suggest that smaller individuals are predominantly found in low variability macroalgal habitat where no reef or open areas exist (Wakefield pers. obs.). Other lethrinid species have also been shown to associate with macroalgal habitat as juveniles before migrating to open, low relief, reef habitats as they mature (Davies 1995; Kimirei et al. 2011). It appears that a similar migration may occur in *L. punctulatus*. With individuals of the 50-125 and 125-200 mm size classes found at similar depths, while 200-275 mm individuals are found across a range of depths and average at medium depths, and the largest individuals mainly found at greater depths and with a stronger correlation with reef building habitat.

Macroalgal habitats have been shown to have important associations with juveniles in many lethrinid species (Kimirei et al. 2011; Evans et al. 2014). The current study suggests some limited importance of macroalgal habitats and demonstrates a strong dissociation between juveniles of *L. punctulatus* and complex coral and sponge habitats. Coral reefs and other complex marine habitats are often well represented in protected areas while other important habitats, such as macroalgal beds, are often overlooked (McNeill 1994). In this study we found clear correlation for juveniles of *L. punctulatus* away from some of these more traditionally protected habitats. With ongoing efforts to create marine sanctuary areas within the Dampier Archipelago, it would seem prudent to include examples of low variability low complexity habitats alongside more complex reef habitats. This would provide protection for habitats that have been found to be important for juveniles of commercially important species, protecting them from the effects of fishing and rapid coastal development in the region, and could ensure continued replenishment of fish stocks (Harrison et al. 2012).

Overall, abundance and biomass data for *L. punctulatus* were not capable of providing a clear picture of ontogenetic change in habitat use. While juveniles show a disassociation with more open habitats, the overall abundance of *L. punctulatus* was best predicted by associations with mid- to low-level relief and by increasing levels of black and octocorals. Only the smallest size class of *L. punctulatus* showed a strong relationship between octocorals and this relationship was a negative one. With juveniles showing preferences for shallow, well sheltered habitats, the sparse more open habitat provided by soft corals is unlikely to provide the necessary ontogenetic niches for smaller individuals to exploit. While adults do not show the same habitat associations as smaller individuals, they do show some preference for mid- to low-level relief habitats at the largest size class. Here abundance peaks in habitats of mid level variability with some relief features amongst mostly flat substrate that was more open than habitats preferred by juveniles. These habitats likely provide less refuge from predators but also an abundance of prey items (Almany 2004). The overall dispersal of most lethrinids (Kimirei et al. 2013) and *L. punctulatus* is likely limited at different sizes by the ability to find plentiful food sources whilst also minimising predation risks. This study reports evidence of an ontogenetic shift across depth and habitat gradients with smaller, juvenile individuals limited to shallow, sheltered habitats and shifting to more varied, open and deeper habitats as they mature. This results in a size-structured population with juveniles limited to shallow unfished waters and the largest adults to greater depths where commercial fishing occurs.

Studies showing the ontogenetic effect of depth on the size distribution of fish are common across the globe (e.g. Bell 1983; Newman et al. 1997) however the majority are limited in their ability to record continuous change using a standardised method. This study is unique in its use of a standardised continuous sampling method across a depth gradient, this gives a greater level of detail on the variability of habitat and depth associations in our indicator species. This study is also unique in its use of accurate length measurements obtained using stereo-BRUV to sample ontogenetic shifts across depth and habitat gradients, opening the door for further ontogenetic studies in this fashion. Ontogenetic studies in the Pilbara region are limited and there have been no studies of this type looking at *L. punctulatus.* This study is the first to obtain detailed length information across a continuous depth gradient in the region and in utilising small scale habitat variables. The use of a continuous design likely provides a more powerful test of depth (Somerfield et al. 2002) but limits the conclusions that can be drawn from this study due to the lack of a random factor at the site or location level. However, conducting future comparisons at multiple locations over a similar depth gradient would provide a further test of the generality of the findings (Beck 1997). The logical next step in investigating the spatial distribution of these species is to compare similar continuous transects in other comparable locations within the Pilbara region. This could prove the significance of these results and provide excellent models for the ontogenetic shift of *L. punctulatus* to be utilised in fisheries and conservation management of the Pilbara region. There are also opportunities for comparative studies with areas of high coastal development to investigate the effects of coastal construction and dredging on the size-distribution of these species.

This study found evidence of a spatially distinct size structure in *L. punctulatus,* and helps to validate current fisheries legislation limiting the depth at which the Pilbara Trawl and Trap Fisheries operate. Management of these fisheries was designed to reduce the risk of negatively influencing the recruitment of targeted fish species including *L. punctulatus*. Juveniles of this species were found to be correlated with macroalgal habitats, however the negative effect of coraline and variable habitat on the distribution of juveniles was more powerful. This suggests that the preservation of shallow, low variance habitat, including macroalgal dominated habitats through fisheries and conservation management, are a priority for the continued protection of nursery grounds for *L. punctulatus.* Continued exclusion of fisheries from shallow waters in the region will ensure that juvenile populations of the endemic indicator species *L. punctulatus* remain relatively undisturbed by fishing as well as conserving and maintaining recruitment of larger individuals into the adult population and active fishery zones.

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10.1.6 REFERENCES

Akaike H (1973) Information Theory and an Extension of the Maximum Likelihood Principle. Proceedings of the Second International Symposium on Information Theory. Petrov BN and Caskie F Akademiai Kiado, Budapest, 267–81.

Almany GR (2004) Does Increased Habitat Complexity Reduce Predation and Competition in Coral Reef Fish Assemblages? Oikos 106(2):275–84.

Althaus F, Hill N, Edwards L, and Ferrari R (2013) CATAMI Classification Scheme for Scoring Marine Biota and Substrata in Underwater Imagery – A Pictorial Guide to the Collaborative and Annotation Tools for Analysis of Marine Imagery and Video (CATAMI) Classification Scheme. Version 1 Http://catami.org/classification.

Anderson M, Ray NG and Robert KC (2008) Permanova+ for Primer: Guide to Software and Statistical Methods.

Beck MW (1997) Inference and Generality in Ecology: Current Problems and an Experimental Solution. Oikos 78(2):265–73.

Bell JD (1983) Effects of Depth and Marine Reserve Fishing Restrictions on the Structure of a Rocky Reef Fish Assemblage in the North-Western Mediterranean Sea. The Journal of Applied Ecology 20(2):357–69.

Bornt KR, McLean DL, Langlois TJ, Harvey ES, Bellchambers LM, Evans SN and Newman SJ (2015) Targeted Demersal Fish Species Exhibit Variable Responses to Long-Term Protection from Fishing at the Houtman Abrolhos Islands. Coral Reefs 34(4):1297–1312.

Burnham KP and Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media.

Cappo M, Harvey E, Malcolm H and Speare P (2003) Potential of Video Techniques to Monitor Diversity, Abundance and Size of Fish in Studies of Marine Protected Areas. Aquatic Protected Areas-What Works Best and How Do We Know? JANUARY 2003: 455–64p.

Cappo M, Speare P and De'ath G (2004) Comparison of Baited Remote Underwater Video Stations (BRUVS) and Prawn (shrimp) Trawls for Assessments of Fish Biodiversity in Inter-Reefal Areas of the Great Barrier Reef Marine Park. Journal of Experimental Marine Biology and Ecology 302(2):123–52.

Chittaro PM, Usseglio P and Sale PF (2005) Variation in Fish Density, Assemblage Composition and Relative Rates of Predation among Mangrove, Seagrass and Coral Reef Habitats. Environmental Biology of Fishes 72(2): 175–87.

Dahlgren CP and Eggleston DB (2000) Ecological Processes Underlying Ontogenetic Habitat Shifts in a Coral Reef Fish. Ecology 81(8):2227–40.

Davies CR (1995) Patterns of Movement of Three Species of Coral Reef Fish on the Great Barrier Reef. Phd, James Cook University. http://eprints.jcu.edu.au/27169/.

DoF (2011) Resource Assessment Framework (RAF) for Finfish Resources in Western Australia. 85. Department of Fisheries Western Australia Fisheries Occasional Publication. http://www.fish.wa.gov.au/documents/occasional_publications/fop085.pdf.

Donaldson TJ (2002) Habitat Association and Depth Distribution of Two Sympatric Groupers of the Genus Cephalopholis (Serranidae: Epinephelinae). Ichthyological Research 49(2):191–93.

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR and Skjoldal HR (2008) Climate Change and Deepening of the North Sea Fish Assemblage: A Biotic Indicator of Warming Seas. The Journal of Applied Ecology 45(4):1029–39.

Evans RD, Wilson SK, Field SN and Moore J (2014) Importance of Macroalgal Fields as Coral Reef Fish Nursery Habitat in North-West Australia. Marine Biology 161(3):599–607.

Faunce CH and Serafy JS (2007) Nearshore Habitat Use by Gray Snapper (Lutjanus Griseus) and Bluestriped Grunt (Haemulon Sciurus): Environmental Gradients and Ontogenetic Shifts. Bulletin of Marine Science 80(3):473–95.

Fletcher WJ, and Santoro K (2015) Status Reports of the Fisheries and Aquatic Resources of Western Australia 2014/15: The State of the Fisheries, Department of Fisheries, Western Australia.

Fox NJ and Beckley LE (2005) Priority Areas for Conservation of Western Australian Coastal Fishes: A Comparison of Hotspot, Biogeographical and Complementarity Approaches. Biological Conservation 125(4):399–410.

Graham MH (2003) Confronting Multicollinearity In: Ecological Multiple Regression. Ecology 84(11):2809–15.

Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim KA, et al. (2012) Larval Export from Marine Reserves and the Recruitment Benefit for Fish and Fisheries. Current Biology: 22(11):1023–28.

Harvey ES, Cappo M, Butler JJ, Hall N and Kendrick GA (2007). Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Marine Ecology Progress Series 350:245–54.

Harvey E and Shortis M (1996). A System for Stereo-Video Measurement of Sub-Tidal Organisms. Marine Technology Society Journal 29(4):10–22.

Hastie TJ and Tibshirani RJ (1986) generalized additive models, statistical science: a review. Journal of the Institute of Mathematical Statistics 43(3):297–310.

Heinlein JM, Stier AC and Steele MA (2010) Predators Reduce Abundance and Species Richness of Coral Reef Fish Recruits via Non-Selective Predation. Coral Reefs 29(2):527–32.

Hutchins JB (2004) Fishes of the Dampier Archipelago, Western Australia. Records of the Western Australian Museum Supplement No. 66 p343–98.

Kimirei IA, Nagelkerken I, Trommelen M, Blankers P, van Hoytema N, Hoeijmakers D, Huijbers CM, Mgaya YD and Rypel AL (2013) What Drives Ontogenetic Niche Shifts of Fishes in Coral Reef Ecosystems? Ecosystems 16(5):783–96.

Kimirei IA, Nagelkerken I, Griffioen B, Wagner C and Mgaya YD (2011) Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. Estuarine, Coastal and Shelf Science 92(1):47–58.

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL, et al. (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. Aquatic Biology 9(2):155–68.

Langlois TJ, Newman SJ, Cappo M, Harvey ES, Rome BM, Skepper CL and Wakefield CB (2015) Length selectivity of commercial fish traps assessed from in situ comparisons with stereo-video: is there evidence of sampling bias?" Fisheries Research 161:145–55.

Legendre P and Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs: Ecological Society of America 69:1–24.

McLean DL, Langlois TJ, Newman SJ, Holmes TH, Birt MJ, Bornt KR, Bond T, et al. (2016) Distribution, abundance, diversity and habitat associations of fishes across a bioregion experiencing rapid coastal development. Estuarine, Coastal and Shelf Science 178:36–47.

McNeill SE (1994) The selection and design of marine protected areas: australia as a case study biodiversity and conservation 3(7):586–605.

Nakazawa T (2014) Ontogenetic niche shifts matter in community ecology: a review and future perspectives. Population Ecology 57(2):347–54.

Newman SJ, Wakefield C, Skepper C, Boddington D, Blay N, Jones R and Dobson P (2015) North Coast Demersal Fisheries Status Report Edited by W J Fletcher and K Santoro Department of Fisheries, Western Australia Department of Fisheries, Western Australia.

Newman SJ and Williams DMCB (2001) Spatial and temporal variation in assemblages of Lutjanidae, Lethrinidae and associated fish species among mid-continental shelf reefs in the central Great Barrier Reef. Marine and Freshwater Research 52(6):843–51.

Newman SJ, Williams DMCB and Russ GR (1997) Patterns of zonation of assemblages of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) within and among mid-shelf and outer-shelf, reefs in the central Great Barrier Reef. Marine and Freshwater Research 48(2):119–28.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, et al. (2016) Vegan: Community Ecology Package. https://CRAN.R-project.org/package=vegan.

Priede IG, Bagley PM, Smith A, Creasey S and Merrett NR (1994) Scavenging deep demersal fishes of the Porcupine Seabight, North-East Atlantic: observations by baited camera, trap and trawl" Journal of the Marine Biological Association of the United Kingdom Marine Biological Association of the United Kingdom 74 (03):81–98.

Raftery AE (1995) Bayesian model selection in social research. Sociological Methodology 25 JSTOR: 111–64.

R Core Team (2015) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Schoener TW (1974) Resource partitioning in ecological communities. Science 185 (4145): 27–39.

Shepherd SA and Brook JB (2007) Distribution and ontogenetic shifts in habitat and abundance of the temperate western blue groper, *Achoerodus gouldii* (Richardson).” Journal of Fish Biology 71 (5):1457–78.

Shortis MR and Harvey ES (1998) Design and calibration of an underwater stereo-video system for the monitoring of marine fauna populations. International Archives of Photogrammetry and Remote Sensing 32:792–99.

Simpson GL (2015) Ggvegan: ‘ggplot2’ Plots for the ‘Vegan’ Package.

Somerfield PJ, Clarke KR and Olsgard F (2002) A comparison of the power of categorical and correlational tests applied to community ecology data from gradient studies. The Journal of Animal Ecology 71 (4):581–93.

Steele MA (1999) Effects of shelter and predators on reef fishes. Journal of Experimental Marine Biology and Ecology 233(1):65–79.

Travers MJ, Newman SJ and Potter IC (2006) Influence of latitude, water depth, day v night and wet v dry periods on the species composition of reef fish communities in tropical Western Australia. Journal of Fish Biology 69(4):987–1017.

Tweedie MCK (1984) An index which distinguishes between some important exponential families. In Statistics: Applications and New Directions: Proc. Indian Statistical Institute Golden Jubilee International Conference, p579–604.

Wand M (2012) KernSmooth: Functions for Kernel Smoothing for Wand & Jones (1995) (version R Package version 2). http://CRAN.R-project.org/package=KernSmooth.

Werner EE and Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15 (1):393–425.

Wickham H (2009) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. http://ggplot2.org.

Wickham H (2016) Tidyr: Easily Tidy Data with `spread()` and `gather()` Functions. https://CRAN.R-project.org/package=tidyr.

Wickham H and Francois R (2016) Dplyr: A Grammar of Data Manipulation https://CRAN.R-project.org/package=dplyr.

Willis TJ and Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. Marine and Freshwater Research 51 (8):755–63.

Wilson SK, Babcock RC, Fisher R, Holmes TH, Moore JAW and Thomson DP (2012) Relative and combined effects of habitat and fishing on reef fish communities across a limited fishing gradient at Ningaloo. Marine Environmental Research 81:1–11

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73:3-36

11. Habitat dependencies

11.1 Distribution, abundance, diversity and habitat associations of fishes across a bioregion experiencing rapid coastal development

Authors: McLean DL, Langlois TJ, Newman SJ, Holmes TH, Birt MJ, Bornt KR, Bond T, Collins DL, Evans SN, Travers MJ, Wakefield CB, Babcock RC, Fisher R.

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ABSTRACT

Knowledge of the factors that influence spatial patterns in fish abundance, distribution and diversity are essential for informing fisheries and conservation management. The present study was conducted in the nearshore Pilbara bioregion of north-western Australia where the dynamic marine environment is characterised by large embayments, numerous islands and islets, coexisting with globally significant petrochemical and mineral industries. Within Western Australia, this nearshore bioregion has high biodiversity and is considered to play an essential role in the recruitment of species of commercial importance. To better inform future investigations into both ecological processes and planning scenarios for management, a rapid assessment of the distribution, abundance and associations with nearshore habitats of fishes across the region was conducted. Baited remote underwater stereo-video systems (stereo-BRUVs) were used to simultaneously sample the fish assemblage and habitat composition. Generalised additive mixed models (GAMMs) were used to determine whether the abundance of fishes were related to habitat and a range of environmental variables (visibility, depth, distance to 30 m and 200 m depth isobars, boat ramps and the nearest large embayment (Exmouth Gulf). A diverse fish assemblage comprising 343 species from 58 families was recorded. The abundance and distribution patterns of fishery-target species and of the five most common and abundant species and families were linked positively with areas of high relief, hard coral cover, reef and macroalgae and negatively with the distance to the nearest oceanic waters (200 m depth isobar). This study provides information that can contribute to future marine spatial planning scenarios for management of the Pilbara using a unique, analytical approach that has broad application in biogeography.

11.1.1 INTRODUCTION

Information on relationships between fish and habitats is essential for understanding the processes driving patterns of fish diversity and abundance. Habitat type and complexity are important determinants of the structure of fish assemblages (Friedlander and Parish 1998; Almany 2004; Travers et al. 2006; 2010; 2012; Giakoumi and Kokkoris 2013; Wakefield et al. 2013). Fish abundance, diversity and distribution has been shown to be positively correlated with the structural complexity of habitats, likely due to the additional refuge from predators and availability of resources (e.g. food) that complex habitats offer (Newman and Williams 1996; 2001; Newman et al. 1997; Friedlander et al. 2003; Willis and Anderson 2003; Wilson et al. 2012). Understanding these relationships and natural patterns in fish abundance and diversity enables natural and anthropogenic impacts to be assessed. Knowledge of the spatial distribution of habitats and their relationship with fish is therefore essential for informing fisheries management and conservation (Curley et al. 2002).

The Pilbara region hosts fish assemblages characterised by high diversity and economically important, but low productivity, fisheries (MPRSWG 1994; Fox and Beckley 2005; Molony et al. 2011; Newman et al. 2014). In addition, rapid coastal development has been occurring at multiple locations throughout the region to support the mineral and petrochemical industries (PDC 2015). This development has the potential to directly impact the biodiversity and productivity of vulnerable nearshore ecosystems via dredging, construction, pollution, shipping and other indirect pressures associated with increased human populations (e.g. fishing) (Pandolfi et al. 2003; Crain et al. 2009; Waycott et al. 2009). Management is challenged with finding a balance between the economic benefits of non-renewables, sustainable fisheries development and maintenance of biodiversity and ecosystem services. Knowledge of the patterns and processes that support productivity biodiversity of these nearshore marine ecosystems is therefore essential for informing management decisions (Parsons et al. 2014).

Nearshore marine habitats in the Pilbara, including macrophyte and sessile invertebrate assemblages, are likely to be vulnerable to coastal development pressures, with these habitats considered to be essential for the recruitment of important fishery species. In this region, recruits and juveniles of important commercial and recreational fishery species are thought to be spatially partitioned from adult populations and associated with different habitats (Evans et al. 2014). Knowledge of fish-habitat relationships across the Pilbara is lacking, but is required for the identification of priority areas for the recruitment of target fish species, areas of high biodiversity and vulnerable habitats. Such information would inform research into how these important areas may be affected by ongoing coastal development associated with the petrochemical and mineral industries.

Buoyed by the construction and operation of major coastal development projects in the Pilbara, levels of boat-based recreational activity peaked in 2012/13 (Fletcher and Santoro 2015; Ryan et al. 2013; 2015). There is a seasonal peak in angling activity during the winter months when local populations are inflated by significant numbers of metropolitan and inter-state tourists in addition to the contribution from the workforce associated with construction or operation of major developments in the region (Fletcher and Santoro 2015). Owing to the large tidal range in the Pilbara, nearshore recreational angling activity is mainly boat based for a variety of finfish species including barramundi (*Lates calcarifer*), mangrove jack (*Lutjanus argentimaculatus*), trevallies (Carangidae) and groupers (Epinephelidae) in nearshore waters. Tropical snappers (Lutjanidae), emperors (Lethrinidae), groupers (Epinephelidae), trevallies (Carangidae), tuskfish (*Choerodon* spp.) and mackerels (Scombridae) are also targeted further from shore (Fletcher and Santoro 2015). The two main commercial fisheries operating within nearshore Pilbara waters are the Onslow and Nickol Bay prawn trawl fisheries that predominantly target banana prawns (*Penaeus merguiensis*) and the mackerel managed fishery that predominantly targets Spanish mackerel (*Scomberomorus commerson*) (Fletcher and Santoro 2015). Commercial fisheries (fish trap, fish trawl and line) operate in continental shelf waters (30-500 m).

The current study is the first contribution from a five-year project aiming to create ecological models for use by management agencies assessing the impacts of coastal development associated with petrochemical and mineral extraction industries on biodiversity values and fisheries productivity in the Pilbara. As part of this integrated study, a novel application of a standardised benthic classification system was adopted to simultaneously collect semi-quantitative measures of habitat from an established fish survey method, baited remote underwater stereo-video (stereo-BRUV). These data were subjected to multivariate analyses to investigate ecological processes underlying the distribution, abundance and diversity of fishes along the extensive coastline of the Pilbara bioregion through the following hypotheses: (1) The relative abundance and diversity (species richness) of fishes are greatest in more structurally complex habitat types such as hard and soft corals, (2) The relative abundance and diversity of fishes will be greatest closer to large embayments where fish nursery habitats occur, (3) The relative abundance and diversity of fishes will be greatest in areas furthest from boat ramp access where fishing pressure may be least. Emphasis will be placed on identifying areas of notable abundance and diversity and the species and family groups mainly responsible for the observed patterns along the length of the Pilbara coastline.

11.1.2 METHODS

Study Site

This study took place in the western Pilbara region of Western Australia spanning a distance of approximately 340 km from the eastern end of the Exmouth Gulf in the south (114° 8' 55.47E, 21° 55' 19.15S) to the Dampier Archipelago in the north (116° 56' 12.945E, 20° 24' 19.94S; Figure 11.1.1). The marine environment is tropical with a component of sub-tropical species, which are more prominent in the assemblage towards higher latitudes (Hutchins 2001).

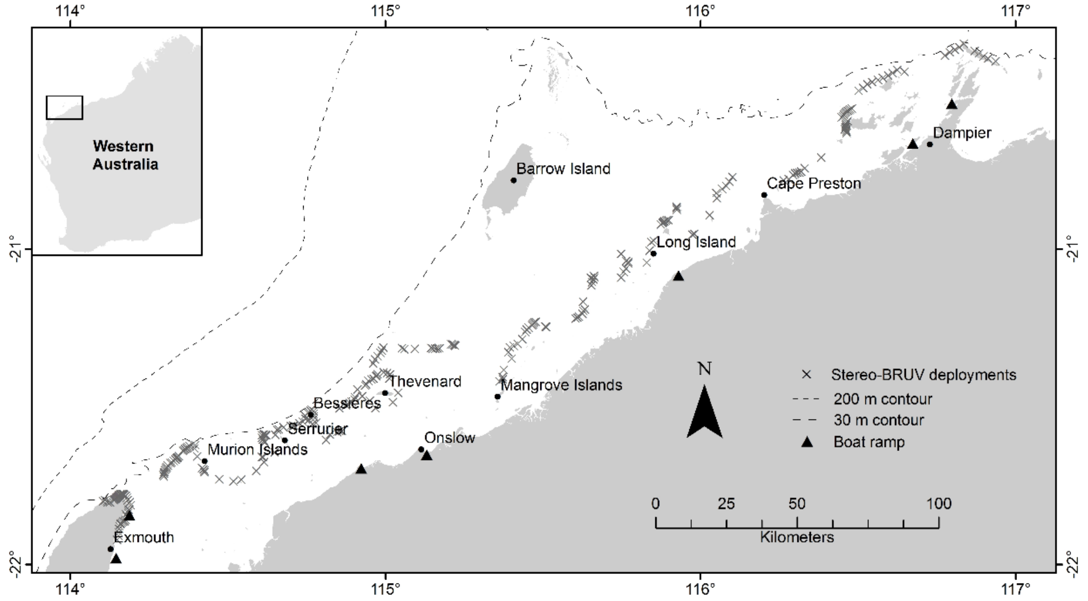

Figure 11.1.1. Location of 212 stereo-BRUV deployments conducted in the Pilbara region of north-western Australia.

Sampling protocol and equipment

Surveys were conducted over a 10 day period in May, 2014 using baited remote underwater stereo-video systems (stereo-BRUVs). A total of 212 deployments were conducted in 6-21 m depth (mean 9.7 ± 0.1 m) across a range of habitat types, in areas open to recreational and charter fishing. Stereo-BRUVs were deployed on reefs or areas in close proximity to reefs with seabed structure present, *i.e.* we attempted to minimise large expanses of sand and as such these habitats are likely underrepresented in this study.

Ten stereo-BRUVs were used concurrently to maximise sampling efficiency. These systems comprised a pair of high definition video cameras, either Canon Legria HFG25 or GoPro Hero3+ (silver and black models) set to record at 25 and 60 frames per second, respectively. The cameras are inwardly converged at 7º to provide an overlapping field of view and are fixed to a galvanised steel bar within a trapezium-shaped frame (see Langlois et al. 2010; Watson et al. 2010; see Video 1). Further information on the design configuration and calibration of these stereo-BRUVs can be found in Harvey and Shortis (1996, 1998). To maximise calibration stability, the systems used a purpose-built, dual housing mounted on a base bar with a design that minimises camera movement within the housing, and between the cameras.

Each stereo-BRUV was baited with approximately ~1 kg of pilchards (*Sardinops* spp.) contained within a plastic-coated wire mesh basket, attached to a conduit rod and positioned 1.2 m in front of the cameras. Bait was crushed to promote dispersal of the flesh and fish oil. Each system was deployed by boat and left to film remotely for at least 60 minutes on the seafloor before being retrieved and re-deployed. Neighbouring deployments were separated by at least 400 m to reduce the likelihood of fish swimming between stereo-BRUVs (see Cappo et al. 2004).

Video Analysis

FISH ASSEMBLAGES

All fish were identified to species where possible, however several species could not be reliably or consistently identified to species level from video images. These included various species of mackerel (herein referred to as *Scomberomorus* spp.), threadfin bream (*Nemipterus* spp.), flounder (*Bothidae* spp.), flathead (*Platycephalus* spp.), whiting (*Sillago* spp.) and two species of coral trout (*Plectropomus leopardus*, *Plectropomus maculatus).* The majority of trout species in the Pilbara region are likely to be *P. maculatus,* but *P. leopardus* also occurs and they cannot consistently be differentiated on video. Here, these important target species are considered together as *Plectropomus* spp. When juvenile lethrinids and scarids (individuals <12 cm) could not be identified to species level, they were recorded as *Lethrinus* spp. and *Scarus* spp. (see Supplementary Material Table S11.1.1).

Stereo-BRUVs were calibrated using the software CAL and subsequent analysis of videos was facilitated through the program EventMeasure (http://www.seagis.com.au). Relative abundance counts were obtained as the maximum number of fish belonging to each species, present in the field of view of the stereo-BRUVs at one time (MaxN; Priede et al. 1994; Cappo et al. 2004). Measures of species richness were obtained as the total number of species observed on each stereo-BRUV deployment. While the stereo-configuration of the video systems allowed us to obtain accurate and precise measurements of fish length using EventMeasure, this data is not reported here. However, the stereo-enabled capacity to measure distance was used to finalise measures of relative abundance by confirming whether each individual comprising MaxN was within our sample boundary of 10 m. Data checking and formatting of EventMeasure MaxN outputs were undertaken using scripts provided in Langlois et al. (2015) using the R language for statistical computing (R Development Core Team 2015).

Five target species were selected from the dataset for focussed analysis with these species being the most common and/or were of significant importance to recreational and commercial fisheries. The selected species were: *Choerodon schoenleinii* (blackspot tuskfish), *Epinephelus multinotatus* (rankin cod), *Lethrinus nebulosus* (spangled emperor), *Lutjanus carponotatus* (stripey snapper) and *Plectropomus* spp. (coral trout). *E. multinotatus* were not analysed in statistical models, however, due to low abundance. In addition, we focussed analyses on the five most commonly observed (% of deployments) fish families and on the five most common fish species.

HABITAT VARIABLES

Measures of habitat and relief were obtained from the stereo-video imagery using the software program TransectMeasure (http://www.seagis.com.au). This method of analysis used a 5 x 4 grid which was overlaid on a high definition image obtained from each stereo-BRUV deployment. Within each grid rectangle, the dominant habitat type was characterised using a novel application of the CATAMI classification scheme (Althaus et al. 2013; Harrison et al. 2014; Hill et al. 2014), with some modification to simplify naming schemes. This resulted in the selection of eight broad habitat types: 1) hard corals, 2) macroalgae, 3) reef (boulders or pavement – including those covered in turfing algae + hard corals + macroalgae), 4) sand/rubble, 5) seagrass, 6) soft corals, 7) sponges and, 8) ascidians. For every deployment we had a list of all habitat types and a corresponding number of grid cells in which it was present. For simplicity we refer to the data as ‘percent cover’ for each habitat type but effectively it is how often each were encountered. When grid rectangles were positioned over open water they were classed as ‘no biota’ and excluded from the overall percent cover and final statistical analyses. In cells where biota was present, estimates of relief were also obtained and ranked as flat (no relief), low (<1 m), medium (1-3 m) and high (>3 m) with an average and standard deviation calculated for each deployment.

ENVIRONMENTAL VARIABLES

The depth (m) and the GPS latitude and longitude position was recorded at the time of each deployment. Rather than examining the relationship between latitude and longitude with fish and habitats, we used positional measures that we considered were most applicable to the marine environment in the western Pilbara region. The first two positional variables were the minimum distance of each stereo-BRUV deployment to the 30 m and 200 m depth isobars. At the northern end of the Pilbara the 200 m depth isobar is approximately 160 km offshore and the marine environment is quite sheltered from the open ocean, while at the southern end the 200 m depth isobar is approximately 15 km offshore and the water is clearer and more readily flushed by oceanic waters. The third positional predictor variable included in analyses was ‘distance to the Exmouth Gulf’, a large shallow embayment approximately 3000 km^2 in area located to the southwest of the Pilbara region. This Gulf’s nearshore waters on the eastern and south-western side are important fish nursery areas (MPRSWG 1994) and therefore a potentially important source of juveniles to the south-western Pilbara region. Lastly, the fourth positional predictor variable included was minimum distance to the nearest boat ramp. There are six boat ramps between Exmouth Gulf and Dampier in the remote Pilbara region. Finally, visibility was recorded as a proxy for turbidity with estimates made by the same experienced analyst for every stereo-BRUV deployment.

Data analysis

The influence of habitat and environmental variables on the abundance of fish was investigated using generalised additive mixed models (GAMMs; Lin and Zhang 1999). GAMMs are an extension of generalised additive models (GAMs; Hastie and Tibshirani 1986) which use a sum of smooth functions to model covariate effects – as opposed to a linear (or some other parametric) form. This allows for more flexible functional dependence of the response variable on the covariates, making GAMs (and GAMMs) useful for capturing the shape of a relationship without making prior assumptions about its parametric form. To accommodate for overdispersion and correlation in the data, which arise in many fields of research (e.g. longitudinal studies, Lin and Zhang 1999), we extend the application of this class of models by including replicates as a random effect (Harrison 2014).

Model selection was based on Akaike Information Criterion (AIC; Akaike 1973) and AIC weights (wAIC; Burnham and Anderson 2002). A full subsets method was used to fit models of all possible combinations up to a maximum of three variables – to prevent overfitting. Models containing variables with correlations > 0.4 were also excluded from the analysis to eliminate strong colinearity, which can cause problems with over-fitting and make interpretation of statistical results difficult. Models with AIC values that differ by less than two units show weak evidence for favouring one over the other (Raftery 1995; Burnham and Anderson 2002). The best model was therefore the one with the fewest variables (most parsimonious) and was within two AIC units of the lowest AIC value (Burnham and Anderson 2002). The wAIC, which represents probabilities or weights of evidence for each model, were used to facilitate interpretation of the best models. Relative support for each predictor variable was obtained by calculating the summed wAIC across all subsets of models containing that variable to obtain its relative importance (Burnham and Anderson 2002). For these variable importance metrics to be meaningful, it is necessary to have the same number of models containing each variable (Burnham and Anderson 2002). As this was not the case due to removal of models with highly collinear predictor variables, we calculated per model averaged variable weights (average wAIC) by dividing each weight (wAIC) by the total number of models containing each variable or class of variables, respectively. These were then rescaled to between 0 and 1 (with 1 being the variable with the highest relative weight). To account for the large differences in the overall fit of the models, these rescaled variable importance values were multiplied by the R2 value of the best model for plotting. This ensured that the overall importance of each variable was presented in the context of explanatory power.

Prior to analyses, three habitat categories (seagrass, sponges, and ascidians) were removed due to their limited coverage. A fourth category, sand/rubble, was also excluded due to strong colinearity with the category reef. Several variables (depth, soft corals, and hard corals) were log10 (x+1) transformed to downplay outlying values and better represent relationships with fish abundance. Since GAMMs can account for data that are not normally distributed, models were fitted to untransformed fish abundance data using a Poisson distribution but allowing for overdispersion with the addition of an observation level random effect. All analyses were performed using the R language for statistical computing (R Development Core Team 2015) with the package GAMM4 version 0.2-3 for GAMMs (Wood and Scheipl 2015).

11.1.3 RESULTS

Patterns in the distribution and abundance of fish

The 212 stereo-BRUV deployments analysed from the nearshore Pilbara region yielded at least 31171 individuals (sum MaxN’s) from 343 species and 58 families (Table S11.1.1). Several protected species (Fish Resources Management Regulation 1995) were observed during the study. These included four *Epinephelus tukula* (potato cod; 946 – 1377 mm fork length) on separate deployments

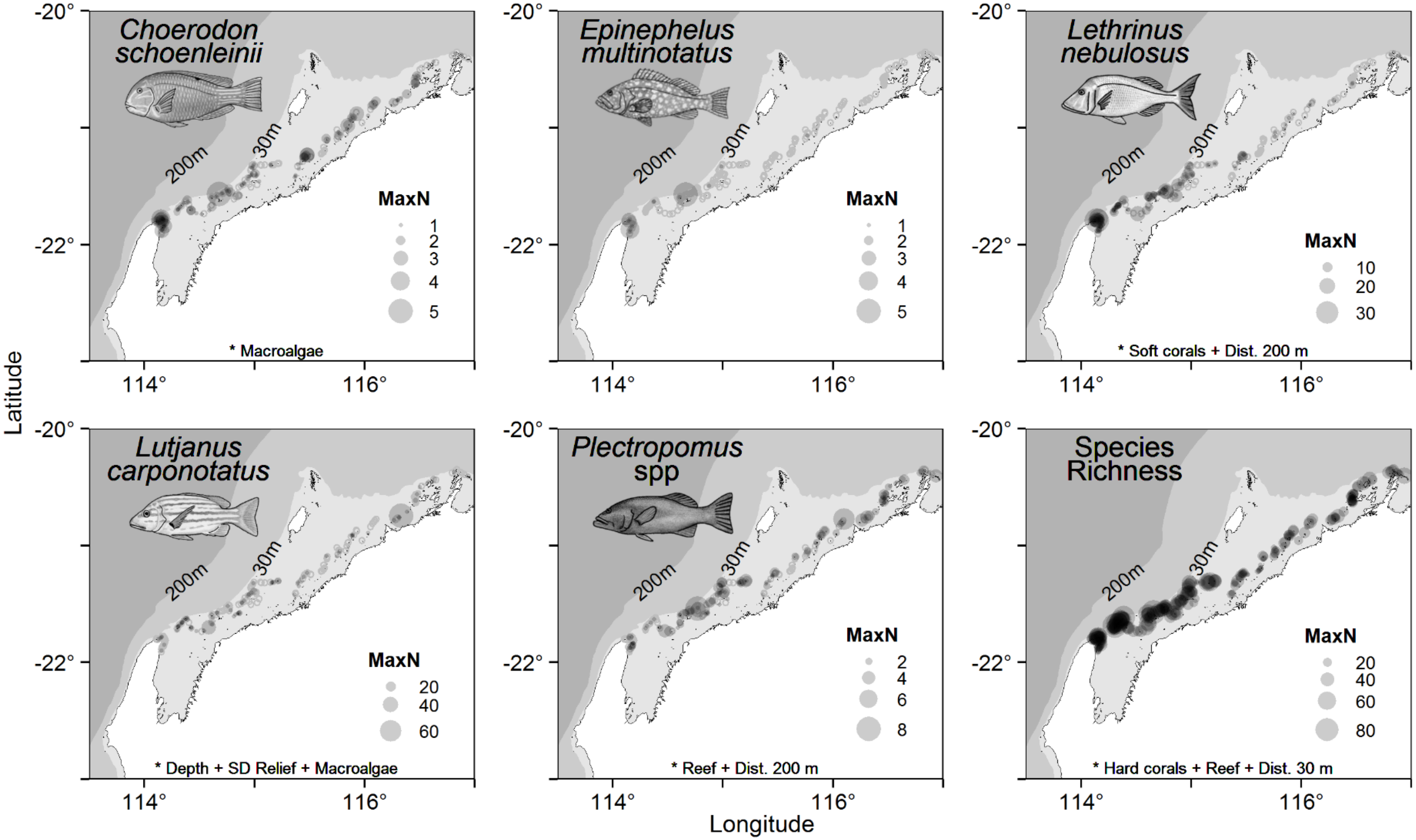

Figure 11.1.2. Spatial distribution of the relative abundance of five fishery targeted species and of species richness observed on stereo-BRUV deployments in the inshore Pilbara region of Western Australia. MaxN bubble sizes reflect actual numbers and therefore sizes on the plot may be larger or smaller than those in the legend, depending on numbers observed. * Most important variables for explaining the relative abundance of each species/group (see Table 11.1.1).

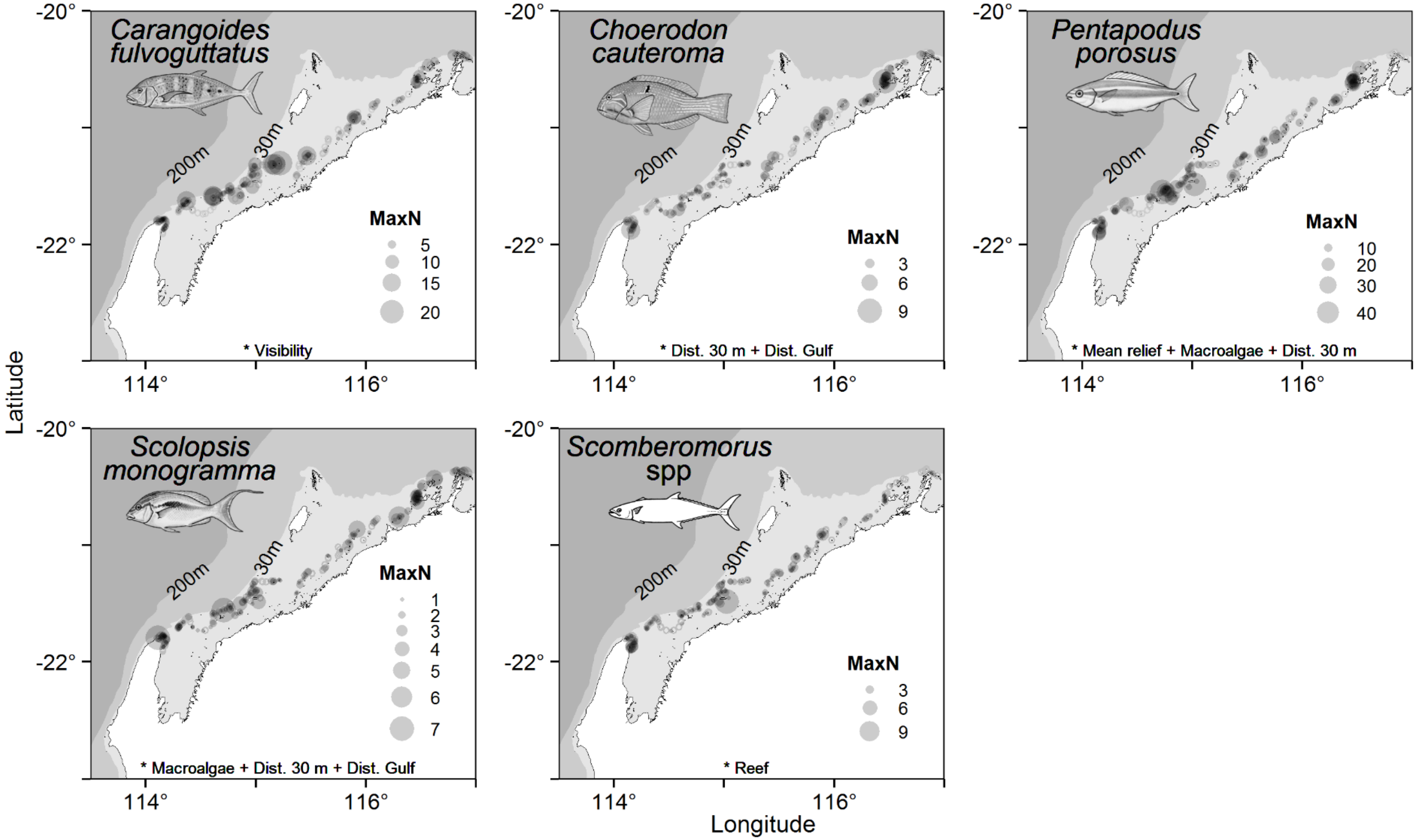

Figure 11.1.3. Spatial distribution of the relative abundance of the five most common fish species observed on stereo-BRUV deployments in the inshore Pilbara region of Western Australia. MaxN bubble sizes reflect actual numbers and therefore sizes on the plot may be larger or smaller than those in the legend, depending on numbers observed. * Most important variables for explaining the relative abundance of each species/group (see Table 11.1.1).

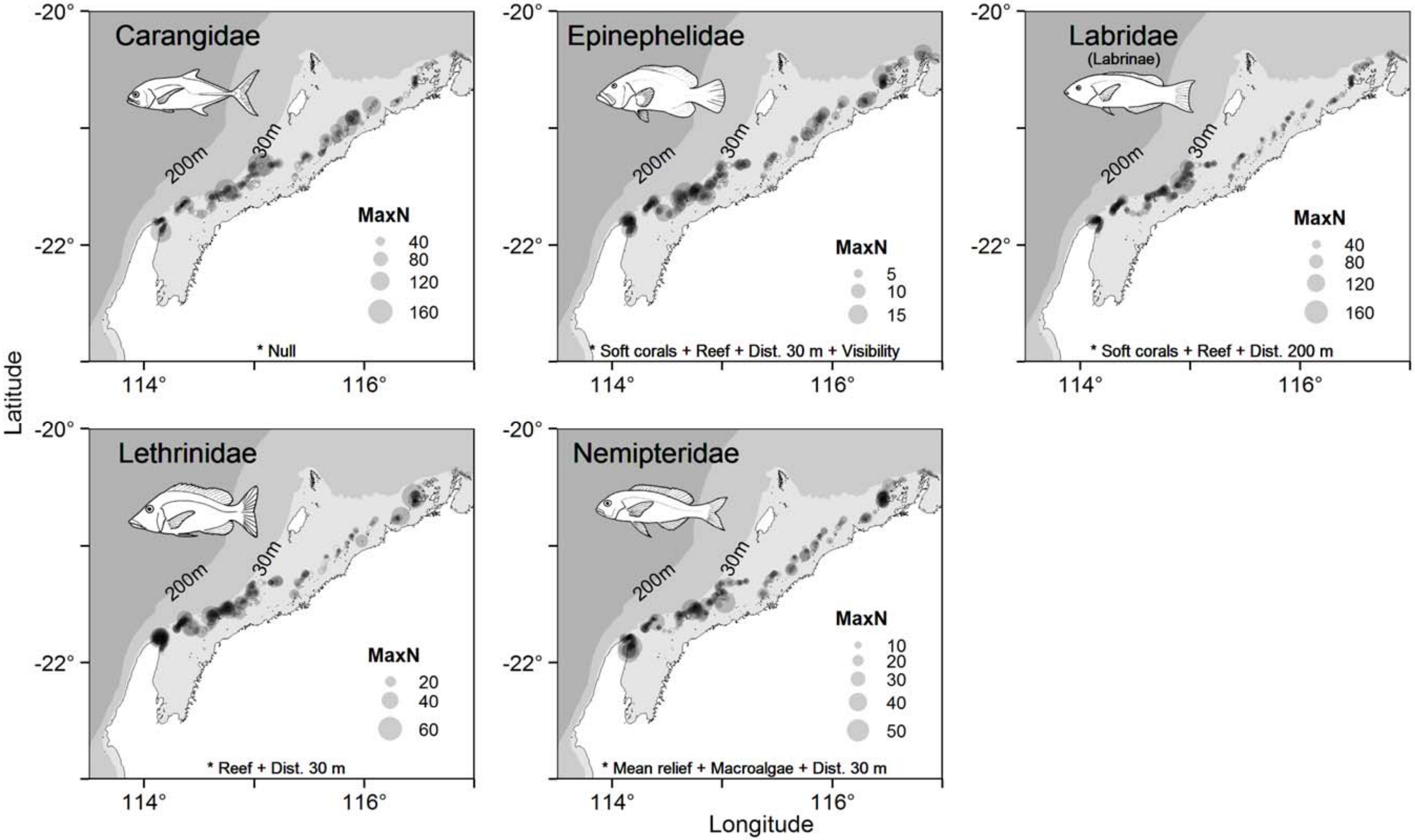

Figure 11.1.4. Spatial distribution of the relative abundance of the five most common fish families observed on stereo-BRUV deployments in the inshore Pilbara region of Western Australia. MaxN bubble sizes reflect actual numbers and therefore sizes on the plot may be larger or smaller than those in the legend, depending on numbers observed. * Most important variables for explaining the relative abundance of each species/group (see Table 11.1.1).

at the Muiron Islands, one 1500 mm *Epinephelus lanceolatus* (Queensland groper) at Legendre Island, Dampier and one *Pristis zijsron* (green sawfish) near Thevenard Island. The sawfish measured 4345 mm in length from rostra tip to tail fork, with a rostra length of 1390 mm. The five most ubiquitous fish species observed were: *Scolopsis monogramma* (rainbow monocle bream; 67% of deployments), *Scomberomorus* spp. (mackerel; 62%), *Choerodon cauteroma* (blue-spotted tuskfish; 58%), *Carangoides fulvoguttatus* (gold-spotted trevally; 56%) and *Pentapodus porosus* (northwest threadfin bream; 51%) (Figure 11.1.3). The most ubiquitous families were: Nemipteridae (threadfin bream; 93% of deployments), Labridae (wrasses and tuskfish; 90%), Lethrinidae (emperors; 81%), Carangidae (trevallies; 80%) and Epinephelidae (groupers and coral cods; 76%) (Figure 11.1.4).

Table 11.1.1. Best generalized additive mixed models (GAMMs) for predicting the abundance of fish in the Pilbara, i.e. those within two units of the lowest Akaike Information Criterion (AIC) value, which have the fewest variables.

	DEPENDENT VARIABLE	DF	R²	AIC	BIC	WAIC	BEST MODEL
	Total Abundance	10.39	0.43	2487.91	2504.69	0.78	Hard corals, Distance to 30 m, Distance to Gulf
	Species Richness	6.53	0.57	1600.45	1617.23	0.99	Hard corals, Reef, Distance to 30 m
Family	Carangidae	–	0	1532.54	1539.19	0.05	Null
	Epinephelidae	6.72	0.20	977.11	993.89	0.24	Soft corals, Reef, Distance to 30 m
	Labridae (Labrinae)	9.54	0.29	1484.35	1501.13	0.76	Soft corals, Reef, Distance to 200 m
	Lethrinidae	6.17	0.11	1315.33	1328.76	0.08	Reef, Distance to 30 m
	Nemipteridae	8.40	0.17	1311.55	1328.34	0.51	Relief, Macroalgae, Distance to 30 m
Common Species	*C. fulvoguttatus*	3.70	0.04	836.33	846.40	0.04	Visibility
	C. cauteroma	5.92	0.24	580.33	593.76	0.12	Distance to 30 m, Distance to Gulf
	P. porosus	9.61	0.20	992.99	1009.78	0.66	Relief, Macroalgae, Distance to 30 m
	S. monogramma	8.61	0.25	582.47	599.26	0.58	Macroalgae, Distance to 30 m, Distance to Gulf
	Scomberomorus spp.	3.07	0.16	531.35	541.42	0.06	Reef
Target Species	*C. schoeleinii*	2.93	0.07	456.57	466.64	0.04	Macroalgae
	L. nebulosus	9.29	0.11	642.38	655.81	0.09	Soft corals, Distance to 200 m
	L. carponotatus	15.04	0.08	495.01	511.79	0.36	Depth, SD Relief, Macroalgae
	Plectropomus spp.	5.96	0.17	553.03	566.46	0.21	Reef, Distance to 200 m

Patterns in the relative abundance of common species, target species and families were remarkably similar across the western Pilbara region (Figure 11.1.2-4). The majority of target species and common species peaked in mean relative abundance in the vicinity of the Serrurier, Bessieres and Thevenard Islands (*C. schoenleinii, E. multinotatus, L. nebulosus, Plectropomus* spp.Figure 11.1.2; *C. fulvoguttatus, P. porosus, S. monogramma, Scomberomorus* spp. Figure 11.1.3). This peak in relative abundance around these islands was also reflected in species richness data (Figure 11.1.2) and at the family level, with the exception of Lethrinidae (Figure 11.1.4). High abundances were also recorded in the north between Cape Preston and Dampier. In this location there were high abundances of *L. carponotatus, Plectropomus* spp. (Figure 11.1.2), *C. cauteroma* and *S. monogramma* (Figure 11.1.3).

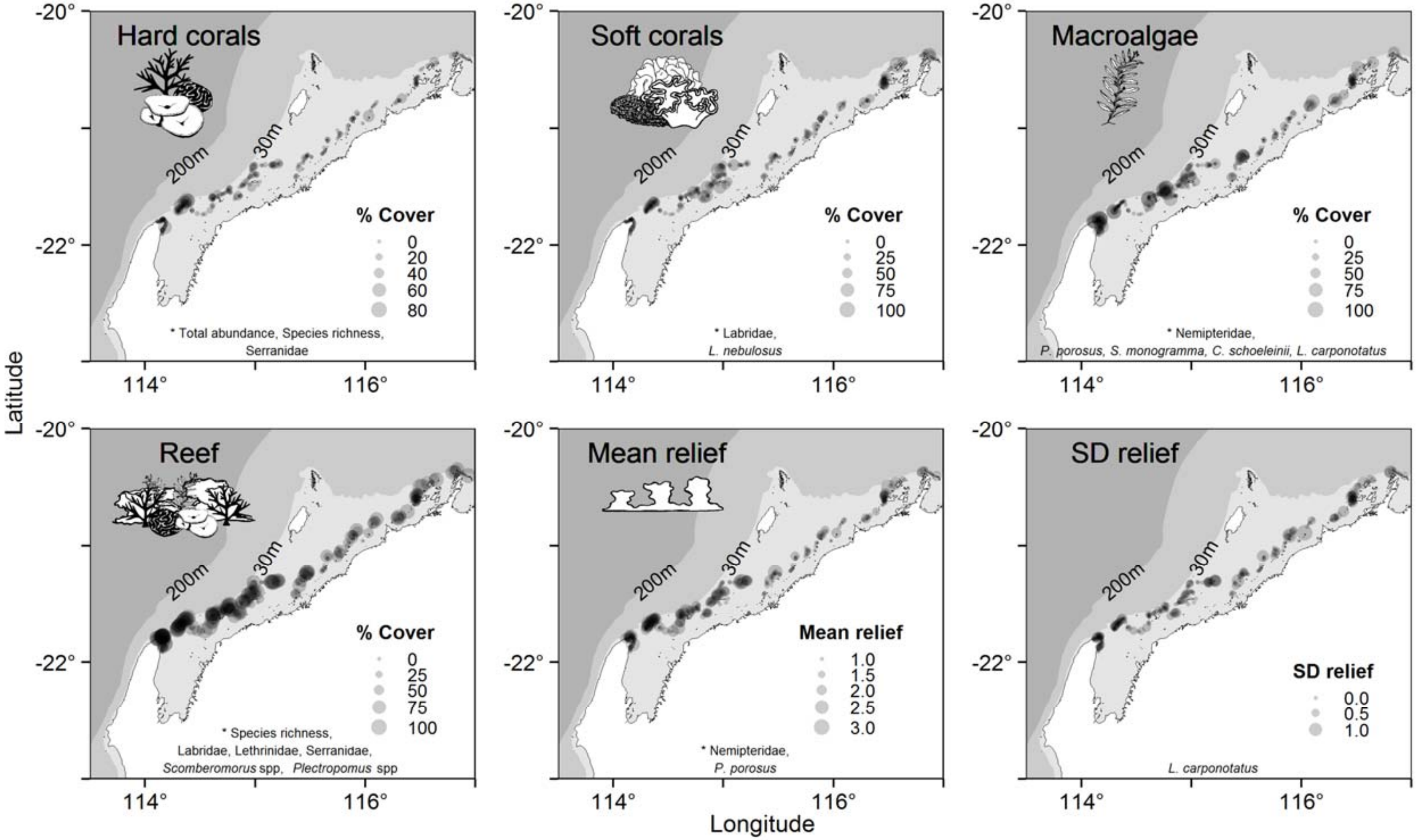

Figure 11.1.5. Percent cover of hard corals, soft corals, macroalgae and reef and estimates of relief and SD relief from stereo-BRUV deployments in the inshore Pilbara region of Western Australia. MaxN bubble sizes reflect actual values and therefore sizes on the plot may be larger or smaller than those in the legend, depending on values observed. * The key species groups for which these variables were important (see Table 11.1.1).

Lethrinids were also particularly abundant between Cape Preston and Dampier, with this pattern not driven by *L. nebulosus* but by other species including *L. atkinsoni* and *L. punctulatus.* The fewest species, and lowest relative abundance measures of common species, target species and families were observed on deployments conducted in the nearshore region between the Mangrove Islands and Long Island (Figure 11.1.2-4).

Habitat distribution

The distribution of structurally complex habitats across the western Pilbara matched closely to areas of peak abundance for fish (Figure 11.1.5). The percent cover of hard coral was greatest at the northern tip of the northwest Cape whilst the percent cover of reef was more uniformly distributed across the region (Figure 11.1.5). Soft corals were observed to exhibit higher cover rates at the offshore Islands south of and including Thevenard Island and in the Dampier Archipelago, a pattern also exhibited by macroalgae (Figure 11.1.5). Percent cover of macroalgae was also high at Islands to the north of Thevenard. Deployments conducted between the Mangrove Islands and Long Island generally had the lowest relief and percent cover of hard corals, soft corals, macroalgae and reef, matching the lowest abundances of common and target fish species.

Importance of environmental and habitat variables for fish

The best-fitted models utilising environmental and habitat variables were generated for species richness and the total abundance of fish in the Pilbara (Table 11.1.1). The variable importance plot (Figure 6) illustrates the strength of these variables in relation to those obtained in the top models for species and families. Positive relationships were obtained between species richness and the percent cover of reef and hard coral (Figure 11.1.7). Total abundances of fish were also greater in areas of higher hard coral cover (Figure 11.1.7). Species richness tended to decline with increasing distance to the 30 m depth isobar and similarly total abundance tended to be greater where the distance to the 30 m depth isobar was <100 km. Total abundance was also greatest closest to Exmouth Gulf and declined with increasing distance from the Gulf (Figure 11.1.7).

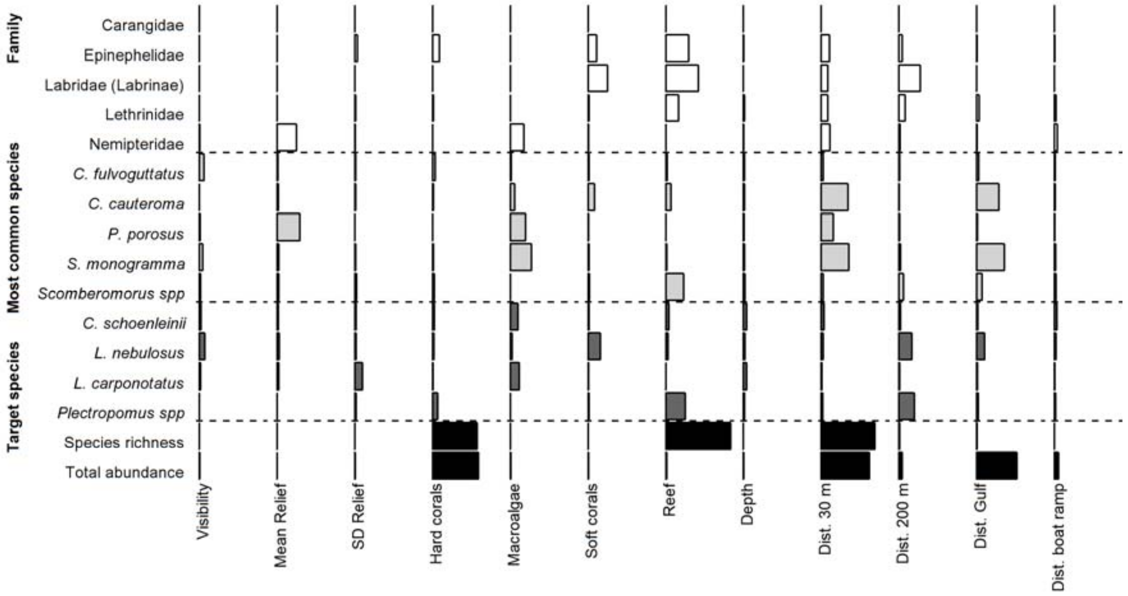

Figure 11.1.6. Relative importance of each explanatory variable in predicting species richness, total abundance and the relative abundance of target and common species and families. Each value was calculated as the average Akaike weight (wAIC) of all subsets of models containing that variable, which was then scaled between 0-1 and multiplied by the R2 of the best fitted model.

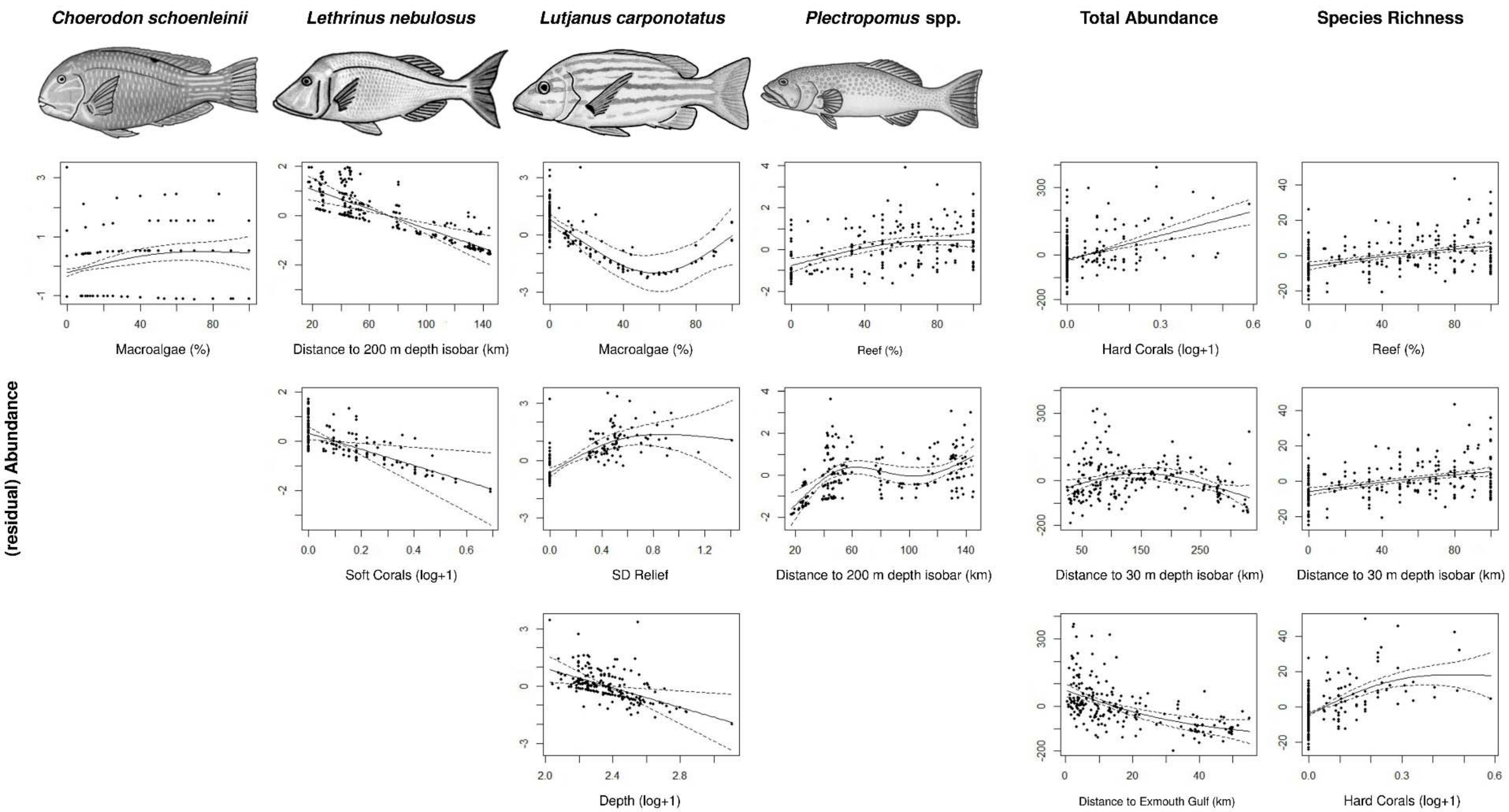

Figure 11.1.7. The total residual abundance, species richness and the residual abundance of four fishery targeted species in the Pilbara relative to their most important explanatory variables (Table 11.1.1). Models were fitted using GAMMs. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 × SE of the estimate.

Despite similar relative abundance distributions of each of the target species across the Pilbara, a variety of different variables were important for these species (Table 11.1.1; Figure 11.1.6). For *C. schoenleinii* the top model included a single variable, macroalgae, but the importance of this variable for influencing the relative abundance of this species was weak (Table 11.1.1; Figure 11.1.6), with only a slight positive relationship between percent cover of macroalgae and abundance (Figure 11.1.7). The relative abundance of *L. nebulosus* declined with the declining cover of soft corals and with increasing distance to the 200 m depth isobar (Figure 11.1.7). The top model for *L. carponotatus* was not strong (Table 11.1.1; Figure 11.1.6) but suggested that the percent cover of macroalgae, SD relief and depth were each, to a small degree, influencing the abundance of this species. *L. carponotatus* were most abundant where macroalgae cover was either <40% or >80%, where SD relief was high (indicating variable relief) and where depths were the shallowest. Of the target species, the strongest model was obtained for *Plectropomus* spp. (Table 11.1.1) with it being most abundant in areas with the greatest percent cover of reef (Figure 11.1.2, Figure 11.1.4, Figure 11.1.7).

Increasing visibility was weakly related to greater abundances of *C. fulvoguttatus* (Figure 11.1.8), however the model strength was low (Table 11.1.1) and the variable relatively unimportant (Figure 11.1.6). Distance to the 30 m depth isobar and distance to the Exmouth Gulf were both important variables for the relative abundance of *C. cauteroma* (Table 11.1.1; Figure 11.1.6). This species was most abundant at mid-distances (20-40 km) from the 30 m depth isobar and increased in abundance with increasing distance from the Exmouth Gulf (Figure 11.1.8). Model strength for *P. porosus* was quite high (Table 11.1.1) with the relative abundance of this species having a strong negative relationship with relief (Figure 11.1.8). There was also a weak positive relationship between abundance and macroalgae cover and a bimodal pattern in abundance with distance to the 30 m depth isobar with higher abundances at distances closest to, and farthest away from this depth contour. *S. monogramma,* the most common fish species observed in the Pilbara, like *C. cauteroma* tended to increase in abundance with increasing distance from the Exmouth Gulf (Figure 11.1.8). A weak negative relationship was observed with *S. monogramma* and the cover of macroalgae and distance to the 30 m depth isobar. Lastly, the top model for *Scomberomorus* spp. contained a single variable, reef (Table 11.1.1), with the highest cover of reef corresponding to lowest abundances for this species (Figure 11.1.8).

The percent cover of reef was present in most of the top models for families (Table 11.1.1; Figure 11.1.6). Increasing cover of reef was associated with increasing abundances of Labridae, Lethrinidae and Epinephelidae (Figure 11.1.9). Distance to the 30 m depth contour was also an important variable in the top models for Lethrinidae, Nemipteridae and Epinephelidae (Table 11.1.1) with each group exhibiting a weak negative relationship between abundance and distance to this depth contour (Figure 11.1.9). For Labridae, additional important variables included distance to the 200 m depth isobar which had a bimodal relationship with abundance (lowest at mid distances), and the percent cover of soft corals which had a positive relationship with abundance (Figure 11.1.9). Important variables for Nemipteridae mirrored those obtained for the most common species of this group, *P. porosus.* Lastly, in addition to reef and distance to the 30 m depth contour, Epinephelidae abundance was greater in areas of high coral cover (Figure 11.1.9).

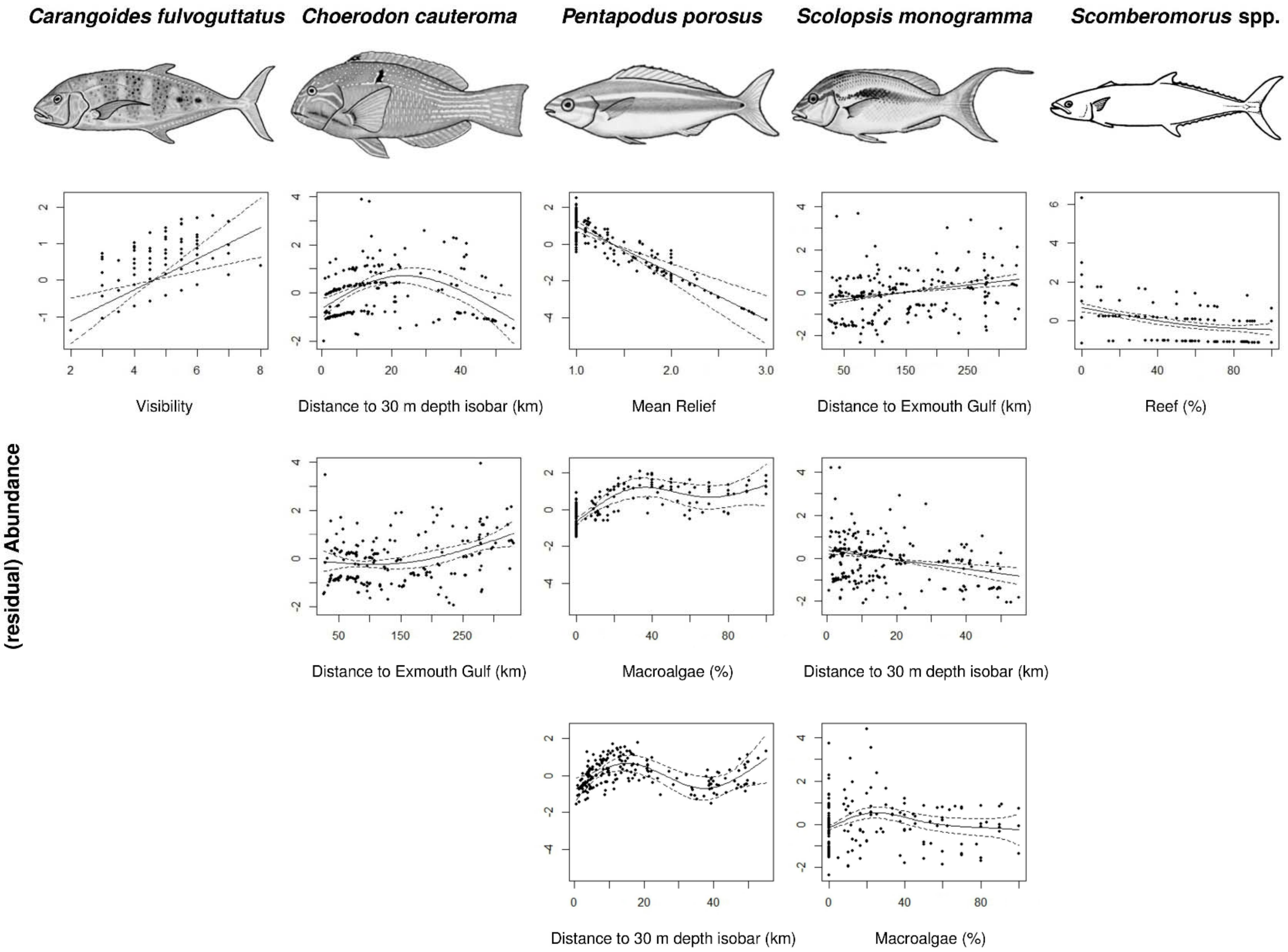

Figure 11.1.8. The residual abundance of the five most common fish species in the Pilbara relative to their most important explanatory variables (Table 11.1.1). Models were fitted using GAMMs. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 × SE of the estimate.

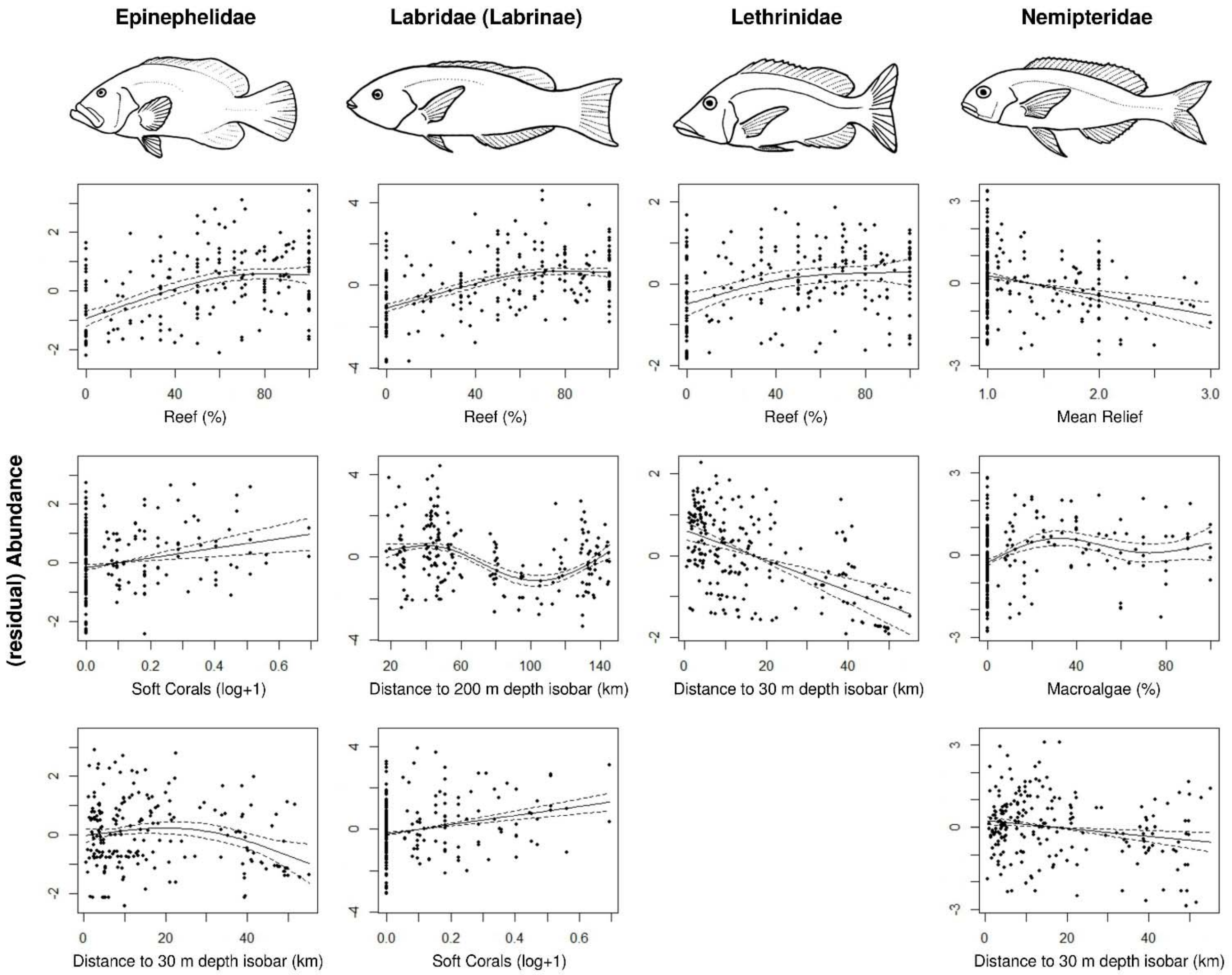

Figure 11.1.9. The residual abundance of the four most common fish families (excluding Carangidae) in the Pilbara relative to their most important explanatory variables (Table 11.1.1). Models were fitted using GAMMs. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 × SE of the estimate. Carangidae is excluded here due to the null model having the best fit.

11.1.4 DISCUSSION

The diverse ichthyofauna in shallow nearshore waters (i.e. <22 m) of the Pilbara region of northwest Australia compares favourably to levels of diversity surveyed in the Kimberley region, approximately 800 km to the north of Dampier (Cappo et al. 2011). Cappo et al. (2011) conducted 154 BRUV deployments in nearshore (<20 m) habitats across ~30 km of coastline, recording 7108 individuals from 116 species. This is markedly less than the 31171 individuals from 343 species recorded from 220 stereo-BRUV deployments conducted along the ~340 km nearshore stretch between Dampier and the Exmouth Gulf (Figure 11.1.1). The disparity is likely primarily due to habitat differences, with those sampled in the Kimberley region being more 'sandy', with low rugosity and a lack of sub-tidal coral reefs (Cappo et al. 2011). Numbers of individuals and species observed in the present study were, however, very similar to those recorded from 1100 BRUV deployments conducted across more than 2000 km of lagoonal and inter-reef waters of the Great Barrier Reef Marine Park of the north-east coast of Australia (39,989 individuals from 347 species; Cappo et al. 2007). These results suggest that the Pilbara region is similar to other sub-tropical and tropical regions around Australia, with fish assemblages characterised by high levels of diversity. This high diversity is likely to be an ecological response to the limited productivity and nutrient deprived marine environments of Western Australia (Molony et al. 2011).

Islands in the south of the Pilbara, including North and South Muiron, Serrurier, Bessieres, Thevenard and Airlie Islands (Figure 11.1.1), possessed the most species-rich assemblages and highest relative abundances of fish, including important fishery-target species and protected species. Around these islands, structurally complex reef systems were present with a high coverage of hard corals, macroalgae and soft corals. Here, the distance to the 30 m and 200 m depth isobars is at a minimum for the region, likely representing increasing exposure to more oceanic water conditions compared to areas further north in the Pilbara. A similar finding was reported by Sandin et al. (2008) who showed that the diversity of Caribbean reef fish increased with increasing connectivity and nearshore productivity and declined with isolation. In the southern Pilbara, a closer proximity to oceanic waters appears to be an important positive driver of high fish diversity (Hutchins et al. 1996; Hutchins 2001).

Whilst coastal coral reefs of the Pilbara are adapted to high levels of natural disturbance (cyclones, tidal currents; Gilmour et al. 2006), corals can be vulnerable to additional anthropogenic disturbances due to limited demographic and genetic replenishment (Underwood et al. 2013). That is, they rely on their own genetic diversity to adapt to environmental change. In this study, strong links were identified between coral cover and fish diversity and abundance at the small offshore islands in the southern Pilbara. Extreme climatic events such as the heat wave that occurred in 2010/2011, combined with pressures associated with significant coastal development supporting the petrochemical and mineral industries, e.g. increased sedimentation, turbidity, and salinity (Gilmour et al. 2006), potentially threaten coral communities, and other sensitive habitats (e.g. benthic primary producers), throughout the Pilbara. Across the globe, a range of anthropogenic (e.g. climate change, overfishing, habitat destruction and pollution) and natural disturbances act in tandem over time to threaten the resilience of habitats and fish communities (Jackson et al. 2001; Bornt et al. 2015; van der Veer et al. 2015). A meta-analysis by Wilson et al. (2006) showed strong links between fish and corals with coral loss (e.g. severe tropical storms) having a greater impact on fishes than coral disturbance (e.g. bleaching). To assist conservation management for the Pilbara, further research into the ecological processes supporting these diverse island communities and the threats to them is warranted.

Bordering the southern Pilbara is Exmouth Gulf, a large, shallow embayment where there is a paucity of information on fish assemblages (Figure 11.1.1). A single study, conducted by Hutchins et al. (1996) documented the presence of fish species along the eastern margins of the Gulf. Exmouth Gulf is a known source of nutrients that support a significant commercial prawn trawl fishery with extensive mangroves and seagrass beds (McCook et al. 1995). Like marine embayments elsewhere in Western Australia (Wakefield et al. 2011) and in other parts of the world (Berkström et al. 2013), the Exmouth Gulf likely provides important nursery habitats for fish. The small offshore islands in the south of the Pilbara, in relatively close proximity to the Gulf, were the only locations where juvenile (<120 mm) lethrinids and scarids, too small to identify to species (Supplementary Data S-Table 1) were recorded. However, with sampling in shallower depths we would expect to also see juveniles where the cover of macroalgae and soft corals was greatest, i.e. between Cape Preston and Dampier in the north with such habitats likely important habitats for juvenile fish (Wilson et al. 2010; Evans et al. 2014). Exmouth Gulf is likely to be a source of nutrients, from the minimal land run-off, and a potential area of juvenile recruitment due to the shallow macrophyte assemblages (McCook et al. 1995). Given these factors and the paucity of information on Exmouth Gulf, the influence of this significant embayment on the whole Pilbara region requires further investigation.

It is generally accepted that fish populations around human population centres will be very different to those on isolated reefs (Stevenson et al. 2007; Williams et al. 2011; Edgar et al. 2014). Along these lines, boat ramp access points within the Pilbara are typically co-located with major human coastal populations and we hypothesised that fish populations furthest from access points would have the greatest abundance of target species (see also Langlois et al. 2012). However, the distance to boat ramp variable was not present in any of the top models and therefore was not found to have a driving influence on the abundance of target fish species. Fish abundance and species richness at the islands in the southern Pilbara were greater than those sampled in more remote locations within the region with no relationship evident with distance to boat ramps.

The lowest species richness and relative abundances of key species groups were observed on deployments conducted between the Mangrove Islands and Long Island (see Figure 11.1.1). Whilst we targeted nearshore reef habitats, in these locations reefs were covered in macroalgae and silty sediment with very little hard coral cover. Here, distances to the 30 and 200 m depth isobars are at a maximum, likely limiting any oceanic flushing through this nearshore region. These habitat and environmental patterns closely match the relative abundances of target and common fish species as indicated in the spatial plots (Figure 11.1.2-4) and residual abundance plots (Figure 11.1.7-9). This distinct mid-region area was well represented in many of the residual abundance plots and is characterised by a bimodal pattern indicating lower abundance and diversity (Figure 11.1.7-9). Coastal habitats inshore of sites sampled in this region are characterised by expansive mangroves crossed by tidal creeks and fronted by intertidal mudflats (Heyward et al. 2006; Human and McDonald 2009). Sediments are likely transported from these coastal areas to the offshore reefs via tidal movements. These nearshore sandy areas in the Pilbara region are notoriously difficult to sample using visual techniques due to high turbidity and very limited visibility. As we avoided sampling bare sandy habitats, there is an underrepresentation of sand-affiliated species in our data (see Supplementary Data S-Table 1). For example, Travers et al. (2010, 2012) recorded high abundances of Synodontidae (lizardfishes) and Monacanthidae (leatherjackets) in soft sediments in the Pilbara, both of which were observed in very low abundances in the current study.

The nearshore marine environment in the northern Pilbara between Cape Preston and Dampier appears to be an important region for coral trout (*Plectropomus* spp.) and lethrinids ((Figure 11.1.2-4). For lethrinids, this reflects greater abundances of particularly the blue-spotted emperor (*L. punctulatus*, Figure 11.1.2). *L. punctulatus,* a north-western Australian endemic species, is perhaps at the centre of its distribution here*,* with adjacent cross-shelf areas having the highest levels of abundance in commercial catches (Newman et al. 2014). This may also explain why the area to the east along the Canning Coast, which lacks these offshore islands and associated habitats, does not appear to exhibit similar levels of abundance for this species. It thus appears that this species likely exhibits life history partitioning between juveniles and adults, with specific habitat associations for juveniles limiting their abundance and distribution along this coastline, despite exhibiting highly productive life history characteristics (e.g. early maturation, protracted spawning period, short lifespan, Wakefield pers. comm.). This situation may also apply to other species with limited distributions (i.e. endemics). Further investigation of the role of these nearshore habitats for juvenile emperor and their links with offshore commercial fisheries in the region is required.

This study is the first example where a standardised habitat classification scheme (CATAMI, Althaus et al. 2013) has been applied to rapidly quantify habitat cover and relief derived from forward facing stereo-BRUVs. Classification of imagery from stereo-BRUVs has previously been demonstrated to be an adequate proxy for hydro-acoustic derived habitat maps for predicting fish habitat suitability (Monk et al. 2011). Here, the simultaneous video sampling of fish and habitats has provided a useful benchmark of the abundance and distribution of fish and fish-habitat relationships across the nearshore Pilbara region of north-western Australia. While the use of bait enables an enhanced survey of a greater abundance and diversity of fish species, the attraction of fish from surrounding areas may limit inferences about fish-habitat relationships, particularly where habitats are patchily distributed. This study also harnesses modern statistical methods to examine the functional trend between variables and a broad range of predictors, assessing whether a trend is evident and if so, what is the form or shape (linear or nonlinear). By combining the use of a standardised habitat classification schemes with GAMMs and full-subsets analyses, a powerful analytical approach for gathering knowledge has been developed that has broad application in biogeography.

11.1.5 ACKNOWLEDGEMENTS

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11.1.6 REFERENCES

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. Proceedings of the Second International Symposium on Information Theory, BN Petrov and F Caskie ds. Akademiai Kiado, Budapest, 267-281.

Almany GR (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *OIKOS* 106:275-284.

Althaus F, Hill N, Edwards L, Ferrari R, et al (2013) CATAMI Classification Scheme for scoring marine biota and substrata in underwater imagery – A pictorial guide to the Collaborative and Annotation Tools for Analysis of Marine Imagery and Video (CATAMI) classification scheme. Version 1. http://catami.org/classification

Berkström C, Lindborg R, Thyresson, M, Gullström M (2013) Assessing connectivity in a tropical embayment: fish migrations and seascape ecology. *Biological Conservation* 166:43-53.

Bornt KR, McLean DL, Langlois TJ, Harvey ES, Bellchambers LM, Evans SN, Newman SJ (2015) Targeted demersal fish species exhibit variable responses to long-term protection from fishing at the Houtman Abrolhos Islands. *Coral Reefs* 34(4):1297–1312.

Burnham KP and Anderson DR (2002) Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, Springer, New York.

Cappo M, Speare P and De'ath G (2004). Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology* 302:123-152.

Cappo M, De'ath G and Speare P (2007) Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. *Marine Ecology Progress Series* 350:209–221.

Cappo M, Stower M, Syms C, Johansson C and Cooper T (2011) Fish-habitat associations in the region offshore from James Price Point – a rapid assessment using Baited Remote Underwater Video Stations (BRUVS). *Journal of the Royal Society of Western Australia* 94:303-321.

Crain CM, Halpern BS and Beck MW Kappel CV (2009) Understanding and managing human threats to the coastal marine environment. *Annals of the New York Academy of Science* 1162:39-62.

Curley BG Kingsford MJ and Gillanders BM (2002) Spatial and habitat-related patterns of temperate reef assemblages: implications for the design of Marine Protected Areas. *Marine and Freshwater Research* 53:1197–1210.

Edgar GE, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett, NS, Becerro MA Bernard, ATF Berkhout J, Buxton CD, Campbell SJ, Cooper AT, Davey M, Edgar SC, Försterra G, Galván DE, Irigoyen AJ, Kushner DJ, Moura R, Parnell PE, Shears NT, Soler G, Strain EMA and Thomson RJ (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216-220Evans R, Wilson S, Field S and Moore J (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia *Marine Biology* 161:599-607.

Fletcher WJ, Santoro K (2015) Status Reports of the Fisheries and Aquatic Resources of Western Australia 2014/15: The State of the Fisheries. Department of Fisheries, Western Australia, 353.

Fox NJ, Beckley LE (2005) Priority areas for conservation of Western Australian coastal fishes: A comparison of hotspot, biogeographical and complementarity approaches *Biological Conservation* 125:399-410.

Friedlander AM and Parish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef *Journal of Experimental Marine Biology and Ecology* 224:1–30.

Friedlander AM Brown EK Jokiel PL Smith WR and Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian Archipelago. *Coral Reefs* 22:291–305.

Giakoumi S and Kokkoris GD (2013) Effects of habitat and substrate complexity on shallow sublittoral fish assemblages in the Cyclades Archipelago, North-eastern Mediterranean sea.

Mediterranean Marine Science 14:58–68.

Gilmour JP, Cooper TF, Fabricius KE and Smith LD (2006) Early warning indicators of change in the condition of corals and coral communities in response to key anthropogenic stressors in the Pilbara, Western Australia. Australian Institute of Marine Science, p. 101.

Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2, e616.

Harrison J, Wyatt M, Marrable D, Gray M and Edwards L (2014) Collaborative and Annotation Tools for Analysis of Marine Imagery and video (CATAMI).

Harvey ES and Shortis MR (1996) A system for stereo-video measurement of subtidal organisms. *Marine Technological Society Journal* 29:10-22.

Harvey ES Shortis MR 1998 Calibration stability of an underwater stereo-video system: Implications for measurement accuracy and precision *Marine Technological Society Journal* 32:3-17.

Hastie T and Tibshirani R (1986) Generalized additive models. Statistical Science 1:297–310.

Heyward A and Revill A Sherwood C 2006 Review of research and data relevant to marine environmental management of Australia’s North West Shelf. North West Shelf Joint Environmental Management Study, Technical Report No. 1. p. 75.

Hill N, Althaus F, Rees T et al (2014) CATAMI Classification Scheme for scoring marine biota and substrata in underwater imagery Version 1.4: December 2014

Human BA and McDonald JI (2009) Knowledge review and gap analysis: Resource condition monitoring in the Pilbara and Kimberley regions of Western Australia. Coastal and Marine Resource Condition Monitoring - Scoping Project. Final NRM Report Project 073007 - Part 1. Department of Fisheries, Government of Western Australia. p. 192.

Hutchins JB (2001) Biodiversity of shallow reef fish assemblages in Western Australia using a rapid censusing technique. Records of the Western Australian Museum 20:247–270.

Hutchins JB, Slacksmith SM, Bryce CW, Morrison SM, Hewitt MA (1996) Marine Biological Survey of the Muiron Islands and the eastern shore of Exmouth Gulf, Western Australia. Report prepared for the Ocean Rescue 2000 Program (G012/94), Western Australian Museum, February 1996. p. 135.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638.

Langlois TJ, Harvey ES and Meeuwig JJ (2012) Strong direct and inconsistent indirect effects of fishing found using stereo-video: Testing indicators from fisheries closures. Ecol. Indic. 23 524-534.

Langlois TJ, Newman SJ, Cappo M, Harvey ES, Rome BM, Skepper CL and Wakefield CB (2015) Length selectivity of commercial fish traps assessed from in situ comparisons with stereo-video: Is there evidence of sampling bias? Fish. Res. 161 145-155.

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G and Watson DL (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. *Aquatic Biology* 9:155-168.

Lin X and Zhang D (1999) Inference in generalized additive mixed models by using smoothing splines. J. R. Statist. Soc. B. 61:381–400.

McCook LJ, Klumpp DW, McKinnon AD (1995) Seagrass communities in Exmouth Gulf, Western Australia: A preliminary survey. Journal for the Royal Society of Western Australia 78:81-87.

Molony BW, Newman SJ, Joll L, Lenanton RCJ, Wise B (2011) Are Western Australian waters the least productive waters for finfish across two oceans? A review with a focus on finfish resources in the Kimberley region and North Coast Bioregion. Journal for the Royal Society of Western Australia 94(2):323-332.

Monk J, Ierodiaconou D, Bellgrove A, Harvey E and Laurenson L (2011) Remotely sensed hydroacoustics and observation data for predicting fish habitat suitability. Continental Shelf Research 31:S17-S27.

MPRSWG (1994) A representative marine reserve system for Western Australia. Report of the Marine Parks and Reserves Selection Working Group. Published by the Department of Conservation and Land Management (now Department of Biodiversity, Conservation and Attractions). June 1994. p. 291.

Newman SJ, Williams DMcB (1996) Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central Great Barrier Reef. Environmental Biology of Fishes 46(2):123-138.

Newman SJ, Williams DMcB and Russ GR (1997). Patterns of zonation of assemblages of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) within and among midshelf and outershelf reefs in the central Great Barrier Reef. *Marine Freshwater Research* 48(1):119-128.

Newman SJ, Williams DMcB (2001) Spatial and temporal variation in assemblages of Lutjanidae, Lethrinidae and associated fish species among mid-continental shelf reefs in the central Great Barrier Reef *Marine Freshwater Research* 52(6):843-851.

Newman SJ, Wakefield C, Skepper C, Boddington D, Blay N, Jones R and Wallis D (2014). North Coast Demersal Fisheries Status Report. pp. 192-209. In: Fletcher WJ and Santoro K (eds). *Status Reports of the Fisheries and Aquatic Resources of Western Australia 2013/14: The State of the Fisheries.* Department of Fisheries, Western Australia, Perth, Australia. 359p.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG et al. (2003). Global trajectories of the long-term decline of coral reef ecosystems*. Science* 301:955-958.

Parsons ECM, Favaro B, Aguirre AA, Bauer AL, Blight LK, Cigliano,] JA, Coleman, MA, Cote IM, Draheim M, Fletcher S, Foley MM, Jefferson R, Jones MC, Kelaher BP, Lundquist CJ, McCarthy J-B, Nelson A, Patterson K, Walsh L, Wright AJ and Sutherland WJ (2014). Seventy-one important questions for the conservation of marine biodiversity. Conservation Biology 28(5):1206-1214.

PDC (2015) Pilbara Development Commission Regional Investment Blueprint: Technical Report. p. 154.

Priede IG, Bagley PM, Smith A, Creasey S, Merrett NR (1994). Scavenging deep demersal fishes of the Porcupine Seabight, North-east Atlantic: observations by baited camera, trap and trawl *Journal of Marine Biological Association* U.K. 74:481-498.

R Development Core Team (2015). RStudio: Integrated development environment for R (version 3.2.2) www.rstudio.com

Raftery AE (1995) Bayesian model selection in social research (with discussion). *Sociological Methodology* 25:111-195.

Ryan KL, Wise BS, Hall NG, Pollock KH, Sulin EH and Gaughan DJ (2013). An integrated system to survey boat-based recreational fishing in Western Australia 2011/12. Fisheries Research Report No. 249, Department of Fisheries, Western Australia. p. 168. http://www.fish.wa.gov.au/Documents/research_reports/frr249.pdf

Ryan KL, Hall NG, Lai EK, Smallwood CB, Taylor SM and Wise BS (2015). State-wide survey of boat-based recreational fishing in Western Australia 2013/14. Fisheries Research Report No. 268, Department of Fisheries, Western Australia.

Sandin SA, Vermeij MJA, Hurlbert AH (2008). Island biogeography of Caribbean coral reef fish. *Global Biogeography and ecology* 17:770-777.

Stevenson C, Katz LS, Micheli F, Block B, Heiman KW, Perle C, Weng K, Dunbar R, Witting J (2007). High apex predator biomass on remote Pacific islands. *Coral Reefs* 26:47-51.

Travers MJ, Newman SJ, Potter IC (2006). Influence of latitude, water depth, day v. night and wet v. dry periods on the species composition of reef fish communities in tropical Western Australia. *Journal of Fish Biology* 69:987-1017.

Travers MJ, Potter IC, Clarke KR, Newman SJ and Hutchins JB (2010). The inshore fish faunas over soft substrates and reefs on the tropical west coast of Australia differ and change with latitude and bioregion. *Journal of Biogeography* 37:148-169.

Travers MJ, Potter IC, Clarke KR and Newman SJ (2012). Relationships between latitude and environmental conditions and the species richness, abundance and composition of tropical fish assemblages over soft substrata *Marine Ecology Progress Series* 446:221-241.

Underwood JN, Wilson SK, Ludgerus L and Evans RD (2013). Integrating connectivity science and spatial conservation management of coral reefs in north-west Australia. *Journal of Nature Conservation* 21:163-172.

Van der Veer HW, Dapper R, Henderson PA, Jung AS, Philippart CJM, Witte JIJ, Zuur AF (2015). Changes over 50 years in fish fauna of a temperate coastal sea: Degredation of trophic structure and nursery function. Estuarine Coastal Shelf Science 155:156-166.

Wakefield CB, Fairclough DV, Lenanton RCJ, Potter IC (2011). Spawning and nursery habitat partitioning and movement patterns of *Pagrus auratus* (Sparidae) on the lower west coast of Australia. Fisheries Research 109(2-3):243-251.

Wakefield CB, Lewis PD, Coutts TB, Fairclough DV, Langlois TJ (2013). Fish assemblages associated with natural and anthropogenically modified habitats in a marine embayment: comparison of baited videos and opera-house traps. *PloS one* 8(3), e59959.

Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ, Shedrawi G (2010). Assessing reef fish assemblage structure: how do different stereo-video techniques compare? *Marine Biology* 157:1237-1250.

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams, SL (2009). Accelerating loss of seagrass across the globe threatens coastal ecosystems. PNAS 106(30):12377-12381.

Williams ID, Richards BL, Sandin SA, Baum JK, Schroeder RE, Nadon MO, Zgliczynski B, Craig P, McIlwai JL, Brainard RE (2011). Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western *Pacific Journal of Marine Biology* doi:10.1155/2011/826234.

Willis TJ and Anderson MJ (2003). Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. Marine Ecology Progress Series 257:209–221.

Wilson SK, Graham NA, Pratchett MS, Jones GP and Polunin NV, (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Glob. *Change Biology* 12:2220-2234.

Wilson SK, Depczynski M, Fisher R, Holmes TH, O'Leary RA and Tinkler P (2010). The importance of coral in the habitat use of juvenile reef fish. *PLoS One* 5, e15185.

Wilson SK, Babcock RC, Fisher R, Holmes TH, Moore JAY, Thomson DP (2012). Relative and combined effects of habitat and fishing on reef fish communities across a limited fishing gradient at Ningaloo. *Marine Environmental Research* 81:1–11.

Wood S and Scheipl F (2015) Package 'gamm4' (version 0.2-3). Generalized additive mixed models using mgcv and lme4. https://cran.r-project.org/web/packages/gamm4/gamm4.pdf

11.1.7 SUPPLEMENTARY MATERIAL

Table S11.1.1 Total number and commonality of all fish species (alphabetical by family then genus) observed on stereo-BRUV deployments in the nearshore Pilbara region of northwest Western Australia.

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
Acanthuridae	*Acanthurus dussumieri*	184	14.62
	Acanthurus grammoptilus	397	39.62
	Acanthurus mata	116	6.13
	Acanthurus nigricans	8	1.89
	Acanthurus nigricauda	9	1.89
	Acanthurus olivaceus	43	9.91
	Acanthurus triostegus	5	0.94
	Ctenochaetus striatus	44	10.38
	Naso annulatus	127	15.09
	Naso brevirostris	31	6.6
	Naso fageni	24	3.3
	Naso hexacanthus	4	1.42
	Naso lituratus	7	1.89
	Naso unicornis	49	6.6
	Naso vlamingii	2	0.94
	Zebrasoma scopas	5	2.36
Apogonidae	*Apogon doederleini*	3	0.94
	Apogon semiornatus	1	0.47
	Ostorhinchus cavitiensis	11	0.47
	Ostorhinchus monospilus	107	1.42
Aulostomidae	*Aulostomus chinensis*	9	4.25
Balistidae	*Abalistes stellatus*	55	17.92
	Balistoides viridescens	2	0.47
	Melichthys vidua	7	2.36
	Pseudobalistes flavimarginatus	1	0.47
	Pseudobalistes fuscus	24	11.32
	Sufflamen chrysopterum	83	24.06
	Sufflamen fraenatum	64	21.7
Blenniidae	*Aspidontus dussumieri*	3	1.42
	Cirripectes filamentosus	3	1.42
	Ecsenius bicolor	21	8.02
	Ecsenius lineatus	4	0.94
	Meiacanthus grammistes	2	0.94
	Meiacanthus luteus	7	2.36
	Plagiotremus rhinorhynchos	60	21.7
	Plagiotremus tapeinosoma	3	1.42
Bothidae	*Bothidae* spp.	3	0.94
Caesionidae	*Caesio caerulaurea*	275	2.83
	Caesio cuning	646	15.57
	Caesio teres	49	3.77
	Pterocaesio digramma	2467	17.45
	Pterocaesio tile	283	3.77
Carangidae	*Alepes vari*	296	8.49

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
	Atule mate	370	16.04
	Carangoides caeruleopinnatus	4	0.94
	Carangoides ferdau	7	1.42
	Carangoides fulvoguttatus	509	55.66
	Carangoides gymnostethus	508	16.51
	Carangoides hedlandensis	5	2.36
	Carangoides orthogrammus	1	0.47
	Caranx ignobilis	26	3.77
	Caranx papuensis	66	4.25
	Elagatis bipinnulata	6	0.94
	Gnathanodon speciosus	608	36.79
	Scomberoides commersonnianus	10	3.3
	Scomberoides lysan	19	3.3
	Selaroides leptolepis	1038	12.74
	Seriolina nigrofasciata	2	0.94
	Trachinotus blochii	5	0.47
	Ulua mentalis	2	0.47
Carcharhinidae	*Carcharhinus amblyrhynchos*	41	17.45
	Carcharhinus amboinensis	2	0.94
	Carcharhinus limbatus	10	4.72
	Carcharhinus melanopterus	27	12.26
	Carcharhinus tilstoni	1	0.47
	Galeocerdo cuvier	20	8.96
	Loxodon macrorhinus	2	0.94
	Negaprion acutidens	7	3.3
	Triaenodon obesus	19	8.49
Chaetodontidae	*Chaetodon adiergastos*	2	0.47
	Chaetodon assarius	30	4.72
	Chaetodon aureofasciatus	91	21.7
	Chaetodon auriga	35	9.43
	Chaetodon citrinellus	10	3.3
	Chaetodon kleinii	11	3.3
	Chaetodon lineolatus	22	4.25
	Chaetodon lunula	24	6.6
	Chaetodon lunulatus	4	0.94
	Chaetodon meyeri	2	0.47
	Chaetodon plebeius	28	7.55
	Chaetodon punctatofasciatus	1	0.47
	Chaetodon speculum	6	1.42
	Chaetodon trifascialis	10	3.77
	Chaetodon unimaculatus	15	2.83
	Chelmon marginalis	142	36.79
	Coradion chrysozonus	15	4.72
	Forcipiger flavissimus	10	2.36
	Heniochus acuminatus	57	15.09
	Heniochus singularius	2	0.47
	Parachaetodon ocellatus	30	7.08
Cirrhitidae	*Cirrhitichthys oxycephalus*	1	0.47

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
	Paracirrhites forsteri	4	1.89
Clupeidae	*Herklotsichthys* spp.	4072	5.66
	Spratelloides gracilis	2	0.47
Dasyatidae	*Neotrygon kuhlii*	8	3.3
	Taeniurops meyeni	6	2.83
Diodontidae	*Diodon hystrix*	8	3.77
Echeneidae	*Echeneis naucrates*	137	34.91
Elopidae	*Elops hawaiensis*	42	13.21
Ephippidae	*Platax batavianus*	28	6.6
	Platax orbicularis	3	1.42
	Platax teira	9	2.83
	Zabidius novemaculeatus	25	1.42
Epinephelidae	*Cephalopholis argus*	14	4.72
	Cephalopholis boenak	15	6.13
	Cephalopholis microprion	1	0.47
	Cephalopholis miniata	10	3.77
	Chromileptes altivelis	3	0.94
	Diploprion bifasciatum	17	4.25
	Epinephelus bilobatus	224	47.17
	Epinephelus coioides	8	3.77
	Epinephelus corallicola	1	0.47
	Epinephelus fasciatus	88	22.64
	Epinephelus fuscoguttatus	3	1.42
	Epinephelus lanceolatus[P]	1	0.47
	Epinephelus maculatus	1	0.47
	Epinephelus malabaricus	13	5.66
	Epinephelus multinotatus	14	4.72
	Epinephelus polyphekadion	3	1.42
	Epinephelus quoyanus	14	3.3
	Epinephelus rivulatus	117	19.81
	Epinephelus tauvina	2	0.94
	Epinephelus tukula[P]	4	0.94
	Plectropomus spp.	203	48.58
	Variola louti	1	0.47
Fistulariidae	*Fistularia commersonii*	35	8.96
Ginglymostomatidae	*Nebrius ferrugineus*	15	6.13
Glaucosomatidae	*Glaucosoma magnificum*	52	1.42
Haemulidae	*Diagramma labiosum*	59	18.87
	Plectorhinchus flavomaculatus	1	0.47
	Plectorhinchus gibbosus	8	2.36
	Plectorhinchus multivittatus	1	0.47
	Plectorhinchus picus	4	1.42
	Plectorhinchus polytaenia	2	0.94
Hemiscylliidae	*Chiloscyllium punctatum*	6	2.83
Holocentridae	*Myripristis kuntee*	1	0.47
	Sargocentron rubrum	1	0.47
Kyphosidae	*Kyphosus vaigiensis*	120	4.25
Labridae (Labrinae)	*Anampses caeruleopunctatus*	2	0.94

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
	Anampses lennardi	51	11.32
	Anampses melanurus	10	2.36
	Anampses meleagrides	2	0.94
	Bodianus axillaris	16	4.72
	Bodianus bilunulatus	45	15.57
	Cheilinus chlorourus	26	11.32
	Cheilinus oxycephalus	2	0.94
	Cheilinus trilobatus	9	3.3
	Cheilio inermis	146	11.79
	Choerodon cauteroma	234	57.55
	Choerodon cephalotes	14	5.19
	Choerodon cyanodus	212	50.47
	Choerodon schoenleinii	139	46.7
	Choerodon vitta	46	13.21
	Cirrhilabrus temminckii	54	6.13
	Coris aygula	28	10.38
	Coris caudimacula	328	31.13
	Coris gaimard	1	0.47
	Coris pictoides	29	8.49
	Cymolutes torquatus	3	0.47
	Epibulus insidiator	2	0.94
	Gomphosus varius	6	2.36
	Halichoeres biocellatus	9	3.3
	Halichoeres chloropterus	2	0.47
	Halichoeres hortulanus	7	2.36
	Halichoeres marginatus	4	1.42
	Halichoeres melanochir	84	20.75
	Halichoeres nebulosus	223	33.02
	Hemigymnus fasciatus	15	7.08
	Hemigymnus melapterus	20	7.55
	Hologymnosus annulatus	44	13.68
	Hologymnosus doliatus	4	1.89
	Iniistius pavo	21	1.42
	Labroides bicolor	4	1.42
	Labroides dimidiatus	212	47.64
	Leptojulis cyanopleura	651	23.11
	Macropharyngodon negrosensis	18	5.66
	Novaculichthys taeniourus	5	1.42
	Oxycheilinus bimaculatus	5	1.42
	Oxycheilinus orientalis	2	0.94
	Oxycheilinus unifasciatus	2	0.94
	Pseudocheilinus evanidus	10	2.36
	Pseudodax moluccanus	2	0.94
	Pteragogus cryptus	2	0.47
	Pteragogus enneacanthus	1	0.47
	Stethojulis bandanensis	41	12.26
	Stethojulis interrupta	15	4.25
	Thalassoma amblycephalum	47	6.13

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
	Thalassoma hardwicke	1	0.47
	Thalassoma jansenii	1	0.47
	Thalassoma lunare	583	41.04
	Thalassoma lutescens	125	16.51
Labridae (Scarinae)	*Calotomus carolinus*	3	0.94
	Chlorurus bleekeri	2	0.47
	Chlorurus microrhinos	8	3.3
	Chlorurus rhakoura	14	2.83
	Chlorurus sordidus	11	4.25
	Hipposcarus longiceps	2	0.94
	Leptoscarus vaigiensis	5	0.47
	Scarus chameleon	51	9.91
	Scarus frenatus	2	0.94
	Scarus ghobban	213	38.21
	Scarus globiceps	4	1.42
	Scarus niger	1	0.47
	Scarus prasiognathos	8	3.3
	Scarus psittacus	8	0.47
	Scarus rivulatus	44	9.91
	Scarus rubroviolaceus	28	5.19
	Scarus schlegeli	27	5.19
	Scarus sp3*[1]	125	25.94
	Scarus spp.*[2]	5	1.42
	Scarus tricolor	2	0.94
Lethrinidae	*Gymnocranius grandoculis*	19	4.72
	Lethrinus atkinsoni	393	32.08
	Lethrinus genivittatus	77	8.96
	Lethrinus laticaudis	139	31.13
	Lethrinus lentjan	46	7.55
	Lethrinus microdon/olivaceus	118	17.45
	Lethrinus miniatus	60	4.72
	Lethrinus nebulosus	351	41.98
	Lethrinus punctulatus	345	14.62
	Lethrinus ravus	52	6.13
	Lethrinus rubrioperculatus	28	3.77
	Lethrinus spp.*[2]	4	1.42
	Lethrinus variegatus	129	5.66
Lutjanidae	*Aprion virescens*	35	9.91
	Lutjanus argentimaculatus	4	1.42
	Lutjanus bohar	9	2.36
	Lutjanus carponotatus	269	35.38
	Lutjanus fulviflamma	30	3.77
	Lutjanus gibbus	1	0.47
	Lutjanus kasmira	6	0.47
	Lutjanus lemniscatus	194	36.32
	Lutjanus quinquelineatus	76	2.83
	Lutjanus rivulatus	1	0.47
	Lutjanus russellii	32	4.72

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
	Lutjanus sebae	4	1.89
	Lutjanus vitta	114	4.25
	Symphorus nematophorus	81	30.19
Microdesmidae	*Ptereleotris evides*	38	2.83
	Ptereleotris microlepis	130	3.3
	Ptereleotris monoptera	220	3.3
Monacanthidae	*Aluterus scriptus*	2	0.94
	Cantherhines dumerilii	5	2.36
	Cantherhines fronticinctus	3	1.42
	Cantherhines pardalis	11	4.72
	Paramonacanthus choirocephalus	22	4.25
	Pseudomonacanthus peroni	1	0.47
Mullidae	*Parupeneus barberinoides*	174	18.87
	Parupeneus barberinus	1	0.47
	Parupeneus cyclostomus	52	8.49
	Parupeneus heptacanthus	33	8.02
	Parupeneus indicus	191	43.4
	Parupeneus multifasciatus	41	10.85
	Parupeneus pleurostigma	30	9.43
	Parupeneus spilurus	67	8.02
	Upeneus tragula	87	10.85
Muraenidae	*Gymnothorax eurostus*	1	0.47
	Gymnothorax flavimarginatus	3	0.94
	Gymnothorax javanicus	2	0.94
	Gymnothorax thrysoideus	8	3.77
	Gymnothorax undulatus	19	8.49
Nemipteridae	*Nemipterus* spp.	16	2.83
	Pentapodus emeryii	300	50
	Pentapodus porosus	1058	51.42
	Pentapodus vitta	83	6.6
	Scolopsis bilineata	27	10.38
	Scolopsis monogramma	246	66.98
	Scolopsis xenochrous	4	1.42
Ostraciidae	*Ostracion cubicus*	7	3.3
	Ostracion meleagris	1	0.47
Pinguipedidae	*Parapercis clathrata*	20	8.02
	Parapercis nebulosa	9	3.77
	Parapercis snyderi	1	0.47
	Parapercis xanthozona	1	0.47
Platycephalidae	*Platycephalus* spp.	3	1.42
Plotosidae	*Paraplotosus butleri*	5	1.89
Pomacanthidae	*Centropyge tibicen*	9	2.83
	Chaetodontoplus duboulayi	115	37.26
	Chaetodontoplus personifer	13	5.19
	Pomacanthus imperator	16	6.13
	Pomacanthus semicirculatus	74	24.53
	Pomacanthus sexstriatus	96	27.36
	Abudefduf bengalensis	131	16.98

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
	Abudefduf sexfasciatus	40	1.42
	Amphiprion clarkii	5	0.94
	Chromis cinerascens	6	0.94
	Chromis fumea	273	10.85
	Chromis margaritifer	11	0.94
	Chromis viridis	12	0.47
	Chromis weberi	261	8.02
	Dascyllus reticulatus	20	1.42
	Dascyllus trimaculatus	23	3.77
	Neoglyphidodon melas	3	1.42
	Neopomacentrus azysron	44	3.77
	Neopomacentrus cyanomos	68	2.83
	Neopomacentrus filamentosus	99	12.74
	Plectroglyphidodon johnstonianus	2	0.94
	Plectroglyphidodon lacrymatus	12	2.83
	Pomacentrus coelestis	3610	39.62
	Pomacentrus limosus	28	2.36
	Pomacentrus milleri	72	11.32
	Pomacentrus moluccensis	2	0.94
	Pomacentrus nagasakiensis	358	24.53
	Pomacentrus nigromanus	2	0.94
	Pomacentrus vaiuli	17	3.77
	Stegastes obreptus	15	6.6
Priacanthidae	*Priacanthus blochii*	1	0.47
	Priacanthus hamrur	4	0.94
Pristidae	*Pristis zijsron*^{P}	1	0.47
Pseudochromidae	*Labracinus lineatus*	5	2.36
	Pseudochromis fuscus	9	4.25
Pteroidae	*Pterois volitans*	1	0.47
Rachycentridae	*Rachycentron canadum*	14	4.72
Rhinidae	*Rhina ancylostoma*	2	0.94
Rhynchobatidae	*Rhynchobatus australiae*	4	1.89
Scombridae	*Cybiosarda elegans*	1	0.47
	Rastrelliger kanagurta	3	0.47
	Sarda orientalis	17	0.47
	Scomberomorus spp.	205	62.26
Scyliorhinidae	*Atelomycterus macleayi*	1	0.47
Serranidae	*Pseudanthias bicolor*	1	0.47
Siganidae	*Siganus argenteus*	63	4.72
	Siganus doliatus	115	20.28
	Siganus fuscescens	633	25.94
	Siganus lineatus	8	0.94
	Siganus punctatissimus	4	0.94
	Siganus punctatus	19	4.25
	Siganus trispilos	4	1.42
Sillaginidae	*Sillago* spp.	7	1.89
Sphyraenidae	*Sphyraena barracuda*	2	0.94
	Sphyraena jello	30	6.6

FAMILY	TAXA	SUM MAXN	% DEPLOYMENTS
	Sphyraena obtusata	18	1.89
	Sphyraena qenie	19	0.94
Sphyrnidae	*Sphyrna lewini*	1	0.47
	Sphyrna mokarran	2	0.94
Stegostomatidae	*Stegostoma fasciatum*	2	0.94
Synodontidae	*Trachinocephalus myops*	13	4.72
Tetraodontidae	*Arothron hispidus*	2	0.94
	Canthigaster coronata	7	2.36
	Feroxodon multistriatus	1	0.47
	Lagocephalus sceleratus	1	0.47
	Torquigener pallimaculatus	15	2.83
Zanclidae	*Zanclus cornutus*	19	7.08

*1 = Likely to be formally recognised as *Scarus hutchinsi* and is distinct from *S. ghobban*.
*2 = Unidentified juveniles (< 120 mm)
*^{P} = Protected under Fish Resources Management Regulations 1995

11.2 Can diver operated stereo-video surveys for fish be used to collect meaningful data on benthic coral reef communities?

Authors: Bennett K, Wilson S, Shedrawi G, McLean D, Langlois T.

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ABSTRACT

Information for monitoring marine communities is increasingly collected using digital imagery and there is a need to understand how data collected using different methods compare. This study investigated the comparability of benthic data collected by downward facing diver operated stereo-video (DOV) with a forward facing stereo-DOV typically used in fish surveys. Data sets were collected by both methods from the same transect along which the benthos visible in each method was identified by taxonomy, growth form or substratum class. Analyses indicated that 77% of taxa were identified by both methods however, forward facing-DOV recorded 35 genera and downward-DOV 43 genera and there were significant ($p<0.05$) differences in the percent cover of dominant benthic categories. The forward facing stereo-DOV detected significantly more vertically erect coral (~10%), specifically branching genera *Acropora*, *Echinopora* and *Porites*, and canopy forming algae, *Sargassum* spp., but proportionally less turf algae (~20%) than the downward facing video. Cost-benefit optimisation indicated that the forward facing video was more cost-effective at detecting broad scale change in coral, but less effective at detecting change in non-canopy forming algae compared to the downward video. Despite differences in detection of coral and algae, Deming regression analyses detected significant relationships between the percentages of common benthos recorded by both methods, enabling direct comparison between the data collected by each method at a broad scale level. Stereo-DOV surveys for fish can also be considered for the description of reef benthos that captures key elements of structural complexity, but not necessarily suitable for taxonomic benthic monitoring.

11.2.1 INTRODUCTION

Coral reefs are facing increasing levels of local and global pressures and it is imperative that effective monitoring programs are is in place to assess the ongoing condition of benthos and associated assemblages (Sweatman et al. 2001; Fisher et al. 2008; Houk and Van Woesik 2013). There is scientific consensus that we are experiencing a drastic global decline in total coral cover due to both natural and anthropogenic stresses (Gardner et al. 2003; Graham et al. 2008; De'ath et al. 2012), which has flow on effects for ecosystem services (Pratchett et al. 2014). As coral cover continues to fall, reliable monitoring data becomes a priority to inform effective management decisions that can prevent a further decline and encourage recovery of coral reefs (Aronson et al. 1994; Houk and Van Woesik 2006; Mantelatto et al. 2013). Yet, coral cover as a criterion alone may be ineffective for guiding management protocols (McClanahan et al. 2011), as future monitoring programs need to consider the overall composition and structure of benthic assemblages and the processes that drive changes in these communities (Hughes et al. 2010).

Deciding upon the most appropriate way to assess change in benthic communities should be based primarily on the type of information required, the repeatability of the method and the level of precision (Dumas et al. 2009; Tyne et al. 2010; Mantelatto et al. 2013). Choice of method is typically constrained by field and analysis time, human expertise and available budget. Hence, compromises must be made between data completeness and cost efficiency (Brown et al. 2004; Hill and Wilkinson 2004).

Throughout long-term monitoring programs it is inevitable that there will be technological advancements, fluctuations in research funding and availability of human resources (Dollar and Grigg 2004; Ramos et al. 2010). This can result in time series data that is collected by different techniques, which may confound biological interpretation of community structure. Precursor method comparison studies are central to understanding method performance and the comparability of data collected (Fairweather 1991). This ensures that trends detected are attributed to actual changes, rather than differences in the ability of methods to quantify different aspects of the benthos (Connell et al. 1998; Nadon and Stirling 2006; Ramos et al. 2010; Tyne et al. 2010). However, the most common outcome of method comparison studies is that no single method is capable of detecting every aspect of change (Brown et al. 2004; Houk and Woesik 2006), hence there is a need to test not only for data comparability, but to determine if data collected by several methods can be combined to provide a more comprehensive and advanced understanding of the marine ecosystem (Cheal and Thompson 1997).

Benthic imagery collected by video or photographic surveys has been used extensively for long-term monitoring, as it is a rapid and cost-efficient technique for collecting field data (Aronson et al. 1994; Carleton and Done 1995; Jokiel et al. 2005; Scopélitis et al. 2010). The initial costs associated with video techniques are often expensive and may inhibit more widespread use of this technique. The costs may be offset by a reduction in field time, observer bias and providing a permanent visual record which allows archived images to be revisited, resampled and contrasted directly against time series data for the detection of spatial and temporal variability (Segal and Castro 2001; Miller et al. 2003; Lam et al. 2006; Lirman et al. 2007; Dumas et al. 2009; Burgess et al. 2010). Moreover, reduced costs of cameras and monitoring procedures are making the use of video techniques more accessible, particularly to researches in developing nations. However, digital imagery techniques are restricted by image quality and issues of water clarity and turbidity which may prevent the detection of obscured or cryptic taxa (Hill and Wilkinson 2004; Leujak and Ormond 2007; Turner et al. 2015). To overcome these limitations, many studies assessing change in benthic communities have utilised a range of spatio-temporal data from multiple studies and monitoring programs (Brown et al. 2004; Jokiel et al. 2005; Speed et al. 2013). However, to maximise spatio-temporal replication in benthic community assessments that utilise data from various techniques, it is paramount to understand their relationships using empirical data from direct comparisons.

Underwater video techniques have also been used for the assessment of shallow water fish assemblages (Harvey and Shortis 1996; Watson et al. 2005; Shortis et al. 2009; Holmes et al. 2013; Mallet and Pelletier 2014; Wartenberg and Booth 2014). Forward facing diver operated stereo-video (stereo-DOV) has been used widely to detect spatial and temporal changes within reef fish communities due to its ability to precisely estimate fish lengths and provide a permanent record for scrutiny (Harvey and Shortis 1996; Watson et al. 2010; Shedrawi et al. 2014). Benthic monitoring through underwater video techniques operate on the same principle however, in benthic surveys the camera is held facing directly downward perpendicular to the substrate, while in fish surveys the camera's field of view is directed forwards, just above the substrate towards the horizon (Lam et al. 2006; Watson et al. 2010). Forward facing stereo-DOV have been used to assess benthic habitat (Shedrawi et al. 2014), although it is unclear how benthic data collected using a forward facing method relates to data collected using a downward facing camera.

This study assesses the comparability of benthic community composition data collected by the two stereo-DOV methods, with the aim of providing a cost effective monitoring option for both fish and benthic communities. The study examines how the two methods differ in their estimates of different habitat components, cost effectiveness and comparability. Our results will determine which method is better suited to answering specific marine monitoring questions, from broad scale structural changes to changes in biotic cover and composition and how data collected for different purposes can be used in meta-analysis to provide a more comprehensive assessment of coral reef assemblages.

11.2.2 METHODS

Study location

This study was conducted on the tropical coral reefs of the Montebello and Barrow Islands Marine Park situated in the Pilbara offshore waters off the north-west coast of Western Australia (20˚27'S) Seven sites were surveyed during 22-26th April 2010, using both downward facing and forward facing stereo-DOV Twelve 25 m long transects were conducted at each site with an average survey depth of 5 m.

Sample collection

Field operation of the two camera methods was conducted by trained personnel in accordance with the standardised approach of the West Australian Department of Biodiversity, Conservation and Attractions (DBCA) (Langlois et al. 2010; Turner et al. 2015). At each site, the forward facing stereo-DOV operator swum the transect, laying out a line of biodegradable cotton string for the downward facing stereo-DOV operator, who followed directly behind. The start of one transect was separated from the end of the preceding transect by a gap of at least 10 m and transects were arranged in a haphazard manner. Both Self-contained Underwater Breathing Apparatus (SCUBA) divers swam at a constant slow speed of ~0.1 ms^{-1}, holding the camera units 1 m above the substrate.

Forward facing stereo-DOV

The forward facing stereo-DOV unit (here after termed forward-DOV) consisted of two high-definition Canon HG21 digital video cameras contained in underwater housings. The cameras were fixed in a stereo configuration on a neutrally buoyant metal bar 70 cm apart, pointing inwardly at an angle of 8˚ (Harvey and Shortis 1996, 1998). This is typical of the camera configuration used for monitoring fish communities (Langlois et al. 2010; Watson et al. 2010; Holmes et al. 2013). A diode positioned 80 cm in front of the camera unit was within the field of view of both cameras to aid frame synchronisation during image analysis. During filming, the forward-DOV was held approximately 1 m above the substrate and angled forward as conducted in Langlois et al. (2010).

Downward facing stereo-DOV

The downward facing stereo-video system (here after termed downward-DOV) consisted of two Canon HG21 digital cameras with Raynox high-definition super wide angle conversion lenses in underwater housings. The cameras were mounted on a neutrally buoyant horizontal metal frame 44.7 cm apart, converging on an angle of 6.66˚. A diode positioned in front of the camera unit was visible in the field of view of both cameras to aid frame synchronisation during image analysis. The SCUBA diver operating the benthic video swum directly behind the diver operating the forward-DOV, over the cotton string, holding the camera unit downward approximately 1 m above the substrate. This recorded a 1-1.5 m wide video belt and ensured the forward and downward facing stereo-DOV recorded the same benthos along the belt transect.

Calibration

To ensure measurement accuracy, both forward-DOV and downward-DOV camera systems were calibrated prior to field work using a 3D calibration cube and *CAL* SeaGISCAL^{TM} software (www.seagis.com.au). Calibration of the video cameras was necessary to quantify internal characteristics of the camera and to define relative three-dimensional orientations of both cameras, i.e. rotation, tilt (y plane) and convergence (x plane) (Harvey and Shortis 1996, 1998). Calibration was also needed for projecting the virtual quadrat, a user defined polygon drawn on images, ensuring the same unit area was sampled in both stereo-systems (Figure 11.2.1).

Video analysis

Stereo-video imagery from forward-DOV and downward-DOV videos was downloaded in the field to external hard drives where raw digital videos were converted to Audio Video Interleaved files (AVI) for laboratory analysis. The AVI files from the left and right cameras for both methods were imported into the program EventMeasure v3.54 (www.seagis.com.au) for the construction of a virtual quadrat using the projective transformation feature. From each transect, 20 image frames were randomly selected. In each frame, six identical 3D points were placed on the left and right images to define the quadrat size. A simple function in the software was set to control the accuracy of the virtual quadrat size and location in three dimensions. This ensured that all points placed on the downward-DOV and forward-DOV images were within a quadrat of comparable size between methods. Images overlaid with the six 3D point measurements were saved as measurement files for further benthic analysis in TransectMeasure v2.24 (www.seagis.com.au).

A 600 × 600 mm quadrat (calibrated projective transformation) was generated using the left camera image from forward-DOV and downward-DOV measurement files. Quadrats projected onto forward-DOV images were offset left 10% and down 10% from the centre of the frame to reposition the superimposed quadrat closer to the camera and lower down within the frame to avoid quadrat projection off the substratum. Six random points were overlaid within the superimposed quadrats in TransectMeasure for benthic classification analysis (www.seagis.com.au) (Figure 11.2.1).

Benthic classification

Identification of benthos was based upon the West Australian DBCA standard set of major benthic categories (Vernon 2000; Kelley 2011). Benthos was identified to taxonomic levels of broad group (coral, algae, octocorals, invertebrates (non-corals), rubble and sand) and genus-morphology (staghorn, branching, foliose etc.), by a trained video analyst with access to a range of appropriate reference resources (Vernon 2000; Kelley 2011). The video analyst had completed a 12-day identification course created by the West Australian DBCA using the Coral Finder and Corals of the World online learning criteria. Where genus identification was not possible, benthos was identified to the next best classification level, and recorded as ‘unknown’ at genus levels. On the rare occasion (less than 1%) where one of the six randomly placed points could not be identified at any level, the point was recorded as “obscured”.

Figure 11.2.1 Calibrated projective transformation (virtual quadrat) projected onto the frame of the (a) forward-DOV and (b) downward-DOV, with six randomly placed points superimposed for benthic identification. The white line seen in image (b) is the biodegradable cotton string. Red text state the ‘Interest area, side length=6000.000’.

Rugosity

Recording benthic community composition using stereo-DOV systems may be influenced by the structural complexity of the reef, and differences between the two methods may be partially explained by the spatial variation in rugosity. Hence the rugosity for each transect was assessed to help explain potential differences in the ability of each method to record benthos under differing reef conditions. Rugosity was assessed during the post processing of the videos by a single analyst familiar with categorising reef substratum. Rugosity was determined by visual assessment at five random points of each forward-DOV transect and following the scale of 0-5 of Polunin and Roberts (1993). Visual assessments are deemed both effective and reliable compared to photogrammetric techniques and in situ measurements (Gratwicke and Speight 2005; Wilson et al. 2007) and are increasingly used to assess reef structural complexity (Wilson et al 2009).

Cost-benefit optimisation

The costs associated with field sampling and image analysis using the downward-DOV and forward-DOV were calculated in terms of staff hours required to complete the task. Costs for each method were classified as cost per site and cost per survey. Cost-benefit optimisation accounted for varied mobilisation of equipment and laboratory costs associated with image analysis (Langlois et al. 2010). Field costs including vessel costs and the number of equipment operators were deemed comparable. Differences in laboratory costs, time spent during video analysis were used to estimate the cost per replicate sample within a site.

Statistical analysis

Counts of benthos for each point in a virtual quadrat were summed to the transect level. The number of points for each benthic category identified were divided by the total number of points for the transect giving a relative abundance of each of the variables detected by each method. Count values were used to calculate percentage cover per transect and describe detection of specific benthic variables identified by each method. A two factor repeated measures experimental design was constructed to investigate differences in benthic habitat compositions recorded by the two methods. The two factors were; method (downward or forward, fixed) and site (seven levels, random). Transect was entered as a repeated measure as benthic habitat data was collected simultaneously by each method along the same transect. Site was treated as a random factor, as primary analysis was aimed at detecting differences in benthos recorded by method rather than differences between habitats at sites. Rugosity was included in the experimental design as a covariate to explain any potential differences in benthic identification between the two methods.

Due to highly left skewed data with a high zero count for many benthic variables, benthic habitat data were analysed using a repeated measures non-parametric permutational analysis of variance (PERMANOVA) (Clarke 1993; Clarke and Gorley 2006; Anderson et al. 2008). PERMANOVA was conducted in the statistical package PRIMER-E v6 (Plymouth Routines in Multivariate Ecological Research; Anderson et al. 2008). Data were fourth-root transformed to meet the assumptions of heterogeneity of dispersions as tested by permutational analyses of multivariate dispersions (PERMDISP). A dissimilarity matrix based on Euclidean distance was constructed and used in the subsequent PERMANOVA analyses. Euclidean distance was selected as it recognises the joint absence of certain habitat variables among samples as a similarity. The inclusion of the covariate in PERMANOVA follows that the sums of squares for each term becomes non-independent, hence Type 1 sequential sums of squares were used (Anderson et al. 2008). PERMANOVA analysis was initially conducted at the broad group classification level with 9999 permutations for variables contributing more than 5% to the data set. A subsequent PERMANOVA analysis was conducted on genus-morphology variables to investigate the difference between methods when assessing at higher taxonomic classifications. Differences in the number of obscured and unknown benthic identifications between methods were examined by an analysis of variance (ANOVA).

To test for significant and predictable relationships between the benthos recorded by the two methods Deming regression, an error-in-variables approach was used. Deming regression was used instead of a classical least square regression as it takes into account errors in both *x* and *y* variables which is appropriate where two sampling methods are compared (Cornbleet and Gochman 1979; Linnet 1993, 1998). Deming regression also minimises the sums of squared errors in both *x* and *y* directions simultaneously to predict a line of best fit through the data points (Dunn 2007).

Deming regression analyses were run on commonly (>5%) observed broad group and genus-morphology variables. We input the initial error ratio (λ) calculated by the ratio of SDx/SDy into the model. We used unweighted Deming regressions and standard deviations were determined by using the actual x and y data and input to develop a simple model that best delivers across a range of mean values (Martin 2000; Manuilova et al. 2014; www.rstudio.com).Thus we did not set a constant coefficient of variation (CV%), otherwise known as a weighted Deming regression. This provided an unbiased estimate of the slope and intercept for the relationship between data collected by the forward-DOV and downward-DOV (Cornbleet and Gochman 1979; Linnet 1993, 1998). Studies have shown Deming regression to be more robust than a classical linear or orthogonal regression model, even when error variance is unknown or mis-specified (Linnet 1993). Residual diagnostic plots were generated to validate the application of the model for the selected benthic variables and to determine if errors were constant or proportional. 95% Confidence intervals were used to indicate if there were significant differences in slope ($\beta \neq 1$) or intercept ($\alpha \neq 0$) estimates from the $y=x$ line (Linnet 1999).

Deming regression analysis calculates a coefficient of determination value Pearson’s r to indicate how well the regression line generated fit the data. In addition to this, two linear regressions were run where each method was used alternatively to predict the other. This generated two R^2 values and enabled a comparison of how well one sampling method was able to predict the other and how the Deming model compared with the linear model. All Deming and standard linear regression analyses were completed using the “mcr” package in RStudio (Manuilova et al. 2014; www.rstudio.com).

11.2.3 RESULTS

Comparison of benthic assemblage composition between methods

A total of 44 benthic genera were identified by the two methods. The downward-DOV detected 43 genera belonging to 27 families, while the forward-DOV detected 35 genera belonging to 24 families. Thirty-four (77%) of the total number of genera were identified by both stereo-DOV methods. Nine (20%) were identified only by the downward-DOV, while a further one (2%) was identified by forward-DOV only.

Assessment of benthic data at the broad group and genus-morphology level indicated that there were significant differences in benthos detected by forward-DOV and downward-DOV methods (p<0.01; Table 11.2.1). The composition of benthic assemblages also differed among sites and was correlated to rugosity (Table 11.2.1). Differences in the rugosity of reefs did not significantly influence methodological assessments of benthic assemblages, however, differences in benthic composition among sites meant the comparability of methods differed from site to site (significant method × site interaction, Table 11.2.1).

Table 11.2.1 Results from PERMANOVA tests assessing benthic community assemblages at broad group and genus-morphology level. PERMANOVA was run on fourth-root transformed data, based on a Euclidean distance matrix of variables contributing >5% to the data set. P-values were set to a significance of α=0.05, bold values <0.05.

		BROAD GROUP		GENUS-MORPHOLOGY	
SOURCE	*df*	PSEUDO-F	*P*(PERM)	PSEUDO-F	*P*(PERM)
Rugosity	1	0.31	0.64	2.22	<0.01
Method	1	49.64	<0.01	4.03	<0.01
Site	6	34.15	<0.01	19.43	<0.01
Rugosity x Method	1	0.44	0.55	0.95	0.51
Site x Method	6	4.41	<0.01	1.75	<0.01
Site x Method x Rugosity	5	0.22	0.97	1.23	<0.01
Residual	147	98.34			
Total	167				

Comparison of total number of obscured and unidentified benthos

Forward-DOV recorded a significantly greater mean value of unknown genus-morphology observations compared to the downward-DOV, however the proportion of coral genera that could not be identified by either method was very small (<1%) (Table 11.2.2). The mean proportion of obscured identifications was also low and statistically similar between the two methods.

Correlation between methods

Comparison of broad-group variables, coral and non-canopy algae, indicated that while there was no difference in slope, intercept estimates for both groups deviated from zero, indicating that forward-DOV and downward-DOV methods were not directly comparable for these observations (Table 11.2.3, Figure 11.2.2). Forward-DOV detected ~10% more coral but ~20% less non-canopy algae than the downward-DOV method, irrespective of local benthic cover. While the two methodologies do not provide equivalent estimates of coral and algae, approximately 70% of the variation in data measured by one method was explained by the other, while the Pearson’s r value indicated a strong linear relationship between methods.

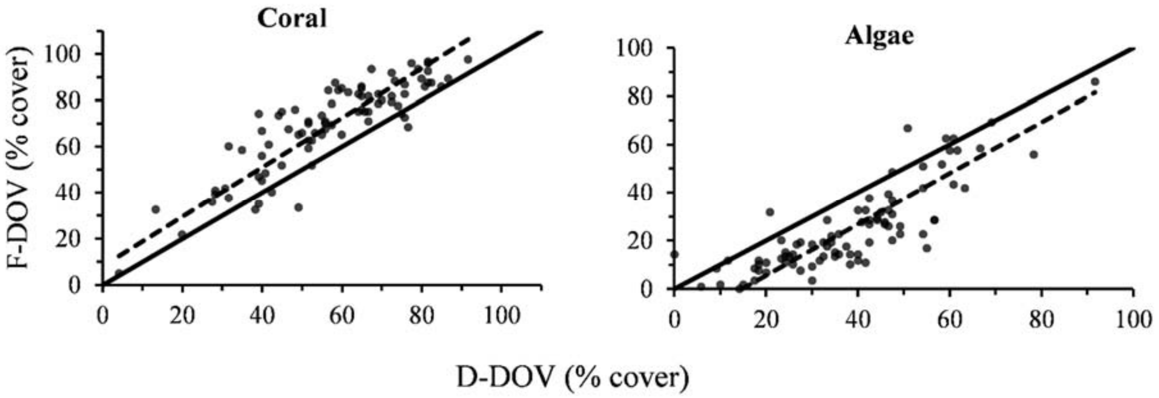

Figure 11.2.2 Scattergram of percent cover of downward (D-DOV) plotted against forward (F-DOV) video system for broad group variables. Solid black line represents y=x and dotted line represents the Deming regression model.

Table 11.2.2 Mean occurrence (±SE) of unknown genus-morphology and obscured benthic identifications level made per site for each using the downward (D-DOV) and forward (F-DOV) methodologies.

TAXONOMIC LEVEL	D-DOV	MEAN (±)	F-DOV	MEAN (±)	*P*-VALUE
Unknown	19	<0.01 (0.03)	95	<0.01 (0.16)	0.01
Obscured	54	0.01(1.90)	152	0.03(0.27)	0.12

*Each site included 12 transects (n=12)

Table 11.2.3 Deming regression results for method comparison of downward (D-DOV) and forward (F-DOV) video systems, *indicates a significant difference in slope or intercept, where β≠ 1 and α≠ 0. R^2 values indicate how well methods predict each other. Pearson's r indicates the strength of the linear relationship between the two methods.

VARIABLE	TAXA	INTERCEPT (95% CI)	SLOPE (95% CI)	R^2 D-DOV PREDICTOR	R^2 F-DOV PREDICTOR	PEARSON'S R DEMING REGRESSION
Broad group	Algae*	**-15.61 (-26.21 to -12.37)***	1.06 (0.98 to 1.33)	0.69	0.69	0.82
	Coral*	**8.16 (1.03 to 16.95)***	1.07 (0.93 to 1.18)	0.75	0.75	0.87
Genus-morphology	corymbose *Acropora*	-0.01 (-0.82 to 0.80)	1.29 (0.89 to 1.71)	0.66	0.67	0.86
	staghorn* *Acropora*	**1.53 (0.53 to 2.54)***	**1.27 (1.14 to 1.40)***	0.85	0.86	0.92
	branching* *Echinopora*	-0.21 (-1.28 to 1.63)	**2.59 (1.53 to 3.57)***	0.32	0.28	0.77
	foliose *Echinopora*	-0.39 (-1.48 to 0.70)	1.13 (0.88 to 1.39)	0.5	0.52	0.84
	submassive *Galaxea*	0.29 (-1.37 to 1.95)	1.17 (0.33 to 2.00)	0.46	0.43	0.76
	foliose *Montipora*	-0.22 (-1.02 to 0.57)	1.14 (0.74 to 1.55)	0.7	0.75	0.84
	branching**Porites*	**-1.44 (-2.19 to -0.53)***	1.65 (0.93 to 1.76)	0.4	0.4	0.79
	massive *Porites*	0.17 (-1.84 to 2.18)	1.18 (0.39 to 1.98)	0.22	0.25	0.6
	Sand*	-0.38 (-0.97 to 0.21)	**0.50 (0.08 to 0.92)***	0.33	0.22	0.64
	Turf reef*	**-12.25 (-17.34 to -4.68)***	1.10 (0.86 to 1.26)	0.59	0.58	0.78
	Turf rubble*	-1.50 (-0.52 to 0.57)	**0.46 (-0.02 to 0.29)***	0.37	0.29	0.57

Table 11.2.4 Cost-benefit analysis for benthic monitoring utilising either downward (D-DOV) or forward (F-DOV) method on broad group variables from the Montebello and Barrow Island region. The most cost effective method for sampling are shown in bold.

			SITES TO DETECT CHANGE OF:			COST (HOURS) PER SURVEY TO DETECT CHANGE OF:		
INDICATOR	METHOD	REPLICATES	10%	25%	50%	10%	25%	50%
Coral	F/D-DOV	7	9	2	1	343	133	103
	F-DOV	**7**	**7**	**2**	**1**	**254**	**104**	**74**
Algae (non-canopy)	**F/D-DOV**	7	**16**	**3**	**1**	**553**	**163**	**103**
	F-DOV	7	46	8	2	1424	284	104

Intercept estimates for the regression model for staghorn *Acropora*, branching *Porites* and turf algae deviated from zero; biplots show this was due to higher estimates of the branching corals and lower estimates of turf algae on the reef when using forward-DOV (Table 11.2.3, Figure 11.2.3). For staghorn *Acropora,* the difference in estimates between methods became more pronounced as percent cover increased. Similarly, a slope significantly greater than one for branching *Echinopora* indicated that forward-DOV was increasingly likely to estimate greater coverage of branching *Echinopora* than the downward-DOV as cover of this coral increases. Conversely, slopes less than one indicated the downward-DOV detected proportionally more sand and turf algae on rubble as the percent cover of these benthic variables increased. Deming regression analysis identified that there were no differences in the way the alternative methods recorded *Acropora* corymbose, *Echinopora* foliose, *Galaxea* submasssive, *Montipora* foliose and *Porites* massive.

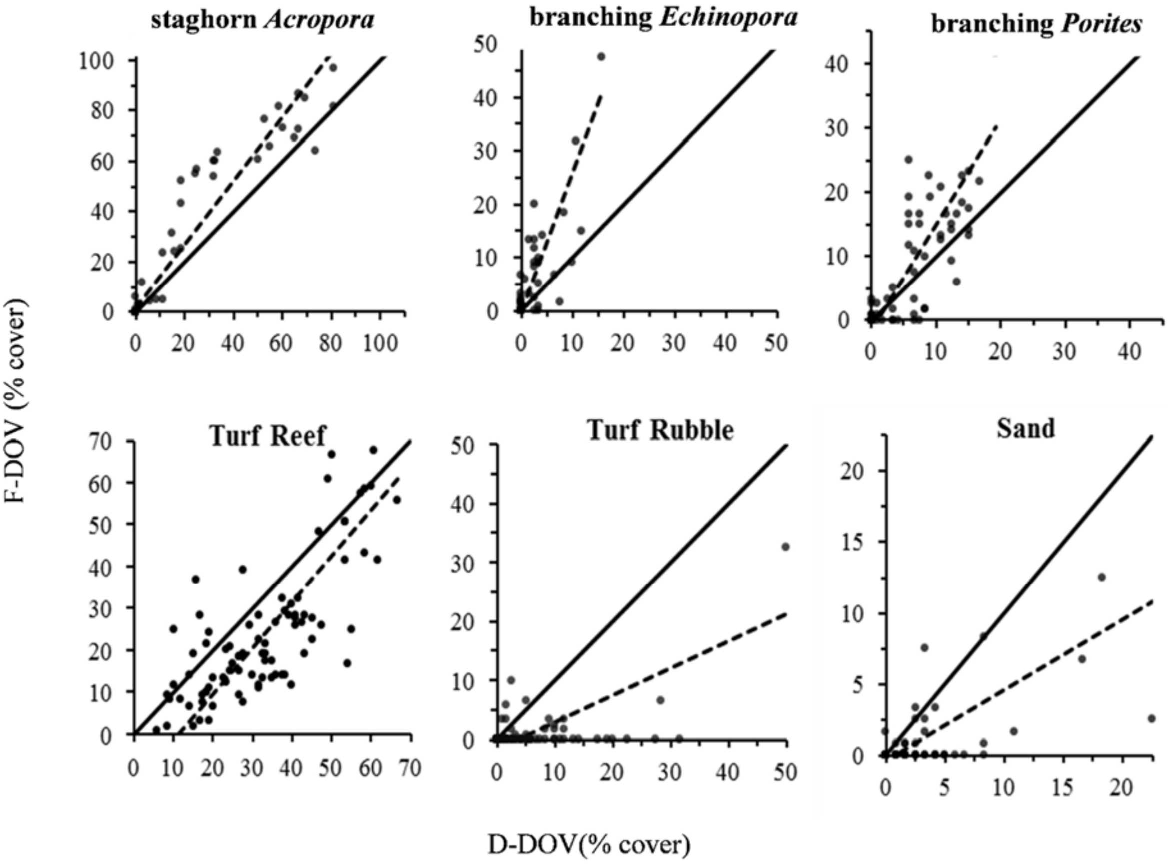

Figure 11.2.3 Scattergram of downward (D-DOV) plotted against forward (F-DOV) video system for genus-morphology variables that had significantly different slopes or interception from y=x. Solid black line represents y=x and dotted line represents the Deming regression model.

The methods were not comparable in their detection of staghorn *Acropora*, however approximately 80% of the variation in the data sets measured by one method could be explained by the other. Coefficients of determination and Pearson's r values suggests that for corymbose *Acropora* (R^2~0.66, r=0.86), foliose *Echinopora* (R^2~0.5, r= 0.84), foliose *Montipora* (R^2~0.7, r=0.84) and turf reef (R^2~0.6, r=0.78) data collected from the two methods were comparable.

Cost-benefit analysis

A cost-benefit optimisation indicated that the forward-DOV may be a more cost-effective option to detect change in total coral cover at the broad group scale (Table 11.2.4). Fewer sites are required to detect a 10% change in coral cover when using the forward-DOV, yet an equal number of sites for each method can be used to detect both a 25% and 50% change in cover (Table 11.2.4). Conversely, optimisation analysis indicated that the downward-DOV would be a more cost-effective option for detecting change in non-canopy algae. To detect a 10% change in non-canopy algae using the forward-DOV would require almost three times the number of sites at 2.5 times the cost compared to the downward-DOV.

11.2.4 DISCUSSION

Methods used for monitoring the status of biological communities often differ in their ability to detect indicators of conditions (Leujak and Ormond 2007). Moreover, methods vary among monitoring programs due to availability of resources, and time due to changes in technology. As a consequence, choosing the appropriate methods and collating data across space and time requires an understanding of how data collected by different methods are related (Jokiel et al. 2005; Safuan et al. 2015). Here, we demonstrate that measures of benthic variables used to assess the condition of coral reefs vary between downward and forward-DOV, however correlations between estimates suggest that through the application of correction factors data collected by two methods can be compared.

Differences in the detection of benthic variables between the two methods can be attributed primarily to the angle of the cameras relative to the substrate. Alternate field of view angles resulted in the methods sampling different aspects of the same benthic assemblage. The downwards angle generated a view of the full vertical diversity of the reef system, particularly turf algae attached to the base of a coral colony or on reef substrate surrounding corals. The forward-DOV employs a near horizontal camera angle that projects vertically out into the water column, which favors the recording of the contours of coral colonies. Therefore, the method may be over representing vertically erect benthos such as branching corals, while failing to detect cryptic benthos and taxa with low morphological profiles, such as turf algae or encrusting corals.

Differences in the way the forward-DOV and downward-DOV detect morphologically flat and vertically erect data suggest that each method may be more suitable to specific monitoring purposes. The forward-DOV recorded a higher proportion of benthic categories that projected into the water column, particularly the common branching taxa *Acropora, Echinopora* and *Porites*, while the ability of the downward-DOV to describe coral morphology and structural complexity is limited by the vertical field of view at which the coral colonies were surveyed (Turner et al. 2015). This suggests that the forward-DOV is potentially a more suitable method for the description and measuring change in the structural complexity and habitat type of reefs. Spatial and temporal differences in reef structure often explain variance in reef fish abundance, diversity and community structure (McCormick 1994; Wilson et al. 2009; Friedman et al. 2013; Graham and Nash 2013). Complex branching growth forms in particular are important to many coral-dwelling fish, due to their provision of refuges and moderate competitive interactions within the manifold of microhabitats (Coker et al. 2009, 2012). Similarly, in macroalgae dominated habitats, erect canopy forming algae are important for juvenile and adult fish (Evans et al. 2014; Lim et al. 2016), changes in branching coral or the structure of macroalgae canopies can alter fish communities (Pratchett et al. 2008; Wilson et al. 2014), suggesting forward-DOV are well suited to collecting and monitoring fish habitat data.

Conversely, the downward-DOV may be more suited to studies and monitoring programs that are specifically interested in capturing the biotic diversity and processes of benthic ecosystems such as species richness, coral recruitment, reef productivity and stability. This method detected proportionally more encrusting and low-lying taxa, particularly turf algae, which are important primary producers (Hatcher 1990; Russ 2003; Chabanet at al. 2005), provide food for many herbivorous species (Choat 1991) and can provide suitable substratum for settlement and recruitment (Bell 1992; Nystrom et al. 2000; Fabricius 2005). The downward-DOV is also capable of identifying small coral recruits on the benthos (Burgess et al. 2010; Turner et al. 2015) which are an indicator of ecosystem recovery after a disturbance event which is a crucial element of monitoring programs.

Rubble is also more likely to be detected by downward-DOV and can be indicative of physical disturbances such as cyclones, trampling, snorkeling or boat anchoring (Chabanet et al. 2005; Moore et al. 2012). Detecting and recording the recovery of ecosystems post-disturbance is essential to enhance learning of recovery regimes, resilience and to educate management and rehabilitation programs (McClanahan et al. 2002; Dollar and Grigg 2004). This method is also more suitable for the description of coral at a more detailed taxonomic level and can be considered a more effective and advanced method for monitoring and detecting change in assemblage structure.

Large-scale monitoring programs often report the long-term trends at broad group taxonomic levels, such as ‘live hard coral cover’ or ‘algae cover’ (Leujak and Ormond 2007; Cruz et al. 2008; Hughes et al. 2010). Despite differences in the detection of broad group variables coral and non-canopy algae, there were strong linear relationships between the percentages observed by each method. Hence, as demonstrated by the Deming regression model, forward-DOV may be used to collect broad scale benthic data for monitoring total coral or algal cover. This may lead to more simplistic and cost-effective monitoring programs aimed solely at the detection of change in coral cover by collecting broad benthic group categories simultaneously with fish surveys. This would enable more surveys to be conducted over a shorter time period increasing efficiency and effectiveness of reef monitoring.

The application of regression models and conversion factors has previously been used to correct fish density estimates from different transect dimensions (Cheal and Thompson 1997), however our study uses the Deming model to account for variation associated with both methods. Importantly, correction factors varied between taxa and for some benthic categories the extent of correction is dependent on their coverage. For example correction factors for branching corals become larger as cover of these corals increases. Thus taxa specific corrections and model development which considers error values proportional to the mean value will be required before transforming results from one method to the other. This allows data collected for different purposes, (e.g. fish and benthic surveys), to be amalgamated with benthic data collected using traditional approaches, facilitating meta-analysis of data from different sources, fostering collaboration and potentially minimising monitoring costs (Moore et al. 2012; Speed et al. 2013).

Conclusions

Comparative studies are fundamental in the determination of whether methods are capable of providing complementary or standalone information useful for monitoring purposes (Brown et al. 2004; Langlois et al. 2010). The results of our study suggest that forward-DOV may provide a better description of taxa that form much of the reefs structural complexity, but is not necessarily suitable for the monitoring of benthic community assemblages at the genus level. At the broad scale, forward-DOV is a cost effective monitoring option which can enable understanding of the composition and structural complexity of benthic assemblages and is comparable, with the appropriate correction factors, to existing data sets recorded by different methods. However, the downward-DOV is more suitable for the overall monitoring of sessile benthic assemblages on coral reefs, specifically changes in percent cover of rubble, algae turfs and the occurrence of coral recruits. The forward-DOV may be considered a suitable method to provide complementary benthic community data on total coral cover and algae cover expanding sources of information for these basic measures over both spatial and temporal scales.

11.2.5 ACKNOWLEDGMENTS

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11.2.6 REFERENCES

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E.

Aronson RB, Edmunds PJ, Pretch WF, Swanson DW, Levitan DR (1994) Large-scale, long-term monitoring of Caribbean coral reefs: Simple, quick, inexpensive techniques. Atoll Research Bulletin 421: 1–19.

Bell PRF (1992) Eutrophication and coral reefs-some examples in the Great Barrier Reef Lagoon. Water Research 26: 553–568.

Brown EK, Cox E, Jokiel PL, Rodgers SK, Smith WR, Tissot BN, Coles SL, Hultquist J (2004) Development of benthic sampling methods for the Coral Reef Assessment and Monitoring Program (CRAMP) in Hawai'i. Pacific Science 58: 145–158.

Burgess SC, Osborne K, Sfiligoj B, Sweatman H (2010) Can juvenile corals be surveyed effectively using digital photography?: implications for rapid assessment techniques. Environmental Monitoring and Assessment 171: 345–351. doi:10.1007/s10661-009-1282-1

Carleton JH, Done TJ (1995) Quantitative video sampling of coral reef benthos: large-scale application. Coral Reefs 14: 35–46.

Chabanet P, Adjeroud M, Andréfouët S, Bozec Y-M, Ferraris J, Garcìa-Charton J-A, Schrimm M (2005) Human-induced physical disturbances and their indicators on coral reef habitats: A multi-scale approach. Aquatic Living Resources 18: 215–230. doi:10.1051/alr:2005028

Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: implications of transect width and species selection. Marine Ecology Progress Series 158: 241–248.

Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic, San Diego, pp 120–155.

Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clarke KR, Gorley RN (2006) PRIMER v6. User manual/tutorial. PRIMER-E.

Coker DJ, Pratchett MS, Munday PL (2009) Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. Behavioural Ecology 20: 1204–1210. doi:10.1093/beheco/arp113

Coker DJ. Pratchett MS, Munday PL (2012) Influence of coral bleaching, coral mortality and conspecific aggression on movement and distribution of coral-dwelling fish. Journal of Experimental Marine Biology and Ecology 414-415: 62–68. doi:10.1016/j.jembe.2012.01.014

Connell SD, Samoilys MA, Lincoln Smith MP, Leqata J (1998) Comparisons of abundance of coral-reef fish: Catch and effort surveys vs visual census. Australian Journal of Ecology 23: 579–586.

Cornbleet PJ, Gochman N (1979) Incorrect least-squares regression coefficients in method-comparison analysis. Clinical Chemistry 25: 432–438.

Cruz I, Kikuchi RK, Leão ZM (2008) Use of the video transect method for characterizing the Itacolomis reefs, eastern Brazil. Brazilian Journal of Oceanography 56: 271–280.

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences 109: 17995–17999. doi:10.1073/pnas.1208909109

Dollar SJ, Grigg RW (2004) Anthropogenic and Natural Stresses on Selected Coral Reefs in Hawai'i: A Multidecade Synthesis of Impact and Recovery. Pacific Science 58: 281–304. doi:10.1353/psc.2004.0016

Dumas P, Bertaud A, Peignon C, Léopold M, Pelletier D (2009) A "quick and clean" photographic method for the description of coral reef habitats. Journal of Experimental Marine Biology and Ecology 368: 161–168. doi:10.1016/j.jembe.2008.10.002

Dunn G (2007) Regression Models for Method Comparison Data. Journal of Biopharmaceutical Statistics 17: 739–756. doi:10.1080/10543400701329513

Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. Marine Biology 161: 599–607. doi:10.1007/s00227-013-2362-x

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50: 125–146. doi:10.1016/j.marpolbul.2004.11.028

Fairweather, PG (1991) Statistical power and design requirements for environmental monitoring. Australian Journal of Marine and Freshwater Resources 42: 555–567.

Fisher WS, Fore LS, Hutchins A, Quarles RL, Campbell JG, LoBue C, Davis WA (2008) Evaluation of stony coral indicators for coral reef management. Marine Pollution Bulletin 56: 1737–1745. doi:10.1016/j.marpolbul.2008.07.002

Friedman A, Pizarro O, Williams SB, Johnson-Roberson M (2012) Multi-Scale Measures of Rugosity, Slope and Aspect from Benthic Stereo Image Reconstructions C. Fulton [ed.]. PLoS ONE 7: e50440. doi:10.1371/journal.pone.0050440

Gardner AT, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301: 958–960.

Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y, Bigot L, Galzin R, Ohman MC, Garpe KC, Edwards AJ, Sheppard CRC (2008) Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems R.P. Freckleton [ed.]. PLoS ONE 3: e3039. doi:10.1371/journal.pone.0003039

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32: 315–326. doi:10.1007/s00338-012-0984-y

Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal Fish Biology 66: 650–667.

Harvey E, Shortis M (1996) A system for stereo-video measurement of sub-tidal organisms. Marine Technology Society Journal 29: 10–22.

Harvey ES, Shortis MR (1998) Calibration stability of an underwater stereo–video system: Implications for measurement accuracy and precision. Marine Technology Society. Marine Technology Society Journal 32: 3.

Hatcher BG (1990) Coral reef primary productivity. A hierarchy of pattern and process. Trends in Ecology & Evolution 5: 149–155. doi:10.1016/0169-5347(90)90221-X

Hill J,Wilkinson C (2004) Methods for Ecological Monitoring of Coral Reefs: Version 1, Australian Institute of Marine Science.

Holmes TH, S. Wilson SK, Travers MJ, Langlois TJ, Evans RD, Moore GI, Douglas RA, Shedrawi G, Harvey ES, Hickey K (2013) A comparison of visual- and stereo-video based fish community assessment methods in tropical and temperate marine waters of Western Australia: Comparison of fish community assessment methods. Limnology and Oceanography: Methods 11: 337–350. doi:10.4319/lom.2013.11.337

Houk, P., and R. Van Woesik. 2006. Coral Reef Benthic Video Surveys Facilitate Long-Term Monitoring in the Commonwealth of the Northern Mariana Islands: Toward an Optimal Sampling Strategy. Pacific Science 60: 177–189. doi:10.1353/psc.2006.0005

Houk P, Van Woesik R (2013) Progress and Perspectives on Question-Driven Coral-Reef Monitoring. BioScience 63: 297-303. doi:10.1525/bio.2013.63.4.10

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution 25: 633–642. doi:10.1016/j.tree.2010.07.011

Jokiel PL, Rodgers KS, Brown EK, Kenyon JC, Aeby G, Smith WR, Farrell F (2005) Comparison of methods used to estimate coral cover in the Hawaiian Islands. PeerJ 3: e954.

Kelley R (2011) Indo Pacific Coral Finder, 2nd ed. BYOG Guides.

Lam K, Shin PKS, Bradbeer R, Randall D, Ku KKK, Hodgson P, Cheung SG (2006) A comparison of video and point intercept transect methods for monitoring subtropical coral communities. Journal of Experimental Marine Biology and Ecology 333: 115–128. doi:10.1016/j.jembe.2005.12.009

Langlois T, Harvey E, Fitzpatrick B, Meeuwig J, Shedrawi G, Watson D (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. Aquatic Biology 9: 155–168. doi:10.3354/ab00235

Leujak W, Ormond RFG (2007) Comparative accuracy and efficiency of six coral community survey methods. Journal of Experimental Marine Biology and Ecology 351: 168–187. doi:10.1016/j.jembe.2007.06.028

Lim IE, Wilson SK, Holmes TH, Noble MM, Fulton CJ (2016) Specialization within a shifting habitat mosaic underpins the seasonal abundance of a tropical fish. Ecosphere 7: e01212.10.1002/ecs2.1212

Linnet L (1990) Estimation of the linear relationship between the measurements of two methods with proportional errors. Statistics in Medicine 9: 1463– 1473. Doi: 10.1002/sim.4780091210

Linnet K (1993) Evaluation of regression procedures for methods comparison studies. Clinical Chemistry 39: 424–424.

Linnet K (1998) Performance of Deming regression analysis in case of misspecified analytical error ratio in method comparison studies. Clinical Chemistry 44: 1024–1031.

Linnet K (1999) Necessary sample size for method comparison studies based on regression analysis. Clinical Chemistry 45: 882–894.

Lirman D, Gracias NR, Gintert BE, Gleason ACR, Reid RP, Negahdaripour S, Kramer P (2007) Development and application of a video-mosaic survey technology to document the status of coral reef communities. Environmental Monitoring and Assessment 125: 59–73. doi:10.1007/s10661-006-9239-0

Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952-2012). Fisheries Research 154: 44–46.

Mantelatto MC, Fleury BG, Menegola C, Creed JC (2013) Cost–benefit of different methods for monitoring invasive corals on tropical rocky reefs in the southwest Atlantic. Journal of Experimental Marine Biology and Ecology 449: 129–134. doi:10.1016/j.jembe.2013.09.009

Manuilova E, Schuetzenmeis A, Model F (2014) Method Comparison. R package Version 1.2.1.

Martin RF (2000) General Deming regression for estimating systematic bias and its confidence interval in metho-comparison studies. Clinical Chemisrty 46:100– 104.

McClanahan T, Polunin N, Done T (2002) Ecological states and the resilience of coral reefs. Conservation Ecology 6: 18.

McClanahan TR, Graham NAJ, MacNeil MA, Muthiga NA, Cinner JE, Bruggemann JH, Wilson SK (2011) Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. Proceedings of the National Academy of Sciences 108: 17230–17233. doi:10.1073/pnas.1106861108

McCormick MI (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Marine Ecology Progress Series 112: 87–96.

Miller MW, Aronson RB, Murdoch TJT (2003) Monitoring coral reef macroalgae: different pictures from different methods. Bulletin of Marine Science 72: 199–206.

Moore JAY, Bellchambers LM, Depczynski MR, Evans RD, Evans SN, Field SN, Friedman, KJ, Gilmour JP, Holmes TH, Middlebrook R, Radford BT, Ridgway T, Shedrawi G, Taylor H, Thomson DP and Wilson SK (2012) Unprecedented Mass Bleaching and Loss of Coral across 12° of Latitude in Western Australia in 2010–11 I. Álvarez [ed.]. PLoS ONE 7: e51807. doi:10.1371/journal.pone.0051807

Nadon M-O, Stirling G (2006) Field and simulation analyses of visual methods for sampling coral cover. Coral Reefs 25: 177–185. doi:10.1007/s00338-005-0074-5

Nystrom M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology and Evolution 15: 413–417.

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Current Opinion in Environmental Sustainability 7: 37–43. doi:10.1016/j.cosust.2013.11.022

Pratchett MS, Munday PL, Wilson SK, Grahan NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes.

Ecological and economic consequences. Oceanography and Marine Biology: Annual Review 46: 251–296.

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 100: 167–176.

Ramos CAC, Amaral FD, de Kikuchi RKP, Chaves EM, de Melo GR (2010) Quantification of reef benthos communities and variability inherent to the monitoring using video transect method. Environmental Monitoring and Assessment 162: 95–101. doi:10.1007/s10661-009-0778-z

Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. Coral Reefs 22: 63–67.

Safuan M, Boo WH, Siang HY, Chark JH, Bachok Z (2015) Optimization of Coral Video Transect Technique for Coral Reef Survey: Comparison with Intercept Transect Technique. Open Journal of Marine Science 05: 379–397. doi:10.4236/ojms.2015.54031

Scopélitis J, Andréfouët S, Phinn S, Arroyo L, Dalleau M, Cros A, Chabanet P (2010) The next step in shallow coral reef monitoring: Combining remote sensing and in situ approaches. Marine Pollution Bulletin 60: 1956–1968. doi:10.1016/j.marpolbul.2010.07.033

Segal B, Castro CB (2001) A proposed method for coral cover assessment: a case study in Abrolhos, Brazil. Bulletin of Marine Science 69: 487–496.

Shedrawi G, Harvey ES, McLean DL, Prince J, Bellchambers LM, Newman SJ (2014) Evaluation of the effect of closed areas on a unique and shallow water coral reef fish assemblage reveals complex responses. Coral Reefs 33: 579–591. doi:10.1007/s00338-014-1160-3

Shortis MR, Harvey ES, Abdo DA (2009) A review of underwater stereo-image measurement for marine biology and ecology applications. Oceanography and Marine Biology: An annual review 47: 257–292.

Speed CW, Babcock RC, Bancroft KP, Beckley LE, Bellchambers LM, Depczynski M, Field SN, Friedman, KJ, Gilmour JP, Hobbs J-P A, Kobryn HT, Moore JAY, Nutt CD, Shedrawi G, Thomson DP and Wilson SK (2013) Dynamic Stability of Coral Reefs on the West Australian Coast I. Álvarez [ed.]. PLoS ONE 8: e69863. doi:10.1371/journal.pone.0069863.

Sweatman HH, Cheal AA, Coleman GG, et al. (2001) Long-Term Monitoring of the Great Barrier Reef, Status Report Number 5.

Turner JA, Polunin NVC, Field SN, Wilson SK (2015) Measuring coral size-frequency distribution using stereo video technology, a comparison with in situ measurements. Environmental Monitoring and Assessment 187: 234. doi:10.1007/s10661-015-4431-8

Tyne JA, Loneragan NR, Krützen M, Allen SJ, Bejder L (2010) An integrated data management and video system for sampling aquatic benthos. Marine and Freshwater Research 61: 1023. doi:10.1071/MF09240

Vernon JEN (2000) Corals of the World. Vol 1-3. Townsville, Australia: Australian Institute of Marine Science.

Wartenberg R, Booth AJ (2014) Video transects are the most appropriate underwater visual census method for surveying high-latitude coral reef fishes in the southwestern Indian Ocean. Marine Biology 45: 633–646.

Watson DL, Harvey ES, Anderson MJ, Kendrick GA (2005) A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. Marine Biology 148: 415–425. doi:10.1007/s00227-005-0090-6

Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ, Shedrawi G (2010) Assessing reef fish assemblage structure: how do different stereo-video techniques compare? Marine Biology 157: 1237–1250. doi:10.1007/s00227-010-1404-x

Wilson SK, Dolman AM, Cheal AJ, Emslie MJ, Pratchett MS, Sweatman HPA (2009) Maintenance of fish diversity on disturbed coral reefs. Coral Reefs 28: 3–14. doi:10.1007/s00338-008-0431-2

Wilson SK, Fulton CJ, Depczynski M, Holmes TH, Noble MM, Radford B, Tinkler B (2014) Seasonal changes in habitat structure underpin shifts in macroalgae-associated tropical fish communities. Marine Biology 161: 2597–2607. doi:10.1007/s00227-014-2531-6

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessment of habitat complexity and benthic composition on coral reefs. Marine Biology 151: 1069–1076. doi:10.1007/s00227-006-0538-3.

11.3 A novel stereo-video method to investigate fish-habitat relationships

Authors: Collins DL, Langlois TJ, Bond T, Holmes TH, Harvey ES, Fisher R, McLean DL.

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ABSTRACT

1. Habitat complexity is known to influence the structure of fish assemblages. A number of techniques have previously been used to measure complexity, including quantitative *in situ* methods, that can be time consuming and labour intensive, and more rapid semi-quantitative visual scoring methods. This study investigated the utility of a novel method for estimating complexity, whereby habitat height was measured using stereo photogrammetry from diver operated stereo-video, traditionally used to sample fish assemblages.

2. This ‘stereo-height’ method was compared to established *in situ* and visual scoring techniques and found to produce similar estimates of complexity. To determine how relevant the proposed method is for assessing ecological relationships, it was then used in conjunction with visual scoring of relief and point-intercept samples of benthic composition to model fish-habitat associations in the Pilbara region of Western Australia.

3. Visual scores of relief were marginally stronger predictors of fish assemblage parameters and functional groups than the stereo-height measurements, providing support for the visual scoring approach. The only exception was for corallivorous fishes, which were more strongly correlated with stereo-height measurements. This study has presented a method for assessing habitat complexity using video imagery that is both comparable to traditional *in situ* techniques and useful for investigating fish-habitat relationships.

4. We suggest that future studies interested in collecting habitat complexity data from new or existing stereo-video samples use both the stereo-height and visual scoring methods presented here. Together these methods enable studies to rapidly and effectively assess fish-habitat relationships across a range of habitats without the need for *in situ* methods or solely relying on field observers trained in visual scoring techniques.

11.3.1 INTRODUCTION

The physical and biological attributes of benthic habitats are known to influence the abundance composition of fish assemblages across marine environments (Connell and Kingsford 1998; Moore et al. 2009; Wilson et al. 2012). An understanding of the relationships between fish and habitat is essential for predicting the impacts of habitat modification and loss on fish populations.

Habitat complexity can be considered as any variance in surface structure (Grigg 1994; Beck 2000). The relationships between fish assemblage metrics and habitat have been well researched, with previous studies demonstrating positive relationships between habitat complexity and the abundance (Luckhurst and Luckhurst 1978; Harman et al. 2003), biomass (Carpenter et al. 1981; Friedlander et al. 2003) and diversity (Willis and Anderson 2003; Wilson et al. 2012) of fishes. Structural features of benthic habitats provide shelter from predators, and modify the availability of resources (e.g. food and shelter) and their rate of acquisition (Friedlander and Parish 1998). Positive relationships between complexity and fish assemblage metrics are typically attributed to the greater availability and variety of these resources in highly complex habitats, which may reduce competition and predation (Friedlander and Parish 1998) and thus promote the co-occurrence of a greater number of individuals and species (Almany 2004; Komyakova et al. 2013).

Another important determinant of fish populations is the composition of benthic habitats (e.g. Ohman and Rajasuriya 1998; Bonaca and Lipej 2005) where the particular requirements of individual species are known to affect their abundance (Williams et al. 2008), biomass (Jennings et al. 1996; Wilson et al. 2012) and spatial distributions (Jennings et al. 1996; Giakoumi and Kokkoris 2013). Species within a given feeding guild have similar dietary requirements, therefore relationships with benthic cover have also been found at this level (Friedlander and Parish 1998; Toller et al. 2010). The abundance and diversity of fish are often found to be greatest on rocky and coral reefs, and decline with increases in the percent cover of macroalgae and sand (e.g. Jenkins and Wheatley 1998; Williams et al. 2008; Wilson et al. 2012; Giakoumi and Kokkoris 2013) – a trend that reflects the structural complexity of these habitats.

A number of *in situ* techniques have been used to estimate complexity, such as measuring rugosity (Risk 1972; Friedlander et al. 2003), habitat height (Parish and Boland 2004; Wilson et al. 2007) and the size and number of reef holes (Friedlander and Parish 1998). Other methods utilise stereo-reconstructions to calculate a rugosity index (Friedman et al. 2012, Bridge et al. 2011). A single method is unlikely to capture all the structural variation in habitat (Roberts and Ormond 1987) and thus may not be a strong predictor for all fish assemblage parameters (e.g. Carpenter et al. 1981; Roberts and Ormond 1987; Wilson et al. 2007). It is becoming increasingly acknowledged that multiple techniques are required to measure various aspects of habitat complexity simultaneously (Friedlander and Parish 1998; Gratwicke and Speight 2005; Friedman et al. 2012; Wilson et al. 2007). However, many techniques are time consuming, labour intensive, or require cumbersome equipment (Gratwicke and Speight 2005, Wilson et al. 2007) and have specialised data collection in the field (Friedman et al. 20012 Bridge et al. 2011; Harborne et al. 2011). Different benthic habitats also require different methods, leading to complications when sampling across a range of habitats (Smale et al. 2012). For example, the chain-tape method (Risk 1972; Luckhurst and Luckhurst 1978; Friedlander et al. 2003; Wilson et al. 2012) commonly used to measure the rugosity of reefs is difficult to apply in seagrass beds where measuring plant height and density would be more appropriate (Gratwicke and Speight 2005). More recently, visual estimates of relief that categorise overall habitat complexity using visual scores have been used (Polunin and Roberts 1993; Jennings et al. 1996; Gratwicke and Speight 2005). Despite being susceptible to observer bias, this rapid technique has been deemed effective and reliable (Gratwicke and Speight 2005; Wilson et al. 2007). However, visual scores are limited in that they only provide semi-quantitative data and typically rely on observations in the field that cannot be validated.

Diver operated stereo-video (stereo-DOV) has been widely used to sample both tropical and temperate fish assemblages (e.g. Harman et al. 2003; Holmes et al. 2013; Goetze et al. 2015). The technique uses stereo-video cameras to rapidly collect imagery in the field, while fish identification, counts and length measurements are subsequently obtained from the stereo-imagery in the laboratory. These videos can be validated and revisited at any time and the accuracy and precision of length measurements obtained is high (Harvey et al. 2001). While visual census methods are still predominantly used on a global scale for collecting information on shallow water fish communities (Edgar et al. 2014), the stereo-DOV method is being increasingly adopted (Holmes et al. 2013) and becoming financially viable with advances in technology producing smaller, cheaper cameras (e.g. GoPro) and cheaper hardware requirements. Since stereo-DOV surveys capture footage of both fish assemblages and benthic habitat simultaneously (Shedrawi et al. 2014), devising a method that is able to quantify habitat complexity from existing imagery would be highly cost-effective.

This study aimed to develop a method to estimate habitat complexity from existing and future stereo-DOV footage that did not rely on additional data collection, and to trial the utility of this method to model fish-habitat relationships. We first determined whether measuring the height of habitat using a virtual point-intercept from stereo-video transects (termed 'stereo-height') is comparable with established *in situ* and visual scoring techniques. Stereo-height measures of complexity were then used to model fish-habitat associations in conjunction with visual scores of relief (termed 'visual-relief') and point-intercept samples of benthic composition in order to determine how relevant and useful the proposed stereo-height method is for investigating ecological relationships.

11.3.2 METHODS

Study areas

To determine whether measures of habitat complexity obtained from stereo-video images were comparable to physical *in situ* methods and visual scores of relief, we conducted studies 1) along an exposed rock shoreline off Perth and 2) in the Pilbara region of northwestern Australia. The first study was conducted out of the water for ease and efficiency of collecting data, enabling a comparison of multiple complexity measures along the same transects. The second study investigated the utility of stereo-height measurements and visual scores of relief to model of fish-habitat relationships. This footage was obtained from ten sites across the Pilbara region of northwestern Australia during November 2013 (Figure 11.3.1).

Comparison of complexity measures

Ten 25 m x 5 m transects were surveyed at a single location across a series of exposed rocky shoreline representing a range of habitat complexity, using three methods: (1) chain-tape, (2) *in situ* height, (3) stereo-height (Figure S11.3.1). In addition, stereo-height and (4) visual scores of relief were compared across 120 transects conducted as part of the fish-habitat study.

For the chain-tape method, five replicate spatially balanced 25 m chain with 38 mm links was successively laid along each transect to conform to all contours and crevices in the rocky shoreline (Figure S11.3.1A, Risk 1972; Luckhurst and Luckhurst 1978; Frost et al. 2005). For the *in situ* height method, five replicate height measurements of the topography were made every 2.5 m along the same five paths followed by the chain, summing to 50 measurements per transect (Figure S11.3.1B). For the stereo-height method, the height of the topography at every 2.5 m interval along each transect was measured at ten evenly spaced points placed on a single video frame within the transect boundaries, summing to 100 measurements per transect (Figure S11.3.1C). To enable the stereo-height method, photogrammetry was used to position a virtual horizontal point-intercept axis ~1 m in front of the cameras. Visual scores of relief for the stereo-video field of view were given a ranking of 0-5 (Polunin and Roberts 1993) where scores of 0 represented areas of no vertical relief (e.g. sand or pavement) and 5 represented exceptionally complex habitats with numerous caves and overhangs. This visual score was used to assess habitat complexity (termed 'visual-relief') every 2.5 m along each transect, summing to 10 measurements per transect and providing a semi-quantitative measure.

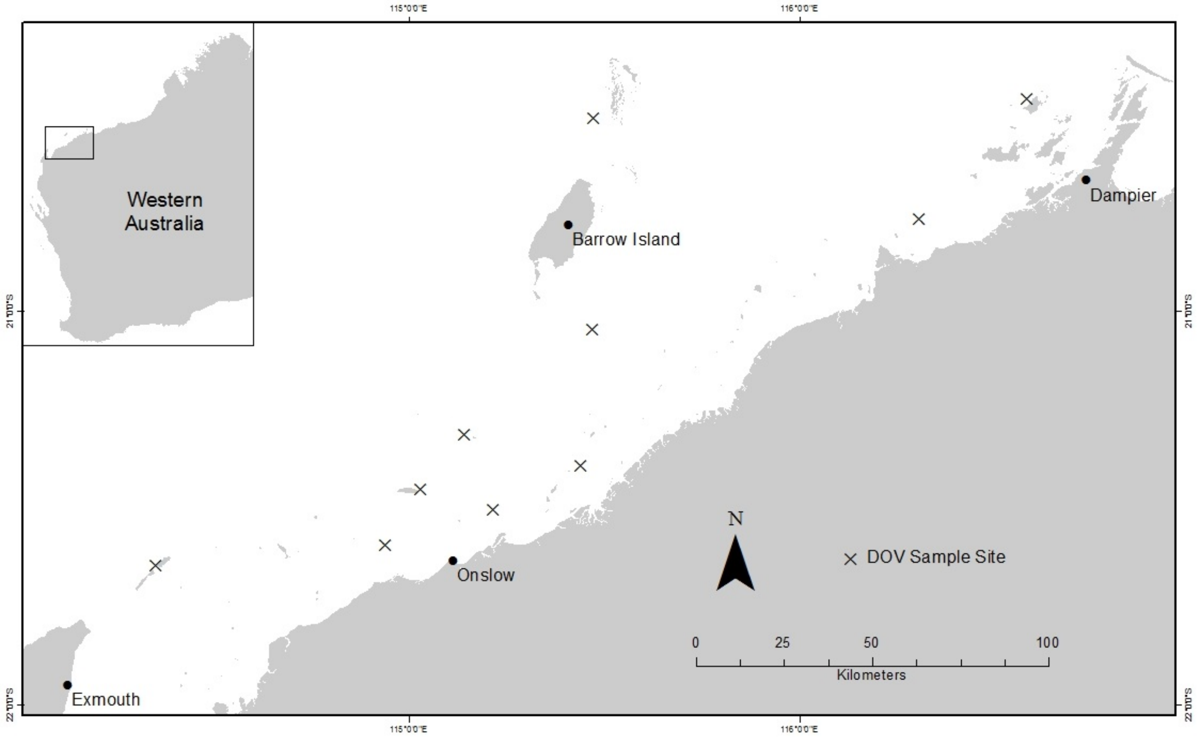

Figure 11.3.1 Location of the study area showing sampling sites along the Pilbara coastline.

The stereo-DOV system consisted of two Sony cx700 digital video camcorders in underwater housings mounted 0.7 m apart on a base bar inwardly converged at eight degrees. The stereo-DOV configuration has been used elsewhere (see Shedrawi et al. 2014), a description of how to calibrate the stereo-video imagery using the program CAL (SeaGIS Pty Ltd 2014) can be found in Harvey and Shortis (1995). To complete the stereo-height method, paired videos from the stereo-DOV system were converted into Audio Video Interleafed (AVI) files using Xilisoft Video Converter Ultimate 6 (Xilisoft Corporation 2014) and viewed in EventMeasure (SeaGIS Pty Ltd 2014).

Fish habitat study

Twelve 25 m transects were swum at each study site, giving a total of 120 transects. The stereo-DOV configuration used was the same as was used in the validation study above. Surveys were conducted by two SCUBA divers simultaneously, one operating the stereo-DOV system and the other measuring the distance swum with a Chainman II® measuring device with biodegradable cotton. Divers swam approximately 30 cm above the seafloor and angled the cameras slightly downwards for a clear view of the habitat and fish above. Each transect took approximately 1 min and 30 s to complete and was separated from the preceding transect by a gap of at least 10 m.

Stereo-DOV footage was viewed in the program EventMeasure (SeaGIS Pty Ltd 2014) where a standardised sample area can be set. Fish further than 2.5 m to the left and right and 7m in front of the camera were excluded. Experienced fish analysts identified fish to the lowest taxonomic unit and counted and measured each individual. Counts were summed per transect to give a relative abundance comparable to other sites using the same method. The relative abundance of all herbivores and corallivores was summed from the assemblage (based on diet; Froese and Pauly 2014) as were families considered targeted by recreational fishers (Lethrinidae, Lutjanidae and Serranidae; Williamson et al. 2006).

Stereo-height measurements and visual scores of relief were collected as described in the comparison of complexity measures methods. *In situ* and chain-tape methods were not included in this analysis as due to logistical constraints we were unable to complete all the complexity measures during the underwater sampling. In addition, the habitat composition beneath each virtual point-intercept was classified into eight categories: (1) hard coral, (2) soft coral, (3) dead coral, (4) macroalgae, (5) pavement, (6) rock, (7) rubble, (8) sand (100 measurements per transect). The proportion of the total number of points that fell on each category was used to estimate percent cover. All assessments were performed by the same person to avoid observer bias, which has previously been noted with this type of visual technique (Wilson et al. 2007).

Data analysis

COMPARISON OF COMPLEXITY MEASURES

For all method comparisons, we used orthogonal regression (Deming 1964), which is designed to examine the linear relationship between two continuous variables while accounting for the measurement error in both the x and y components. The orthogonal regression used to compare complexity measurements included a test for significance (i.e. if the slope is significantly different to 1 and if the intercept is significantly different to 0) (Deming 1964). For the chain-tape method, rugosity (r) is calculated as the ratio between the mean contoured distance and the horizontal distance of each transect (r = chain length / transect tape length). The mean and standard-deviation of stereo-height and *in situ* height measurements were compared to chain-tape rugosity estimates, after normalising all data. In addition, the mean and standard-deviation of stereo-height and *in situ* height measurements were compared using raw data. The mean and standard-deviation of stereo-height measurements and visual scores of relief were also compared, after normalising all data.

FISH-HABITAT STUDY

The fish assemblage metrics were modelled as a function of the percent cover of each habitat type for each transect, scores from principal component axes 1 and 2 which characterised habitat cover, the mean and standard deviation of stereo-height (n=120) and visual scores of relief (n=120). Species richness (# species), total fish abundance and the abundance of herbivores, corallivores and target families were summed for each transect. These feeding guilds were selected given their strong direct link with habitat (in contrast to other feeding guilds such as invertivores).

Collinearity among explanatory variables is inherent in ecological data, which can cause problems with model selection (Graham 2003; Freckleton 2011). Strategies for dealing with this include using PCA to create a reduced set of orthogonal variables and by using full subsets approaches where all possible combinations of variables are considered, but where highly co-linear variables are not included in the same model). For the percent cover habitat data we used principal components analysis (PCA) to generate a reduced number of uncorrelated variables that characterised the differences in benthic composition among transects (Figure S11.3.2). Principal component axis one (PC1) explained 60% of the variation in benthic composition and largely represented the distinction among sites dominated by dead coral from those dominated by macroalgae (Figure S11.3.2). Principal component axis two (PC2) explained 15% of the variation and distinguished pavement, rock and soft coral from sand, macroalgae and dead coral (Figure S11.3.2).

A limitation of PCA lies in its biological interpretation (Graham 2003) and the inability to disentangle the independent effects and predictive strength of correlated variables on the same principal components axis (Freckleton 2011). Therefore, we included both PCA scores and the percent cover of individual habitat categories as predictor variables when modelling fish-habitat relationships. Correlation matrices identified strong colinearity ($r > 0.7$) among all measures of habitat complexity. However, the individual strength of each complexity variable was of a direct interest to this study and these were therefore not included in the PCA.

The influence of habitat complexity (stereo-height measurements, visual scores of relief) and benthic composition on species richness and abundance of the fish assemblage metrics was investigated using generalized additive mixed models (GAMMs; Hastie and Tibshirani 1986; Lin and Zhang 1999). Because of strong collinearity a full subsets approach was used to fit all combinations of predictor variables up to a maximum of three (to prevent overfitting and ensure models remained ecologically interpretable). Models containing combinations of variables with correlations >0.4 were excluded. To contrast the utility of stereo-height and visual scores of relief for modelling fish-habitat relationships we performed the full subset method twice, either including (a total of 238 fitted models) or excluding visual scores of relief (a total of 138 fitted models). Model selection was based on Bayesian Information Criteria (BIC) and BIC weights (wBIC), with the best model being that with the lowest BIC. Relative support for each predictor variable was obtained by calculating the summed wAIC across all subsets of models containing that variable to obtain its relative importance (Burnham and Anderson, 2002). To account for the differing number of models each variable was included in we first divided variables weights by the number of models (in which that variable was included), rescaled these per model weights to zero and one, and then multiplied these by the R^2 value of the best model to ensure that the overall importance of each variable was presented in the context of explanatory power.

As recommended in recent literature (O'hara and Kotze 2010) we used untransformed fish assemblage metrics as our response variables. Models of total abundance and species richness, which met the assumptions of normality and homogeneity of variances, were fitted using a Gaussian distribution. Models of target families and feeding guild abundance were fitted using a Poisson distribution, and over dispersion was accommodated for by including an observation level random effect. Several explanatory variables were either logx+1 (SD stereo-height, hard coral, soft coral, rubble, and sand) or square-root (mean stereo-height, dead coral, and rock) transformed to ensure that their values were evenly distributed across the observed range. All analyses and plots were performed using the R language for statistical computing (R Development Core Team 2015) with the package MGCV version 1.8 - 6 for GAMMs (Wood 2011) and ggplot2 (Wickham 2009).

11.3.3 RESULTS

Comparison of complexity measures

EFFICACY OF STEREO-HEIGHT

Proxies for habitat complexity (mean and SD) derived from both the *in situ* and stereo-height methods demonstrated positive relationships with rugosity estimated using the chain-tape method (Figure 11.3.2). These relationships were weaker for the stereo-height proxies than their *in situ* counterparts (Figure 11.3.2). Strong positive relationships were found between each corresponding *in situ* and stereo-height proxy (Figure 11.3.3). Stereo-height measurements were generally lower than those obtained *in situ* and was exacerbated for the mean height as habitat complexity increased (Figure 11.3.3).

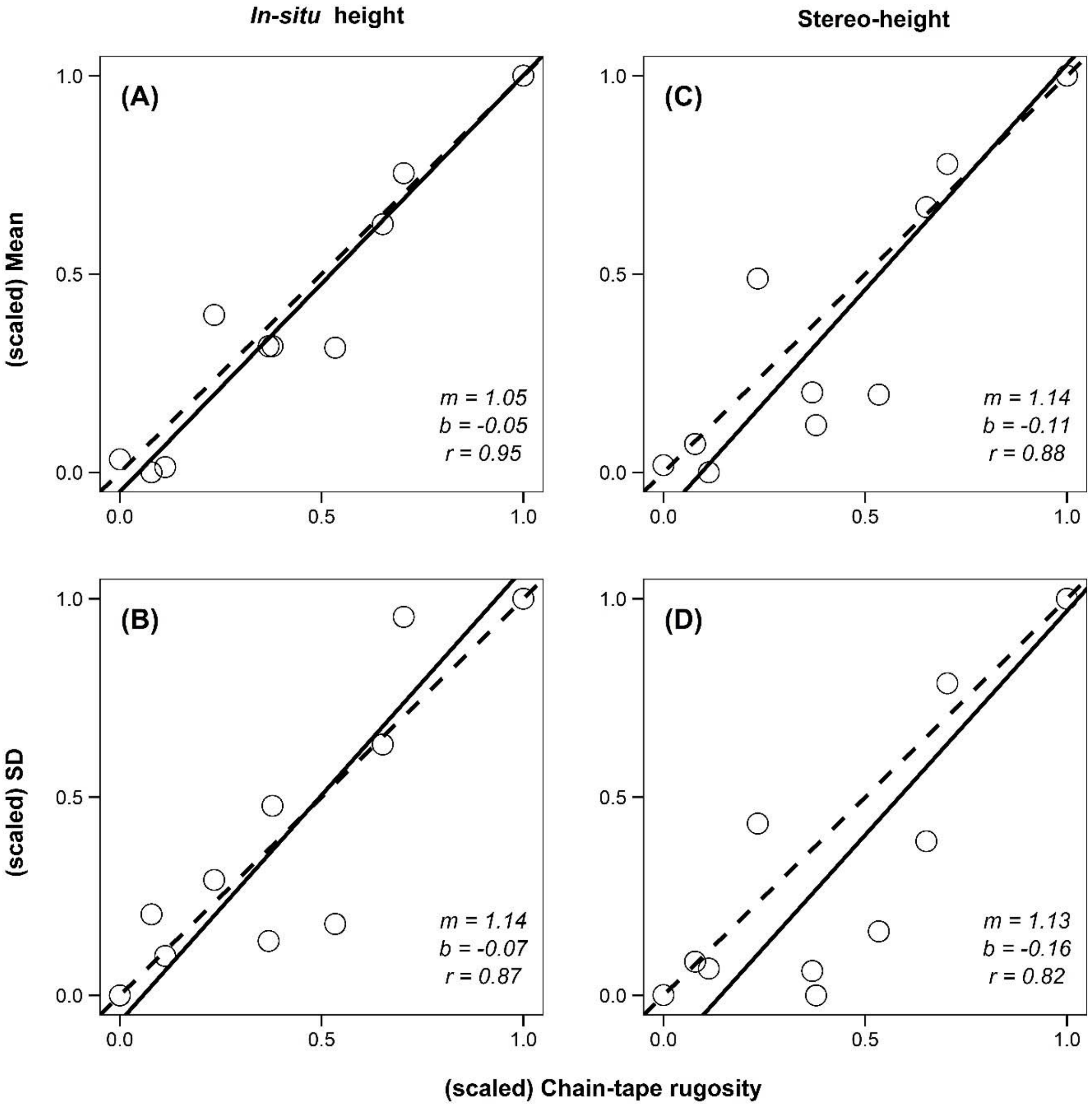

Figure 11.3.2 Comparison of the average and standard deviation of *in situ* height and stereo-height vs. chain-tape rugosity. The slope, intercept and correlation coefficient of each regression are denoted by m, b and r respectively. All measurements were scaled between 0-1. Broken lines represent a 1:1 ratio. (a) mean *in situ* height vs. chain tape rugosity, (b) mean stereo-height vs. chain-tape rugosity, (c) standard deviation of *in situ* height vs. chain-tape rugosity, and (d) standard deviation stereo-height vs. chain-tape rugosity.

STEREO-HEIGHT VS. VISUAL-RELIEF

Positive relationships were found between each corresponding proxy of complexity (mean and SD) derived from stereo-height measurements and visual scores of relief (Figure 11.3.4). The relationship between mean stereo-height measurements and mean visual-relief was stronger than that between the standard deviations of each method (Figure 11.3.4). Mean stereo-height measurements were significantly lower than mean visual scores; however this difference did not increase with habitat complexity (Figure 11.3.4). Conversely, the difference between the SD proxies increased significantly with complexity, with the SD of stereo-height measurements remaining lower than the SD of visual-relief (Figure 11.3.4).

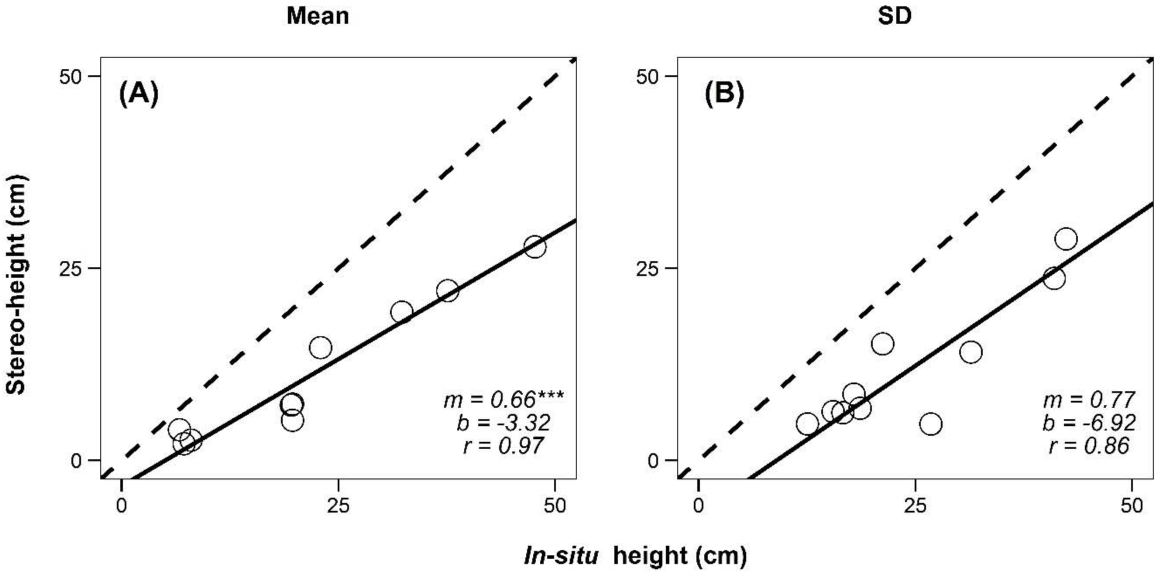

Figure 11.3.3 Comparison of the average and standard deviation of *in situ* height vs. stereo-height. The slope, intercept and correlation coefficient of each regression are denoted by m, b and r respectively. An asterisk indicates the level of significance for *P* (* < 0.001). Broken lines represent a 1:1 ratio. (a) mean stereo-height vs. *in situ* height, and (b) standard deviation of stereo-height vs. *in situ* height.**

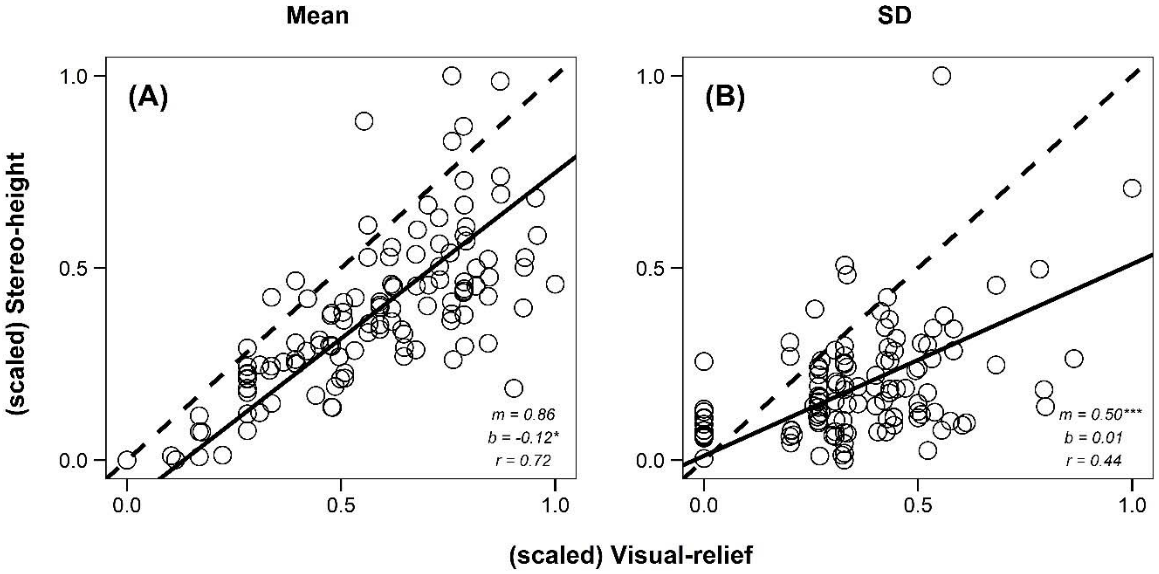

Figure 11.3.4 Comparison of the average and standard deviation of visual relief vs. stereo-height. The slope, intercept and correlation coefficient of each regression are denoted by m, b and r respectively. An asterisk indicates the level of significance for *P* (* < 0.05, * < 0.001). Broken lines represent a 1:1 ratio. (a) mean stereo-height vs. visual-relief, and (b) standard deviation of stereo-height vs. visual relief.**

Fish habitat study

VISUAL SCORES OF RELIEF

Mean visual-relief was present in the best model for predicting total abundance, species richness, and the abundance of herbivores and target families (Table 11.3.1). For total abundance and species richness, mean visual-relief was the second most important predictor variable while for herbivores and target families, it was the most important (Figure 11.3.5). Species richness, total abundance, and the abundance of herbivores and target families were all positively correlated with mean visual scores of relief (Figure S11.3.3, Figure S11.3.4 and Figure S11.3.5), indicating that each increased with habitat complexity. Mean visual-relief was a relatively strong predictor of total abundance and species richness, accounting for ~30% and ~50% of the variation in this data, respectively, when combined with other explanatory variables (Table 11.3.1). However, relationships between mean visual scores of relief and the abundance of herbivores and target families was weak since mean visual-relief accounted for < 11% of the variation in both groups (Table 11.3.1). This indicates that the models were a poor fit and that mean visual-relief was not a strong predictor of herbivore and target family abundance, despite its relative importance. The SD of visual-relief was not present in any of the best models (Table 11.3.1), indicating that it was a poor predictor of total fish abundance and species richness.

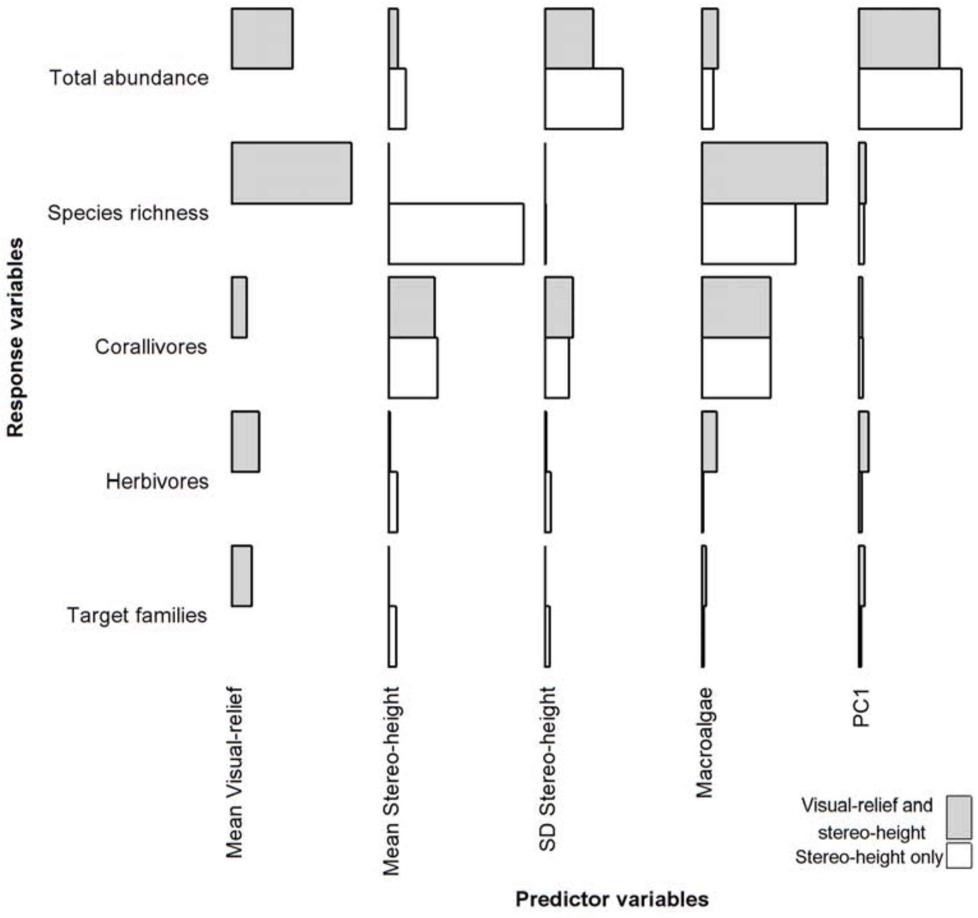

Figure 11.3.5 Relative importance of explanatory variables in predicting fish abundance and species richness in the Pilbara. Models were fitted using GAMMs both with and without visual relief being included in the analysis. Only those explanatory variables that contributed more than 5% are shown.

Table 11.3.1 Best generalized additive mixed models (GAMMs) for predicting the abundance and species richness of fish in the Pilbara. Model selection was performed twice, both with and without visual estimates of relief ('visual-relief') being included as predictor variables. The best models are those with the lowest Bayesian Information Criterion (BIC).

DEPENDENT VARIABLE	VISUAL-RELIEF INCLUDED?	DF	R²	BIC	BEST MODEL
Total Abundance	Yes	4.65	0.33	1482.76	Mean Visual-relief, PC1
	No	6.66	0.42	1483.14	SD Stereo-height, PC1
Species Richness	Yes	6.7	0.51	751.79	Mean Visual-relief, Macroalgae
	No	7.25	0.55	764.99	Mean Stereo-height, Macroalgae
Corallivores	Yes	4.37	0.28	311.07	Mean Stereo-height, Macroalgae
	No	4.37	0.28	311.07	Mean Stereo-height, Macroalgae
Herbivores	Yes	6.8	0.11	791.65	Mean Visual-relief, Macroalgae
	No	3.99	0.14	797.51	Dead coral
Target Families	Yes	3.63	0.08	563.4	Mean Visual-relief
	No	3.92	0.03	576.17	SD Stereo-height

STEREO-HEIGHT

Mean stereo-height was in the best model for predicting the abundance of corallivores regardless of whether visual-relief proxies were included as predictor variables during model selection (Table 11.3.1). Mean stereo-height accounted for ~28% of the variation in their abundance when combined with macroalgae (Figure 11.3.5; Table 11.3.1). Corallivores increased in abundance until the habitat reached an intermediate height and declined thereafter (Figure S11.3.4), suggesting they were most abundant in habitats of moderate complexity.

When visual-relief was excluded from model selection, stereo-height was present in the best model for species richness, total abundance, and the abundance of target families (Table 11.3.1). Mean stereo-height was the most important predictor for species richness and accounted for ~55% of the variation in this data when combined with macroalgae (Figure 11.3.5; Table 11.3.1). For total abundance and target families, the SD of stereo-height had the second greatest and greatest relative importance, respectively (Figure 11.3.5). The SD of stereo-height was a relatively strong predictor for total abundance, accounting for > 40% of the variation in this data (Table 11.3.1). Species richness, total abundance, and target families were all positively correlated with stereo-height (Figure S11.3.3 and Figure S11.3.5), indicating that each increased with habitat complexity. However, the relationship with target families was again weak with stereo-height accounting for < 1% of the variation in their abundance (Table 11.3.1). Since this model was a poor fit, the SD of stereo-height was not a strong predictor of the abundance of target families, despite its relative importance. Both the mean and SD of stereo-height were among the least important predictors for herbivores regardless of whether or not visual scores of relief were included in model selection (Figure 11.3.5).

PRINCIPAL COMPONENTS

PC1, which characterised macroalgae and dead coral (see Supplementary material Figure S11.3.2), was present in the best model for total abundance both with and without visual scores of relief being included in model selection (Table 11.3.1). It was a particularly strong predictor of total abundance, accounting for the greatest value of relative importance for this response variable (Figure 11.3.5). Total abundance increased relatively linearly with PC1 scores, indicating that abundance was typically low in areas dominated by macroalgae, and greater in areas dominated by dead coral (~60% variation, Figure S11.3.3). PC2, which separated pavement, rock and soft coral from sand, macroalgal and dead coral, did not appear in any of the best models and had generally low values of relative importance (Table 11.3.1; Figure 11.3.5), probably reflecting the relatively weak explanatory power (~15% of variation, see Figure S11.3.2) of this axis to adequately represent these habitats.

HABITAT CATEGORIES

Macroalgae and dead coral were the only individual habitat categories found among the best models for predicting fish abundance and species richness (Table 11.3.1). Macroalgae was the most important predictor of species richness and the abundance of corallivores, which both declined as macroalgae increased (Figure 11.3.5, S3 and S4). When visual-relief proxies were included in the model selection process, macroalgae was also present in the best model for predicting the abundance of herbivores (Table 11.3.1). Macroalgae was the second most important variable for herbivores, which declined in abundance as macroalgae cover increased (Figure 11.3.5 and S4). When visual-relief was excluded from model selection, dead coral was the most important predictor for herbivores and was therefore present in the top model for this feeding guild (Figure 11.3.5, Table 11.3.1). This was a positive relationship, with herbivores increasing in abundance as dead coral cover became more widespread (Figure S11.3.4). However, macroalgae and dead coral cover accounted for < 11% of the variation in herbivore abundance (Table 11.3.1), indicating that these models were a poor fit.

11.3.4 DISCUSSION

The method comparisons demonstrated that measuring stereo-height produces comparable estimates of habitat complexity to those obtained by measuring rugosity using the established chain-tape method, *in situ* habitat height measurements and visual scores of relief. This supports previous studies that found a significant correlation between average height and visual scores of relief on coral reefs using *in situ* field based assessments (Wilson et al. 2007). However, likely due to the much greater level of replication, this study revealed a stronger relationship between *in situ* height and visual estimates of relief compared to that found by Wilson et al. (2007), and has thus added further support for the use of rapid visual scoring techniques for estimating habitat complexity.

The stereo-height method was effective at estimating habitat complexity, however, relationships between chain-tape rugosity and stereo-height measures (mean and SD) were weaker than their *in situ* counterparts. Since measurements taken from stereo-video were generally lower than those obtained *in situ*, the stereo-height method tended to underestimate complexity particularly as the habitat became more complex. This was likely the result of limitations of the stereo-DOV field of view. As habitat complexity increases, there are a greater number of obstructions of the field of view which can confound stereo-height measurements by shadowing sections of the benthos. Therefore the stereo-height method may not account for certain structural features that other techniques pick up. Previous studies have found similar limitations when measuring complexity from stereo-photographs, which also resulted in underestimations for more rugose surfaces (Butler et al. 1998; Frost et al. 2005; Abdo et el. 2006). Imprecise estimates of complexity could reduce its predictive power, leading to either weak ecological relationships or a null result, whereby it is concluded that there is no relationship between habitat complexity and an ecological variable (Frost et al. 2005). It may be possible to develop a correction factor for the stereo-height underestimation based on thorough studies comparing video measurements with *in situ* measurements across a range of habitat types and complexity levels. Even without such correction, however, this method provides accurate relative measurements that are strongly correlated with other widely used methods (e.g.

chain-tape). By using both the stereo-height and visual-relief methods simultaneously the current study has obtained comprehensive and reliable estimates of habitat complexity that capture fine scale (and simple vertical relief) along with broader scale features such as overhangs.

While stereo-DOV transects are relatively easy and rapid to conduct in the field (Holmes et al. 2013), all quantitative measures of habitat height were time consuming. However, the stereo-height method required only slightly more time (~5 minutes) in the laboratory than the chain-tape method takes underwater (e.g. Grigg 1994; Connell and Kingsford 1998; Friedlander et al. 2003; Wilson et al. 2012) (See Supplementary Material – *Time Requirements)*. Nevertheless, the stereo-height method requires no additional time underwater compared to the chain-tape and *in situ* height methods, with the added benefit of collecting information on fish communities without any additional field effort. Where field time is a limiting factor or where stereo-DOV's are already utilised as a part of fish research or monitoring programs, the stereo-height method is a useful alternative. The stereo-height method would also be useful in circumstances where there is existing stereo-video footage with no concomitant measures of *in situ* rugosity. Indeed, our finding that relevant complexity measures can be also successfully extracted from stereo-DOV transects creates the exciting possibility that organisations with limited capacity when it comes to detailed *in situ* UVC could use stereo-DOV instead (following a one-off investment in equipment) to simultaneously collect data on fish, benthos and complexity.

Habitat complexity was an important determinant of the abundance and diversity of fish assemblages in the Pilbara. Every proxy of complexity, except the SD of visual scores of relief, was correlated with at least one of the fish assemblage parameters. This indicates that both the stereo-height and visual estimate techniques were effective in capturing aspects of complexity that were important for explaining variation in the fish assemblage. However, the mean visual score of relief was a stronger and more consistent predictor compared to stereo-height, being the most important variable in most of the best models. Similarly, Wilson et al. (2007) showed that the same visual technique (applied *in situ*) explained a significantly greater proportion of the variation in species richness than measuring habitat height *in situ*. This suggests limitations in using the stereo-height method on its own as a proxy of habitat complexity. Measures of habitat height cannot quantify certain structural features, such as the presence of caves and overhangs (McCormick 1994), which contribute to the overall complexity of benthic habitats. The visual scoring technique, however, has the advantage of accounting for such features, and can therefore provide more holistic estimates of complexity at the reef-scale (Wilson et al. 2007). However, Wilson et al. (2007) also found that visual estimates of relief were poor at characterising small scale variation in habitat complexity. This was reflected in the current study by the importance of the finer-scale stereo-height measures for predicting the abundance of corallivores, which were most abundant in habitats of intermediate height.

The best models for predicting the abundance of herbivores were generally poor, indicating that despite the high relative importance of certain variables (e.g. mean visual estimates, macroalgae, and dead coral), none were strong predictors for this group. Herbivore abundance may have been governed by other factors, such as the rate of algal production (Russ 2003), that were not covered in this study. However, it is also likely that the broad categorisation of families into feeding guilds confounded the relationships between herbivores and benthic habitat, since the dietary requirements of species can vary considerably even within the same taxonomic group. A future improvement to this study would therefore be to categorise individual species into finer resolution feeding guilds to better represent these relationships, and thus more accurately determine how structural complexity and other habitat characteristics affect the abundance of herbivores and other feeding guilds.

Mean visual scores of relief was the second strongest predictor for total abundance and species richness, which emphasises the importance of larger-scale habitat complexity for fish communities in the Pilbara. These findings are consistent with previous studies that have found strong positive relationships between complexity and fish assemblages (Luckhurst and Luckhurst 1978; McCormick 1994; Gratwicke and Speight 2005; Wilson et al. 2012). The visual scoring technique presented here has previously been correlated with the biomass of particular fish species (Jennings et al. 1996) and the abundance of fish 10-30cm TL (Wilson et al. 2007). However, unlike the current study, Wilson et al. (2007) found that it was not a strong predictor for the total abundance of fish. By using replicate scores of relief to obtain mean (and thus more representative) estimates of habitat complexity, the current study has potentially demonstrated an improvement in the visual scoring technique that can better predict the total abundance of fish and be easily applied to existing or future stereo-video samples. Mean visual scores of relief was also positively correlated with the abundance of fish families primarily targeted by extractive fishing practices, suggesting that more complex habitats in the Pilbara region are important for these species. An understanding of the natural variation in fish assemblages driven by habitat characteristics is vital for effectively detecting impacts of fishing pressure (Langlois et al. 2012). Therefore, future studies that examine effects of fishing in the Pilbara region should consider natural variation in the abundance of targeted families that is governed by habitat complexity.

This study showed that in addition to habitat complexity, benthic cover was an important determinant of the total abundance and species richness of the fish assemblage. The variation in each of these parameters among benthic habitats was strongly influenced by the percent cover of macroalgae and dead coral. This was true for the individual variables, but also through PC1 (which largely characterised these habitat categories). Abundance was typically low in areas dominated by macroalgae, and greater in areas dominated by dead coral (~60% variation, Figure S11.3.3). These relationships are consistent with those found for habitat complexity, suggesting that although the majority of corals were not live, they still currently provide much of the complex structure that is important to fish assemblages in the Pilbara. Previous studies have demonstrated positive relationships between live coral cover and the abundance and diversity of fish assemblages (Carpenter et al. 1981; Connell and Kingsford 1998; Komyakova et al. 2013). However, in the current study, the percent cover of (live) hard and soft corals was low (~8% combined) compared to dead corals (~25%) possibly due to a bleaching event in March 2013 (Lafratta et al. 2016) (Figure S11.3.6); hence the observed relationships between fish assemblages and dead coral cover (as also indicated by macroalgae) were stronger. Corallivores also declined in abundance as the percent cover of macroalgae increased, indicating that they were frequently associated with dead coral. Live coral serves as a food source for corallivores, and thus their distribution and abundance is largely determined by the amount of appropriate live coral present (Friedlander and Parish 1998). However, dead coral habitat that has retained its structural complexity may continue to support fish communities (Lindahl et al. 2001).

This study has demonstrated that the proposed stereo-height method is comparable to traditional *in situ* techniques for estimating habitat complexity, and that it is a useful tool for investigating ecological relationships. A single method is unlikely to capture all of the variation in habitat complexity (Roberts and Ormond 1987), and previous studies have recommended using multiple techniques (McCormick 1994; Friedlander and Parish 1998; Gratwicke and Speight 2005; Wilson et al. 2007). Here we have shown that both the stereo-height and visual scoring methods can be used to capture different aspects of habitat complexity simultaneously, and that together they provide useful information to model the relationships between complexity and fish assemblages. Furthermore, this study has also highlighted the importance of structurally complex habitats for supporting a greater abundance and diversity of fish assemblages in the Pilbara, which should be considered for future spatial marine management of the region.

11.3.5 ACKNOWLEDGEMENTS

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11.3.6 REFERENCES

Abdo DA, Seager JW, Harvey E S, McDonald JI, Kendrick GA, Shortis MR (2006) Efficiently measuring complex sessile epibenthic organisms using a novel photogrammetric technique. Journal of Experimental Marine Biology and Ecology 339:120-33.

Almany GR (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? OIKOS 106:275-284.

Beck MW (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. Journal of Experimental Marine Biology and Ecology 249: 29-49.

Bonaca MO, Lipej L (2005) Factors affecting habitat occupancy of fish assemblages in the Gulf of Trieste (Northern Adriatic Sea). Marine Ecology 26:42-53.

Bridge TCL, Done TJ, Beaman RJ, Friedman A, Williams SB, Pizarro O, Webster JM (2011) Topography, substratum and benthic macrofaunal relationships on a tropical mesophotic shelf margin, central Great Barrier Reef, Australia. Coral Reefs 30:143-153.

Butler JB, Lane SN, Chandler JH (1998) Assessment of dem quality for characterizing surface roughness using close range digital photogrammetry. *The Photogrammetric Record*, 16, 271-291.

Carpenter KE, Midat RI, Albaladejo VD, Corpuz VT (1981) The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. Proceedings of the 4th International Coral Reef Symposium, Vol. 2. (eds Gomez ED, Birkeland CE, Buddemeier RW, Johannes RE, Marsh Jr. JA, Tsuda RT), pp. 495-502. Marine Science Center, University of the Philippines, Manilla, Philippines.

Connell SD, Kingsford MJ (1998) Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. Coral Reefs 17:49-57.

Deming WE (1964) Statistical adjustment of data. Dover Publications, New York.

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, et al. (2014). Global conservation outcomes depend on marine protected areas with five key features. Nature 506(7487):216–20.

Freckleton RP (2011) Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. Behavioural Ecology and Sociobiology 65:91-101.

Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian Archipelago. Coral Reefs 22:291-305.

Friedlander AM, Parish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224:1-30.

Friedman A, Pizarro O, Williams SB, Johnson-Roberson M (2012) Multi-Scale Measures of Rugosity, Slope and Aspect from Benthic Stereo Image Reconstructions. PLoS ONE 7 (12).

Froese F, Pauly D eds (2014) FishBase. World Wide Web electronic publication. URL http:/www.fishbase.org

Frost NJ, Burrows MT, Johnson MP, Hanley ME, Hawkins SJ (2005) Measuring surface complexity in ecological studies. Limnology and Oceanography: Methods 3:203-210.

Giakoumi S, Kokkoris GD (2013) Effects of habitat and substrate complexity on shallow sublittoral fish assemblages in the Cyclades Archipelago, North-eastern Mediterranean Sea. Mediterranean Marine Science 14:58-68.

Goetze JS, Jupiter SD, Langlois TJ, Wilson SK, Harvey ES, Bond T, Naisilisili W (2015) Diver operated video most accurately detects the impacts of fishing within periodically harvested closures. Journal of Experimental Marine Biology and Ecology 462:74-84.

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809-2815.

Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650-667.

Grigg RW (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. Marine Ecology Progress Series 103:25-34.

Harborne AR, Mumby PJ, Ferrari R (2012). The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. Environmental Biology of Fishes 94(2):431–442.

Harman N, Harvey ES, Kendrick GA (2003) Differences in fish assemblages from different reef habitats at Hamelin Bay, south-western Australia. Marine and Freshwater Research 54:177-184.

Harvey ES, Shortis M (1995) A system for stereo-video measurement of sub-tidal organisms. Marine Technology Society Journal 29:10-22.

Harvey E, Fletcher D, Shortis M (2001) A comparison of the precision and accuracy of estimates of reef-fish lengths determined visually by divers with estimates produced by a stereo-video system. Fishery Bulletin 99:63-71.

Hastie T, Tibshirani R (1986) Generalized additive models. Statistical Science 1:297-310.

Holmes TH, Wilson SK, Travers MJ, Langlois TJ, Evans RD, Moore GI, Douglas RA, Shedrawi G, Harvey ES, Hickey K (2013) A comparison of visual- and stereo-video based fish community assessment methods in tropical and temperate marine waters of Western Australia. Limnology and Oceanography: Methods 11:337-350.

Jenkins GP, Wheatley MJ (1998) The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: Comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. Journal of Experimental Marine Biology and Ecology 221:147-172.

Jennings S, Boulle DP, Polunin NVC (1996) Habitat correlates of the distribution and biomass of Seychelles reef fishes. Environmental Biology of Fishes 46:15-25.

Komyakova V, Munday PL, Jones GP (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. PLoS ONE 8(12): e83178. doi:10.1371/journal.pone.0083178.

Lafratta A, Fromont J, Speare P, Schönberg CHL (2016). Coral bleaching in turbid waters of north-western Australia. Marine and Freshwater Research.

Langlois TJ, Harvey ES, Meeuwig JJ (2012) Strong direct and inconsistent indirect effects of fishing found using stereo-video: Testing indicators from fisheries closures. Ecological Indicators 23:524-534.

Lin X, Zhang D (1999) Inference in generalized additive mixed models by using smoothing splines. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 61:381-400.

Lindahl U, Öhman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. Marine Pollution Bulletin 42(2):127–131.

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49:317-323.

McCormick MI (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Marine Ecology Progress Series 112:87-96.

Moore CH, Harvey ES, Van Niel KP (2009) Spatial prediction of demersal fish distributions: enhancing our understanding of species-environment relationships. ICES Journal of Marine Science 66:2068-2075.

O’hara RB, Kotze DJ (2010). Do not log-transform count data. Methods in Ecology and Evolution 1:118-122.

Ohman MC, Rajasuriya A (1998) Relationships between habitat structure and fish communities on coral and sandstone reefs. Environmental Biology of Fishes 53:19-31.

Parish FA, Boland RC (2004) Habitat and reef-fish assemblages of banks in the Northwestern Hawaiian Islands. Marine Biology 144:1065-1073.

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 100:167-176.

R Development Core Team (2015) R: A language and environment for statistical computing (version 3.2.2). R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org

Risk MJ (1972) Fish diversity on a coral reef in the Virgin Islands. Atoll Research Bulletin 153:1-6.

Roberts CM, Ormond RF (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Marine Ecology Progress Series 41:1-8.

Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. Coral Reefs 22:63-67.

SeaGIS Pty Ltd (2014) EventMeasure (Stereo). SeaGIS Pty Ltd, Bacchus Marsh. URL http:/www.seaGIS.com.au

Shedrawi G, Harvey ES, McLean DL, Prince J, Bellchambers LM, Newman SJ (2014) Evaluation of the effect of closed areas on a unique and shallow water coral reef fish assemblage reveals complex responses. Coral Reefs 33:579-591.

Smale DA, Kendrick GA, Harvey ES, Langlois TJ, Hovey RK, Van Niel KP, Waddington KI, Bellchambers LM, Pember MB, Babcock RC, Vanderklift MA, Thomson DP, Jakuba MV, Pizarro O, Williams SB (2012) Regional-scale benthic monitoring for ecosystem-based fisheries management (EBFM) using an autonomous underwater vehicle (AUV). ICES Journal of Marine Science 69:1108–1118.

Toller W, Debrot AO, Vermeij MJA, Hoetjes PC (2010) Reef fishes of Saba Bank, Netherlands Antilles: Assemblage structure across a gradient of habitat types. PLoS ONE 5(5): e9207. doi:10.1371/journal.pone.0009207.

Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer, New York.

Williams GJ, Cameron MJ, Turner JR (2008) Quantitative characterisation of reef fish diversity among nearshore habitats in a northeastern New Zealand marine reserve. New Zealand Journal of Marine and Freshwater Research 42:33-46.

Williamson PC, Sumner NR, Malseed BE (2006) A 12-month survey of recreational fishing in the Pilbara region of Western Australia during 1999-2000. Fisheries Research Report No. 153, Department of Fisheries, Western Australia.

Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. Marine Ecology Progress Series 257:209-221.

Wilson SK, Babcock RC, Fisher R, Holmes TH, Moore JAY, Thomson DP (2012) Relative and combined effects of habitat and fishing on reef fish communities across a limited fishing gradient at Ningaloo. Marine Environmental Research 81:1-11.

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151:1069-1076.

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 73:3-36.

Xilisoft Corporation (2014) Xilisoft Video Converter Ultimate 6. URL http://www.xilisoft.com [accessed December 2014]

11.3.7 SUPPLEMENTARY MATERIAL

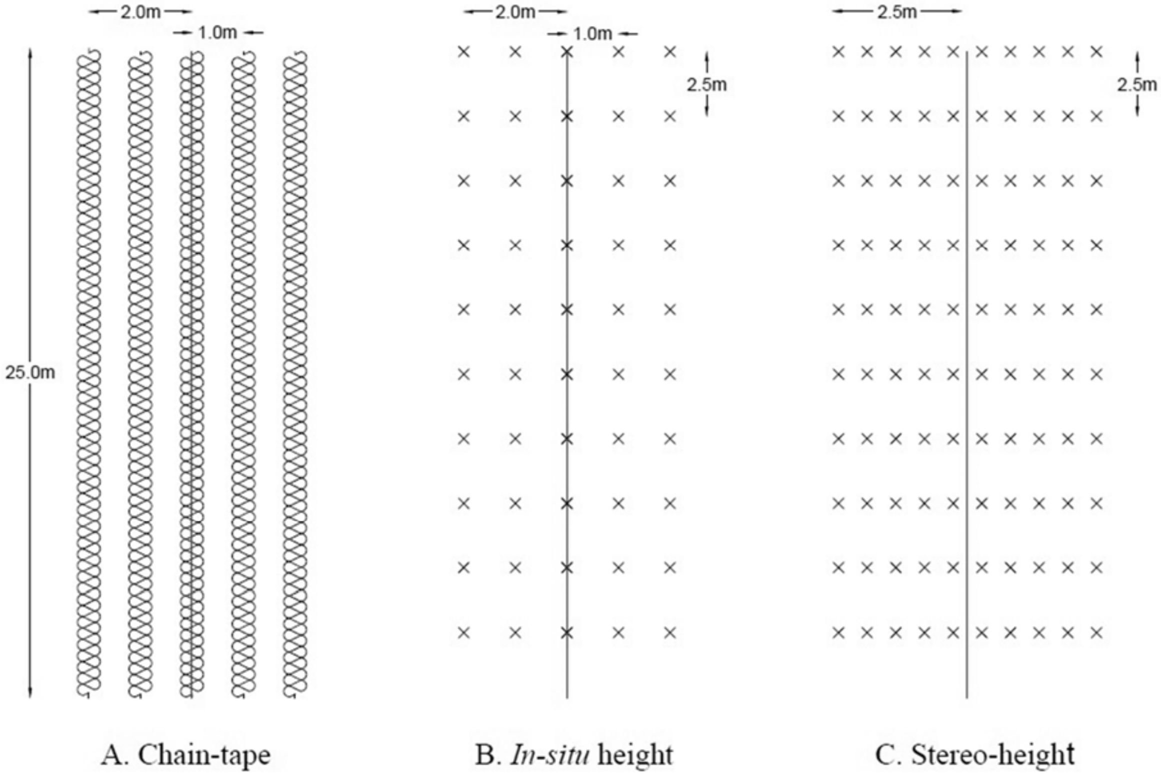

Figure S11.3.1 The sampling design of each method used in the validation study to measure structural complexity: (A) rugosity measured using the chain-tape method; (B) habitat height measured *in situ*, and; (C) habitat height measured from stereo-video. The positions of transects, chains, and height measurements are represented by solid lines, wavy lines, and crosses respectively.

Time requirements

Paired t-tests revealed significant differences in the time taken to measure complexity between each of the three methods (Table S11.3.1). On average, measuring habitat height *in situ* required the least amount of time per transect (mean 11.0 ± 2.6 SE mins); whereas obtaining these measurements from stereo-video was the most time consuming method (31.5 ± 4.3 mins). Although it was significantly quicker to estimate rugosity using the chain-tape method (26.8 ± 3.2 mins) compared to measuring height from stereo-video, the difference between these methods was small (~5 min; Table S11.3.1). However, these results should be interpreted cautiously, as this study was carried out on land and results may differ if sampling was conducted underwater.

Table S11.3.1 Results of paired t-test comparisons between the times taken to complete each method of measuring structural complexity. The lower left of the table shows t values and the upper right (filled) of the table shows P values. Df = 9 for each test.

	CHAIN-TAPE RUGOSITY	*IN SITU* HEIGHT	STEREO-HEIGHT
Chain-tape rugosity	—	< 0.001	0.046
***In situ* height**	6.382	—	< 0.001
Stereo-height	-2.312	-7.186	—

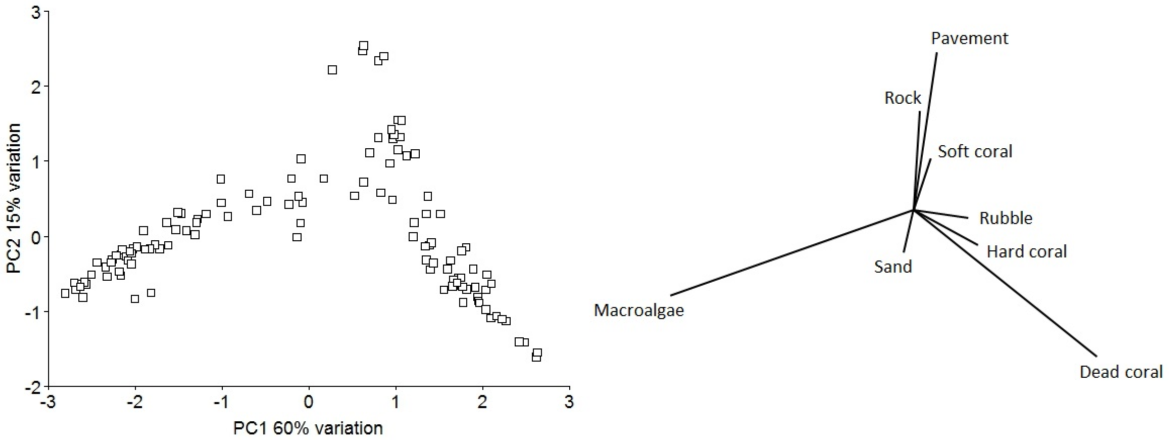

Figure S11.3.2 Bi-plot of the first two components of a principal components analysis (PCA) used to characterise benthic composition among transects.

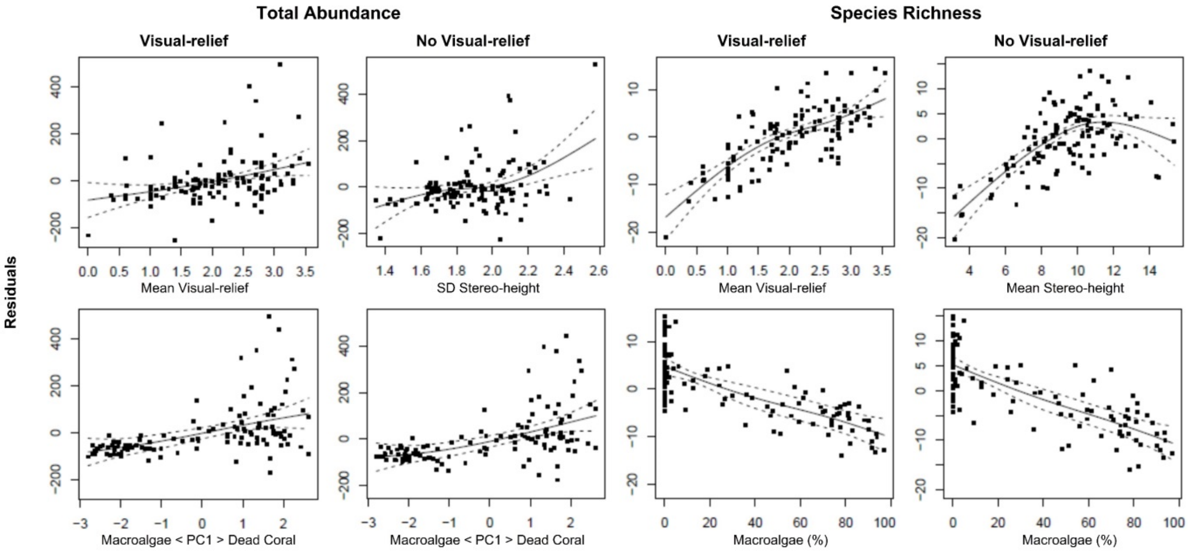

Figure S11.3.3 The residual total abundance and species richness of fish in the Pilbara relative to the most important predictor variables (Table 11.3.1). Models were fitted using GAMMs both with and without visual-relief being included in the analysis. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 × SE of the estimate.

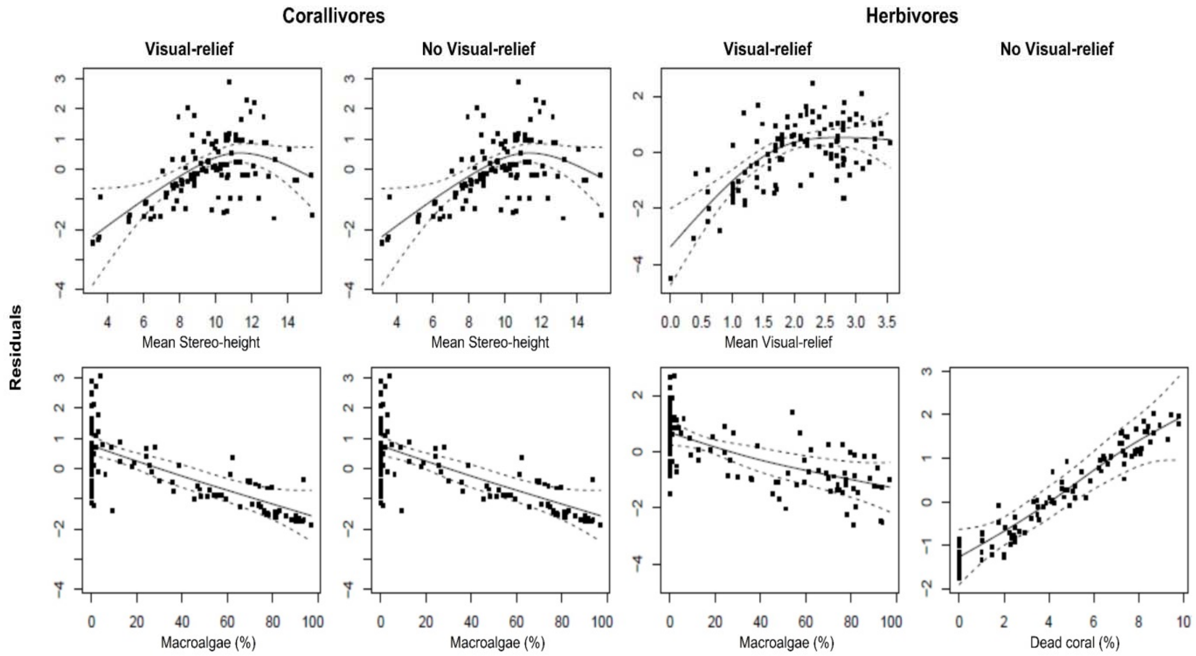

Figure S11.3.4 The residual abundance of corallivores and herbivores in the Pilbara relative to the most important predictor variables (Table 11.3.1). Models were fitted using GAMMs both with and without visual-relief being included in the analysis. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 × SE of the estimate.

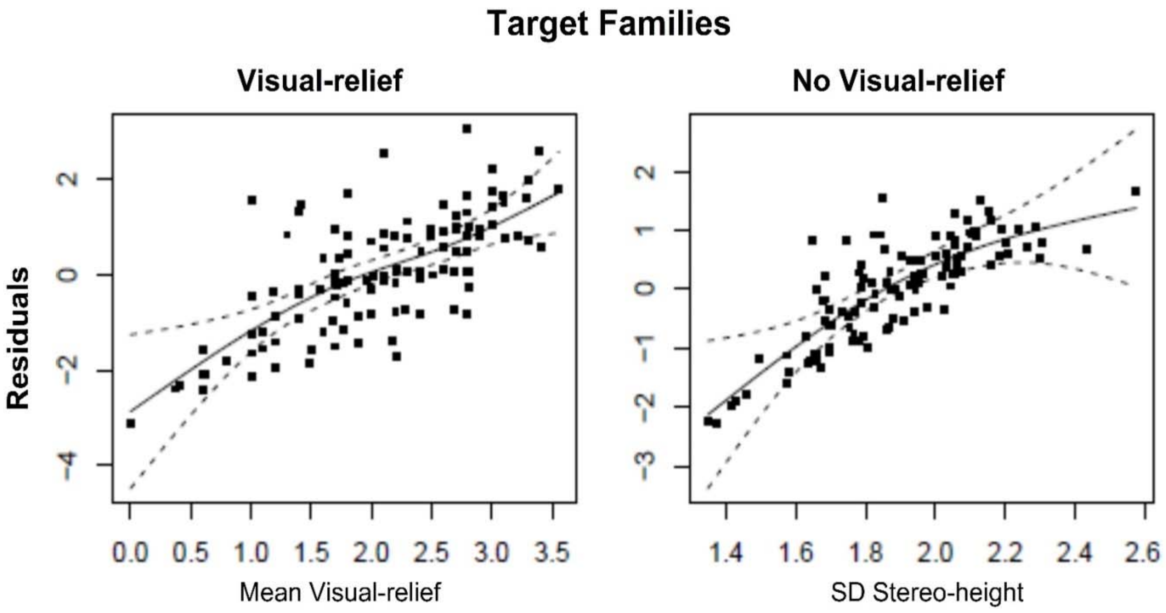

Figure S11.3.5 The residual abundance of target fish families in the Pilbara relative to the most important predictor variables (Table 11.3.1). Models were fitted using GAMMs both with and without visual-relief being included in the analysis. The solid black line represents the estimated smoothing curve and dashed lines represent ±2 × SE of the estimate.

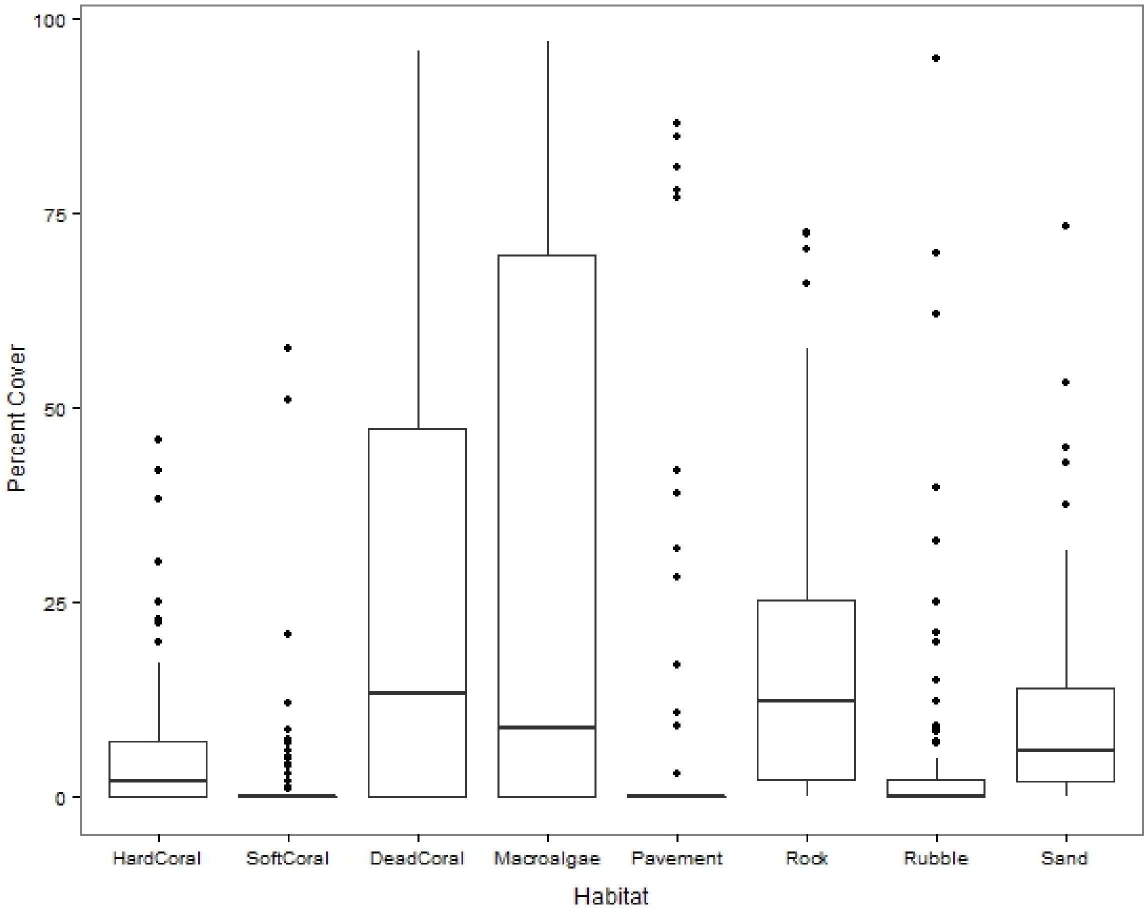

Figure S11.3.6 Percent cover of each habitat type scored from stereo-DOVs.

11.4 Suspended sediment negatively affects herbivorous scrapers and planktivorous omnivores on coral reefs in northwest Australia

Authors: Moustaka M, Langlois T, McLean D, Bond T, Fisher R, Fearns R, Dorji P, Evans R.

Submitted to Oecologia.

ABSTRACT

This study investigated the relationships between short and long term suspended sediment regimes and fine-scale habitat composition on coral reef fish across a cross-shelf turbidity gradient in the nearshore Pilbara region of Western Australia. Underwater visual census was used to sample the fish assemblage and quantify habitat composition and complexity at 16 sites across the turbidity gradient. Generalised additive mixed models were used to explore the relationships between broad-scale environmental variables (including suspended sediment), fine-scale habitat variables, and fish assemblage metrics. Species richness declined with increasing levels of turbidity. Two feeding guilds (planktivorous omnivores and herbivorous scrapers) decreased in abundance at high turbidity sites. Total biomass of herbivorous scrapers was lower at turbid sites, whilst the biomass of planktivorous omnivores was not related to any of the predictor variables. Changes in the abundance, biomass, and behaviour of these functional groups can have severe consequences for the resilience and recovery of coral reefs. Whilst inshore coral reef communities generally consist of species with higher tolerance to suspended sediments, they are less likely to recover from anomalous disturbance events, such as thermal stress, due to lower levels of functional redundancy than their offshore counterparts. This study identified two key functional groups of fish that are vulnerable to elevated suspended sediment loads. The direct effects of long-term elevation of suspended sediment on functional groups of fish needs to be considered when designing management plans for anthropogenic activities that will influence the suspended sediment regime of coastal regions where coral reef communities exist.

11.4.1 INTRODUCTION

Understanding the influence of different environmental drivers on fish assemblage composition and structure is essential when predicting the influence that, and designing management plans for, natural or anthropogenically-induced variation in environmental conditions may have on marine ecosystems (Gil et al. 2016; Gilby et al. 2016). One such environmental driver is suspended sediment, which increases sedimentation and enhances the attenuation of light, reducing the amount of photosynthetically active radiation reaching the benthos (Suedel et al. 2008). The detrimental effects of suspended sediment on coral reefs are well known and unequivocal, including large-scale mortality caused by smothering, reduced growth rates, range contraction, and decreased larval settlement (De'ath and Fabricius 2010; Kemp et al. 2011; Erftemeijer et al. 2012). As habitat composition, complexity, and connectivity largely determine the structure and composition of fish assemblages, degradation of coral reef habitat caused by suspended sediment negatively impacts dependent organisms through habitat loss, resulting in decreased species richness and abundance of fish (Jones et al. 2004; Wilson et al. 2006; Pittman and Brown 2011; Wenger et al. 2017).

Conversely, the direct effects of suspended sediment on coral reef fish are poorly understood and are difficult to isolate from effects attributed to decreased habitat quality or availability (Wenger et al. 2017). Small-scale aquaria studies have found evidence of decreased feeding success, predator avoidance, reproductive success, and impaired habitat choice in coral reef fish in response to elevated suspended sediment (Wenger and McCormick 2013; Collin and Hart 2015; Jones et al. 2016). Feeding guilds have exhibited differential responses to elevated turbidity, with planktivorous omnivores and herbivorous scrapers consistently exhibiting decreased feeding success in high turbidity conditions (Wilber and Clarke 2001; Bellwood and Fulton 2008; Bonaldo and Bellwood 2008; Madin et al. 2010; Wenger et al. 2011; Goatley and Bellwood 2012; Wenger et al. 2012; Johansen and Jones 2013; O'Connor et al. 2015; Goatley et al. 2016). Negative physiological changes have also been observed (particularly in juvenile individuals), including negative changes in mortality and growth rates, gill damage, and decreased reproductive success (Wenger and McCormick 2013; Hess et al. 2015). However, many of these adverse effects caused by elevated suspended sediment focused on one functional group are yet to be consistently observed in field settings (and have not been reported in Western Australia), and the findings of aquaria studies are difficult to extrapolate into realistic management strategies.

Terrestrial runoff and riverine outputs combined with wave, wind, and tidal activity can create cross-shelf gradients of suspended sediment load in coastal waters (Maella et al. 2007). This continuum of high turbidity inshore to low turbidity further offshore, influences the abundance and diversity of fish. Several studies have reported increasing species richness and abundance moving offshore particularly of small-bodied, juvenile, and herbivorous fish species (Maella et al. 2007; Malcolm et al. 2010; Bejarano and Appeldoorn 2013). However, these trends are not universal with Fabricius et al. (2005) reporting similar species richness and decreasing herbivore density at offshore sites. As species play different functional roles in key ecosystem processes, changes in fish assemblages across turbidity gradients will impact ecosystem resilience and capacity for recovery from disturbance (Folke 2006; Best et al. 2015; Nash et al. 2016). These differential responses highlight the need for location-specific knowledge of the influences of suspended sediment on functional groups, or feeding guilds, when designing management plans.

The nearshore waters of the Pilbara region of Western Australia are a prime example of a cross-shelf suspended sediment gradient and provide an ideal opportunity to assess the variation in fish assemblage driven by suspended sediment (Gilmour et al. 2006). In contrast to locations like the Great Barrier Reef (Cooper et al. 2007; Kroon 2009), the Pilbara catchment is arid with very little agriculture, so therefore investigations of sediment effects on reef inhabitants in the Pilbara are less complicated by the pollutants ensuant with agricultural practices. Daily mean turbidity ranges between 1-6 nephelometric turbidity units (NTU), but can reach 80 NTU during natural disturbance events, such as cyclones and intense seasonal rainfall, which frequently occur in the study region (Gilmour et al. 2006). In addition to frequent natural disturbance events, the nearshore Pilbara region experiences high levels of anthropogenic disturbance due to coastal development, shipping activity, construction, and dredging associated with Liquified Natural Gas (LNG) processing in the Wheatstone gas field and maintenance dredging of the existing shipping channels (Crain et al. 2009; McLean et al. 2016).

This study utilised a combination of methods to investigate the relationships between fish assemblage structure, habitat composition and complexity, and suspended sediment in the nearshore Pilbara region. Analyses were based on the following hypotheses: If suspended sediment levels decrease moving offshore across the shelf 1) the habitat composition (particularly coverage of consolidated substrate, macroalgae, and stony corals) will change markedly and will be correlated to changes in fish assemblages; 2) the species richness, total abundance, and total biomass of fish assemblages will increase; 3) planktivorous omnivore and herbivorous scraper abundance and biomass will increase.

11.4.2 MATERIALS AND METHODS

Study location

This study was conducted throughout the western Pilbara region off Onslow, Western Australia (Figure 11.4.1). Sampling spanned approximately 120 km between Fly Island (114°5’51.3 E, 21°8’05.98 S) and West Island (115°4’49.79 E, 21°3’09.76 S). The Pilbara is a tropical region with a component of subtropical species and an array of benthic habitats including coral reefs, macroalgal beds, filter feeder communities, seagrass meadows, and mangroves (Hutchins 2001; McLean et al. 2016). The 16 sampling sites were selected based on the location of compliance monitoring buoys that were placed throughout the region as part of dredging impact monitoring for the Wheatstone project and were distributed across the natural cross-shelf suspended sediment gradient (Figure 11.4.1).

Underwater visual census

An underwater visual census (UVC) was conducted over five days in January 2016, with six stationary five-minute UVC point counts being conducted at each of the 16 sites following methods used by Lowry et al. (2012). The six point count locations were haphazardly chosen across the reef area, with a minimum of 10 m between point count boundaries. A single stationary diver recorded the species, number, and approximate length of all fish sighted within a 3.5 m radius in all directions. A total of 96 point counts were conducted across the 16 sites (Figure 11.4.1).

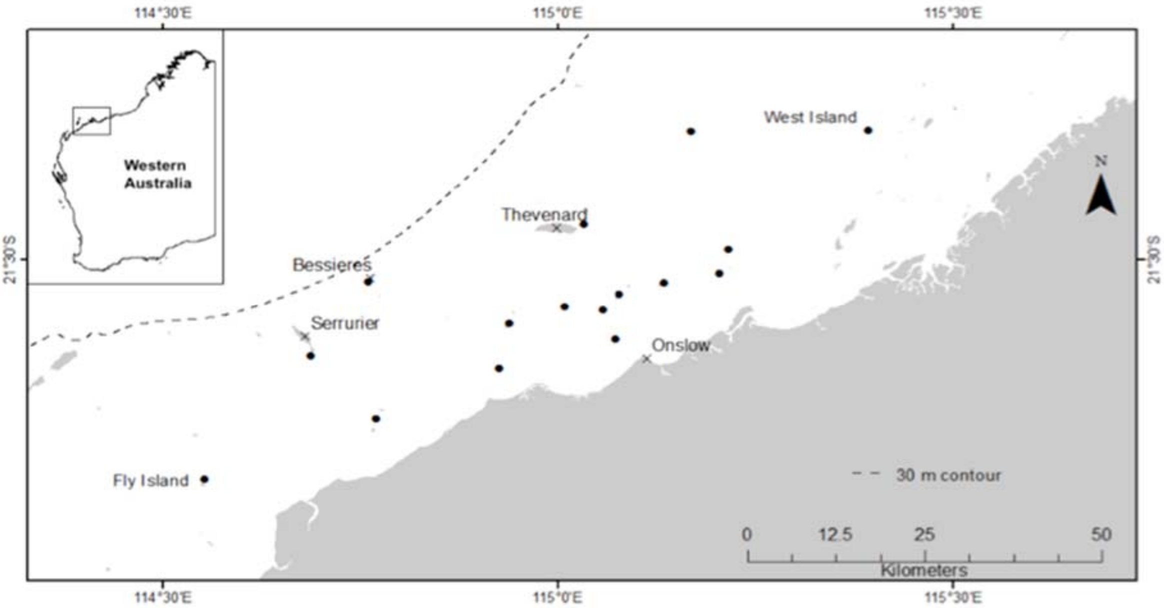

Figure 11.4.1. Location of sampling sites. The 30 m depth isobar is indicated by the dashed line.

Fine-scale habitat predictors

As this study aimed to investigate the influence of broad-scale environmental variables, point count replicates were performed across similar coral reef habitats to minimise the influence of fine-scale habitat variability (i.e. percentage cover of substrate and structural relief). However, as it was impossible to completely control for habitat variation, diver operated stereo-video (stereo-DOV) was used to quantify the habitat at each of the point count replicates (after Bennett et al. 2016). After each point count was completed, a diver took a short 360̊ video, with the stereo-DOV angled slightly downwards to capture the habitat within the UVC radius. Still habitat images were taken every 90̊ from each 360̊ stereo-DOV video. Quantification of habitat was conducted using the TransectMeasure^{TM} software and the CATAMI classification scheme as per McLean et al. (2016); Althaus et al. (2013); SeaGIS Pty Ltd (2016). Habitat was broadly classified as stony coral (e.g. *Acropora*, Tabulate, and *Porites* corals), soft coral, consolidated substrate (rock), unconsolidated substrate (sand/rubble), macroalgae, reef (combined cover of consolidated substrate + stony corals + macroalgae), sponges, or open water (Althaus et al. 2013). Each fine-scale habitat variable was quantified as 'percent cover' of the replicate. Relief was quantified on a scale of 1-5, with 1 indicating a flat surface and 5 representing a vertical surface or very steep overhang, taking into account rugosity and structural complexity (Evans and Russ 2004).

Broad-scale predictor variables

Water quality monitoring buoys were in place between May 2011 and May 2015 and collected data on turbidity (NTU), SST, salinity, and pressure at 30-minute intervals (Chevron 2012). Turbidity data from the water quality loggers was visually inspected to ensure data integrity and spurious turbidity results, such as spikes and zero readings were removed. For further details of data processing and quality control steps see Jones et al. (2015).

MODIS band 1 data and a semi-analytic sediment model (SASM) developed by Dorji et al. (2016), calibrated using TSS concentration and bio-optical properties of the coastal waters of the Onslow region, were used to derive estimates of TSS concentration for the study sites. The SASM model has been shown to produce estimates of the concentration of TSS with reasonable accuracy and at adequate spatial and temporal resolution to be of use for coastal water quality monitoring (Dorji and Fearns 2016). For further details of TSS calculations see Supplementary material.

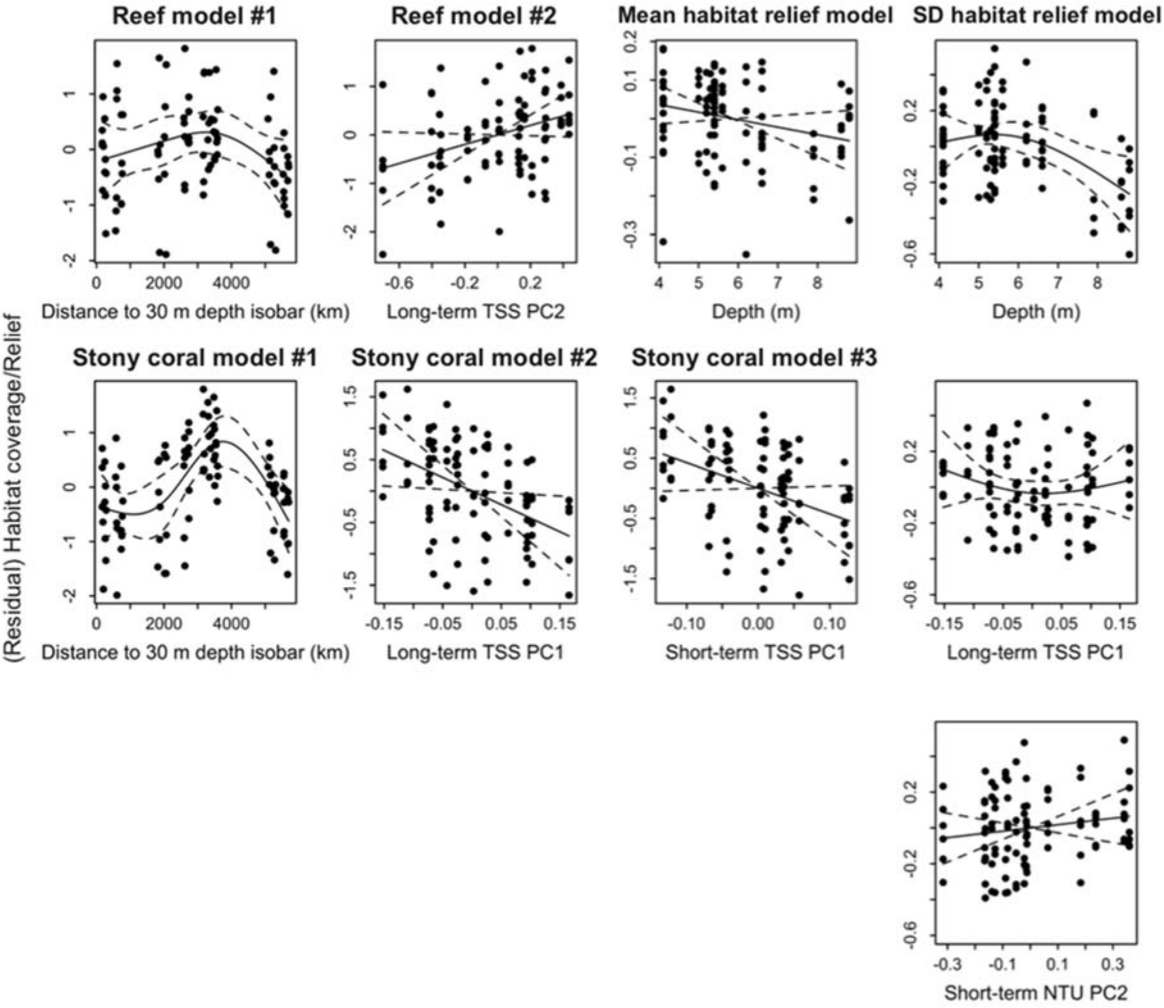

Figure 11.4.2 Partial residual plots of proportional coverage of reef and stony coral habitat, and mean and standard deviation (SD) of habitat relief of fine-scale habitat relative to the explanatory variables in their best models (Table 11.4.1). The solid black line represents the estimated smoothing curve and dashed lines represent ± 2×SE of the estimate. Plots are not presented where model performance was weak.

Due to the large temporal scale over which the TSS and NTU data were recorded, the turbidity profile for each site was characterised by the first two axes of a principal coordinates analysis (PCoA) generated using the pco function from the ecodist package in R based on the TSS data (Figure S11.4.1; R Core Team 2017). PCoA's were conducted on the TSS data for both the long-term (pre-NTU logger deployment) and short-term (whilst NTU loggers were deployed) datasets. The first axis (PC1) accounted for 90.2%, and 93.3%, of the variability for the long-term TSS and short-term TSS respectively, and in both cases this was strongly positively correlated with high values of turbidity across all time scales and percentile summaries (Figure 11.4.2, Figure 11.4.3). As such, the PC1 axes for TSS characterise the differences in the general suspended sediment regime between sites, with higher positive scores indicating high turbidity. The second axes (PC2) accounted for 6.6%, and 4.1% of the variability for the long-term TSS and short-term TSS, respectively (Figure 11.4.2, Figure 11.4.3), and in both cases was strongly negatively correlated with high values of TSS across short time frames, but only for the extreme percentiles (Figure 11.4.2, Figure 11.4.3). Therefore, low values of PC2 indicate the occurrence of extreme, discrete turbidity events. The first axis (PC1) for short-term in situ turbidity (NTU) represented 90.3% of variability and was strongly negatively correlated with high values of turbidity across all time scales and percentile summaries (Figure 11.4.3B). Therefore, for short-term in situ turbidity (NTU), high values of PC1 indicate less turbid water quality conditions. The second axis (PC2) for short-term in situ turbidity represented 5.9% of the remaining variation, with positive values indicating greater frequency or intensity of discrete spikes in turbidity (Figure 11.4.3B). For detailed methods and plotted PCoA's see Supplementary material – Methods and Figure S11.4.1, Figure S11.4.2, Figure S11.4.3.

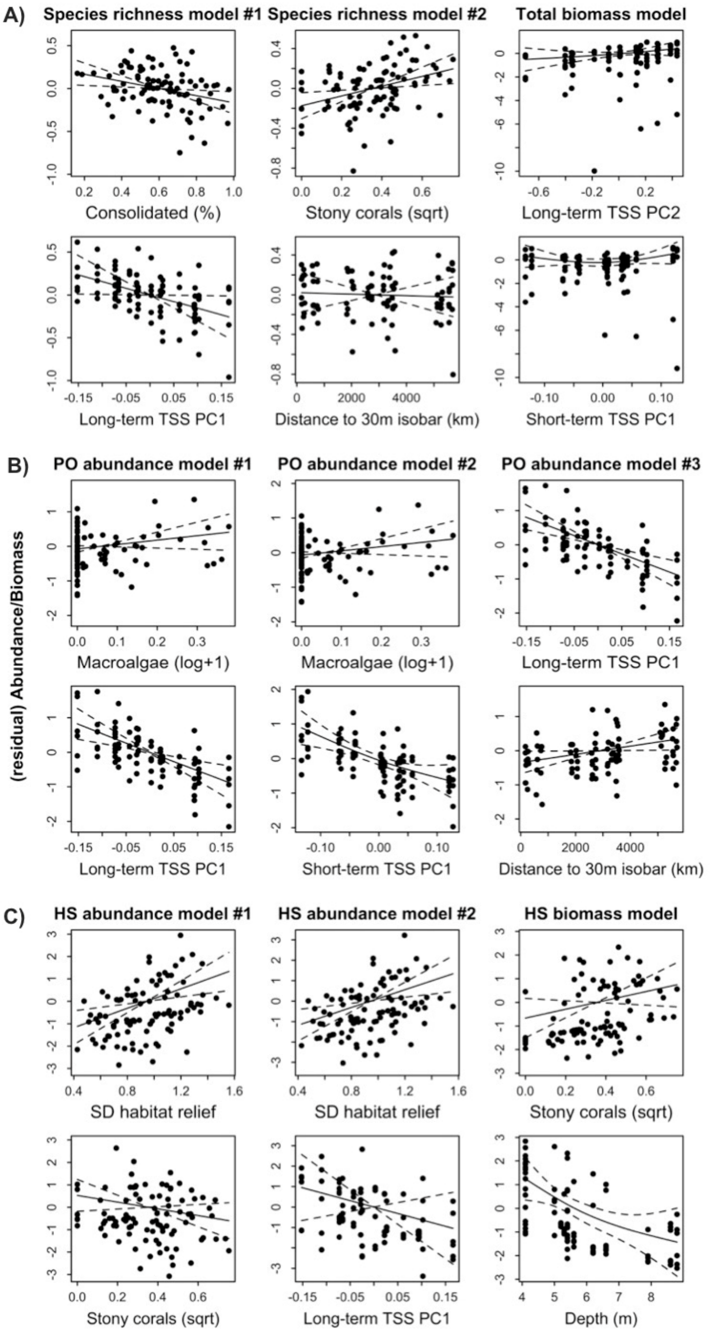

Figure 11.4.3 Partial residual plots of A) species richness and total biomass, B) abundance of planktivorous omnivores (PO), and C) abundance and total biomass of herbivorous scrapers (HS) of fish assemblages relative to the explanatory variables in their best models (Table 11.4.1). The solid black line represents the estimated smoothing curve and dashed lines represent ± 2×SE of the estimate. Plots are not presented where model performance was weak.

To complete the set of environmental variables, distance to the 30 m depth isobar was generated using bathymetry data from NOAA (https://www.ngdc.noaa.gov/mgg/global/) and was used as an indicator of oceanic conditions (Amante and Eakins 2009). Therefore, the full set of broad-scale environmental variables included; depth, distance to the 30 m contours two long-term and short-term TSS Principle coordinate analysis axes, and a single NTU (turbidity) principal coordinate analysis axis. Data checking and analysis was conducted using scripts provided in Langlois et al. (2015) using the R language for statistical computing (R Development Core Team 2015). Information on the feeding guild of each species was retrieved from Fishbase (Froese and Pauly 2016) and cross-checked with records from the Department of Biodiversity, Conservation and Attractions Marine Science Monitoring Program. Biomass was calculated using length-weight relationships retrieved from Fishbase (Froese and Pauly 2016).

Data Analysis

The influence of both fine-scale habitat and broad-scale environmental variables on fish assemblage were analysed using generalised additive mixed models (GAMMs; Wood and Scheipl 2015). GAMMs use a sum of smooth functions to model covariate effects, allowing for more flexible functional dependence of the response variable on the covariates, without requiring prior assumptions about the parametric form of the relationship. Site was included as a random effect to increase the inferential power of the models and to account for overdispersion and correlation in the data (Harrison 2014). A full-subset method was used to fit models of all possible combinations of variables (Fisher et al, in review). Models were limited to three explanatory variables and models containing variables with correlations exceeding 0.28 were excluded to avoid issues with colinearity among predictor variables, which can cause overfitting and difficulty interpreting results (Graham et al. 2005). The most parsimonious model(s) (i.e. had the fewest predictor variables) in the subset of top models (those within 2AICc of that with the lowest AICC, Burnham and Anderson 2002) was selected as the best model. R2 values were used to provide an indication of the predictive power of the model. Therefore, whilst this study was primarily concerned with investigating the relationship between suspended sediment levels and the structure and composition of the fish assemblage in the Pilbara, both broad-scale environmental (depth, distance to the 30 m depth isobar, and TSS/turbidity PCoAs) and fine-scale habitat (composition of biota and complexity) were included as predictor variables in models. Additionally, fine-scale habitat data was modelled against broad-scale environmental predictors to identify any potentially confounding variables.

Models were run on abundance and biomass of common (present in >20% of samples) families, feeding guilds, and unique species. Prior to analysis several predictor variables were removed due to collinearity >0.8, and predictor variables were plotted, assessed for normal distributions, and transformed accordingly (see Supplementary material for details). Fish data was not transformed as generalised modelling and selection of an appropriate error distribution (in this case a Tweedie distribution) accounts for non-normal distribution of data (McLean et al. 2016). Tweedie error distributions were selected for all analyses, except the relationship between fine-scale habitat and broad-scale environmental predictor variables, due to their capacity to adequately model zero-rich data (Shono 2008). For analyses of the relationship between fine-scale habitat composition and broad-scale environmental predictors, fine-scale habitat data was transformed using a logit transformation and models used a Gaussian error distribution, due to the nature of the data (proportional cover, which is bounded by 0 and 1). All statistical analyses were conducted using the R language for statistical computing and the gamm4 (version 0.3) and mgcv (version 12) packages (Wood and Scheipl 2015; R Core Team 2017).

11.4.3 RESULTS

Depth was the most consistent descriptor of variation in fine-scale habitat relief (rugosity), with habitat relief typically lower as depth increased (Figure 11.4.2, Table 11.4.1, Table S11.4.1). Null models were the best representation of variation in macroalgae and consolidated substrate coverage, indicating that none of the predictor variables explained the variation in coverage (Figure 11.4.2, Table 11.4.1). Whilst distance to the 30m isobar was present in one of the top models for reef ('Reef #1), no directional relationship was present (Figure 11.4.2, Table 11.4.1). Conversely, low frequency of anomalous turbidity events (high values for long-term TSS PC2), were linked to high percentage cover of reef in the second top model for reef ('Reef #2; Figure 11.4.2, Table 11.4.1). Lower percentage cover of stony corals was present at very high turbidity sites based on both long-term and short-term metrics, however these results should be interpreted cautiously as the null model was just outside the top models (models with an AIC value less than 2; delta AIC = 2.08; Figure 11.4.2, Table 11.4.1, Table S11.4.2).

Table 11.4.1. Best generalised additive mixed models (GAMMs) for predicting the relief of substrate (mean and standard deviation [SD]) and percent cover of fine-scale habitat type; the total species richness, abundance, biomass of fish assemblages, total abundance and biomass of planktivorous omnivores (PO) and herbivorous scrapers (HS) in the fish assemblages of the Pilbara. The Akaike information criterion (corrected for finite sample sizes; AICc), delta AIC (AIC differences), model weight (wi.AICc), and the coefficient of determination (R^2) were also reported. All models within two units of the lowest AICc value are reported in Table S11.4.3.

DEPENDENT VARIABLE	AICC	ΔAICC	WI.AICC	R^2	BEST MODEL
Mean habitat relief	108.16	0	0.13	0.3	Depth
SD habitat relief	-20.32	0	0.84	0.4	Depth, Long-term TSS PC1 Short-term NTU PC2
Consolidated	-78.7	0.7	0.04	1	Null
Macroalgae	-187.27	0	0.03	0.7	Null
Stony corals #1	-165.28	1.64	0.02	0.6	Distance to 30 m
Stony corals #2	-165.15	1.77	0.02	0.6	Long-term TSS PC1
Stony corals #3	-165.02	1.9	0.02	0.6	Short-term TSS PC1
Reef #1	-112.18	1.98	0.02	0.4	Distance to 30 m
Reef #2	-122.2	1.96	0.02	0.4	Long-term TSS PC2
Species richness #1	546.95	0.92	0.06	0.6	Consolidated, Long-term TSS PC1
Species richness #2	547.74	1.71	0.04	0.6	Stony corals (sqrt), Distance to 30 m
Total abundance	996.73	0.57	0.02	0.5	Null
Total biomass	225.53	0.44	0.15	0.6	Long-term TSS PC2, Short-term TSS PC1
PO abundance #1	617.83	0	0.04	0.6	Macroalgae(log+1), Long-term TSS PC1
PO abundance #2	617.88	0.05	0.04	0.6	Macroalgae(log+1), Short-term TSS PC1
PO abundance #3	619.7	1.87	0.02	0.5	Long-term TSS PC1, Distance to 30 m
PO biomass	-169.88	1.22	0.02	0.1	Null
HS abundance #1	389.66	0.95	0.06	0.6	SD habitat relief, Stony corals (sqrt)
HS abundance #2	389.83	1.11	0.05	0.6	SD habitat relief, Long-term TSS PC1
HS biomass	228.27	0	0.46	0.4	Stony corals (sqrt), Depth, Short-term TSS PC2

The 96 point counts conducted yielded a total of 8,067 individuals from 126 species and 31 families (Table S11.4.2). Species richness of fish assemblages increased at sites with lower levels of long-term TSS and higher stony coral cover, however as percentage cover of stony corals is negatively correlated to long-term TSS the 'Species Richness #2 model may simply represent a secondary effect of long-term TSS (‘Species Richness #1 model; Figure 11.4.3A, Table 11.4.1). Top models for species richness also suggested a negative relationship with consolidated substrate and whilst distance to the 30 m depth isobar was an important predictor variable, no directional relationship was apparent (Figure 11.4.3A, Table 11.4.1). Suspended sediment-related variables were present in all models within 2 units of the lowest AICc value (Table S11.4.2).

No habitat or environmental variables were found to relate to the total abundance of fish assemblages (Table 11.4.1). Suspended sediment (both general characteristics (PC1) and discrete events (PC2) and both long-term and short-term measures) were included in the best model describing the distribution of fish biomass. However the residual plots suggest a relatively weak directional relationship (Figure 11.4.3A). Suspended sediment-related variables (i.e. TSS and NTU PC1 and PC2) were present in all top models for total biomass (Table S11.4.3).

Different feeding guilds exhibited varying responses to fine-scale habitat and broad-scale environmental variables, however responses by planktivorous omnivores and herbivorous scrapers were the most pronounced. The planktivorous omnivores recorded in this study were all from family Pomacentridae (Table S11.4.2). Total planktivorous omnivore abundance was lower at sites characterised by higher levels of suspended sediment over both the long-term and the short-term time scales (TSS PC1; Figure 11.4.3B, Table 11.4.1). A relationship with macroalgae was also detected but the directionality was weak. Predictor variables related to suspended sediment were present in all top models for planktivorous omnivore (Table S11.4.3). Total planktivorous omnivore biomass was not related to any of the predictor variables (Table 11.4.1, Table S11.4.2).

All herbivorous scraper species recorded in this study were from the Scarinae subfamily (Table S11.4.2). Total herbivorous scraper abundance increased with increasing structural relief of habitat (Figure 11.4.3B, Table 11.4.1). A negative relationship was also observed between long-term TSS PC1 (the general suspended sediment regime) and total herbivorous scraper abundance, and indeed, suspended-sediment related predictor variables were present in all top models Figure 11.4.3B, Table S11.4.3). Herbivorous scraper biomass decreased with depth and increased with increasing levels of stony coral cover (Figure 11.4.3B, Table 11.4.1).

11.4.4 DISCUSSION

Increasing suspended sediment is linked to decreasing species richness in the Pilbara region, supporting previous studies on the influence of cross-shelf turbidity gradients on fish assemblages (Figure 11.4.3A; Fabricius et al. 2005; Maella et al. 2007; Malcolm et al. 2010; Bejarano and Appeldoorn 2013). However, this study found no relationship between total abundance of fish and suspended sediment, contradicting patterns observed in other large-scale field studies (Figure 11.4.3A; Fabricius et al. 2005; Maella et al. 2007; Malcolm et al. 2010; Bejarano and Appeldoorn 2013). The consistency of total fish abundance yet decreasing species diversity across the shelf suggests that increased levels of turbidity may not negatively impact some functional groups or species, as is the case for benthic filter feeding communities in this region (Abdul Wahab et al 2017). However, decreased species richness has been linked to decreased ecosystem resilience, productivity, and recovery after disturbance (Worm et al. 2006; Cheal et al. 2013). Consequently, the diminished species richness observed at high turbidity sites indicates that whilst these inshore reef assemblages have a higher tolerance threshold for suspended sediment than offshore reefs, they are likely less resilient to the additive effects of additional natural and anthropogenic disturbance events, due to decreased functional redundancy (Gilmour et al. 2006; Gil et al. 2016). The coral bleaching events between 2011 – 2013 (Lafratta et al. 2016) have already dramatically reduced the coral cover of this region and the habitats supported by inshore reefs have been identified as important areas for recruitment of many fish species, thus the loss of these habitats could significantly erode the biodiversity of the Pilbara region (Gilmour et al. 2006; McLean et al. 2016). Reefs experiencing increased turbidity levels, decreased coral cover, and decreased abundances of functionally-valuable herbivorous scrapers may take longer to recover than their clear water offshore counterparts, due to diminished efficacy of the processes underpinning recruitment and growth on coral reefs (Gilmour et al. 2006; Nash et al. 2016).

Environmental monitoring is time-consuming and costly, therefore it is crucial to identify the coarsest resolution (such as family or feeding guild) that can be studied whilst still providing sufficient detail to inform management (Best et al. 2015). Two key functional groups showed decreasing abundance with increasing suspended sediment: planktivorous omnivores and herbivorous scrapers (Figure 11.4.3B). This is consistent with past studies that have reported that these fish are generally found in clear water and are less abundant on inshore reefs (Fabricius et al. 2005; Malcolm et al. 2010; Johansen and Jones 2013). These results also support aquaria-based experiments that reported decreased foraging success, declines in growth rate and body condition, and increased mortality rates with increasing turbidity (Wenger et al. 2012; Johansen and Jones 2013; O'Connor et al. 2015). While planktivorous omnivore abundance decreased at more turbid sites, no predictor variables were found to relate to the total biomass of this feeding guild (Table 11.4.1). This may suggest that whilst a lower number of individuals are present at more turbid sites, the individuals present are generally of a larger size. This study provides field-based evidence to support lab-based studies that have reported higher magnitude negative influences of suspended sediment on small-bodied fish, and therefore large-bodied individuals are present at turbid sites, whilst smaller-bodied individuals cannot tolerate the turbid conditions (Wenger and McCormick 2013). Planktivorous omnivores play a vital functional role in coral reef ecosystems by importing pelagic nutrients into the system and by providing a trophic link between secondary production and fish biomass (Hamner et al. 2007; Johansen and Jones 2013). Decreased abundance or loss of this feeding guild from an ecosystem may have significant impacts on energy transfer, leading to an erosion of trophic diversity and decreased ecosystem resilience (Johansen and Jones 2013). Planktivorous omnivores are a possible candidate for functional group-level monitoring, as productivity of this feeding guild has been shown to be resilient to diversity loss (Messmer et al. 2014). However, this study demonstrated variable responses between species and Johansen and Jones (2013) found that planktivorous species exhibited different preferred levels of turbidity. The interspecific variation of responses to increasing turbidity in this functional group requires further study to determine if they can be grouped, and an indicator species utilised, for monitoring purposes.

Herbivorous scrapers demonstrated more complex responses to increasing suspended sediment (Figure 11.4.3C, Table 11.4.1). Habitat rugosity was the most important predictor variable, showing a strong positive relationship with herbivorous scraper abundance, concurring with previous studies (Figure 11.4.3C; Wilson et al. 2006; Graham and Nash 2012; Bejarano and Appeldoorn 2013). TSS predictor variables were also important, exhibiting both indirect and direct relationships with herbivorous scraper abundance (Figure 11.4.3C). The negative impacts of sediment on coral cover (including increased mortality, decreased growth, and range contraction) are well documented and were reflected in this study, with decreased percentage cover of stony corals at high turbidity sites (Figure 11.4.2, Table 11.4.1; Fabricius et al. 2005; De'ath and Fabricius 2010; Erftemeijer et al. 2012). Herbivorous scrapers are less common on reefs with high live coral coverage, as they graze on the turf algae that establishes on consolidated substrate and dead coral (Gilmour et al. 2013; Han et al. 2016). This trend was reflected in the results of this study, with herbivorous scraper abundance declining with increasing coral cover (Figure 11.4.3C). This provides an example of an indirect positive effect of suspended sediment on herbivorous scrapers, through decreased stony coral cover. These results must be interpreted cautiously as current live coral cover in the region from other recent studies ranges between 0-10% due to recent bleaching events (Moore et al. 2012; Clausing et al. 2016; Lafratta et al. 2016). However, increased TSS was also directly related to herbivorous scrapers, with increasing turbidity linked to decreased abundance and biomass of this functional group (Figure 11.4.3C). This relationship is likely due to increased sediment in the epilithic algal matrix deterring grazing by herbivorous species, as has been reported on the Great Barrier Reef, Australia (Bellwood and Fulton 2008; Gil et al. 2016; Gordon et al. 2016). These multidirectional ecological interactions are similar to those reported by Gil et al. and Clausing et al. in their 2016 field studies on the Great Barrier Reef and in French Polynesia, respectively, and highlight the importance of an ecosystem-based approach to studying the influences of turbidity on coral reef communities. Herbivorous scrapers play a vital role in preventing coral reefs from shifting to a macroalgal-dominated state after a disturbance event by maintaining space for coral propagules to settle and re-establish (Adam et al. 2011; Han et al. 2016; Nash et al. 2016). Studies have also found that different species and size classes of herbivorous scrapers graze differently, and thus have different impacts on ecosystem function (Bonaldo and Bellwood 2008). Changes in herbivorous scraper assemblage caused by elevated suspended sediment, or size-selective fishing effort, may therefore reduce the resilience and recovery capacity of coral reefs (Madin et al. 2010; Bellwood et al. 2012; Han et al. 2016). The species composition of fish and coral on the offshore reefs is typical of reefs with less sediment influence than the inshore reefs. These reefs would be more susceptible to long-term natural or anthropogenic induced increases in suspended sediments. However, whilst these assemblages may be more vulnerable to the negative effects of increased in turbidity, the increased diversity and functional redundancy of these assemblages means they are likely more resilient to disturbance events, such as discrete sediment pulses caused by storms or dredging. Comparatively, although inshore reefs have a higher tolerance threshold to suspended sediment, recent coral bleaching, high sediment loads, and low abundance of herbivorous scrapers combined will reduce ecosystem resilience and recovery if a disturbance event elevates suspended sediment levels above this threshold. The relative importance of indirect effects (through decreased live coral cover) and direct effects (through decreased ability to graze) of suspended sediment on structuring herbivorous fish assemblages must be understood if the impacts of discrete disturbance events that increase turbidity are to be understood, predicted, and managed appropriately.

Whilst this study has identified several broad-scale ecological trends in response to high levels of suspended sediment, it is by no means a comprehensive assessment of the influences of suspended sediment on fish in the Pilbara region. The long-term impact of discrete disturbance events depends on the length and intensity of the perturbation, recovery rates of habitat, and the ecological plasticity of species within the assemblage (Wenger et al. 2017). Therefore BACI (before-after-control-impact) style studies are key to developing predictive models to assess the influence of discrete events that elevate suspended sediment. Further studies on interspecific and intraspecific variation in the functional roles of planktivorous omnivores and herbivorous scrapers must be conducted to determine whether monitoring fish assemblages at a functional group resolution provides an adequate indication of ecosystem health (Bonaldo and Bellwood 2008; Messmer et al. 2014; Best et al. 2015). Once an appropriate monitoring resolution has been identified, indicator species should be identified and aquaria-based experiments should be conducted to determine tolerance thresholds for suspended sediment. Localised adaptation to high turbidity has been reported, therefore the fish used in aquaria experiments must be sourced from the Pilbara region for such studies (Wilber and Clarke 2001). Future research on the impacts of suspended sediment on coral cover and recruitment in the Pilbara region will clarify the currently unclear relationship between suspended sediment and stony coral cover reported in this study. Finally, multiple studies have identified the importance of reef patch context; that is how reef patches are spatially related to each other in structuring fish assemblage (Grober-Dunsmore et al. 2007; Pittman and Brown 2011). Future studies should aim to include measures of connectivity of reef patches, both genetically and for the physical movement of mobile species (Adam et al. 2011).

This study demonstrated a negative relationship between species richness, and abundance of key functional groups and suspended sediment in the fish assemblage of the nearshore Pilbara region. Whilst the turbid inshore reef assemblages of the region have higher tolerance thresholds for suspended sediment, they are likely less resilient and have less capacity to recover from anomalous disturbance events, than more sensitive but more functionally redundant offshore reefs with lower sediment regimes. Considering the frequency of natural disturbance events in the Pilbara region, this decreased functional redundancy has significant implications for management, particularly regarding dredging activities. Elevating suspended sediment levels above the thresholds that inshore coral reef communities are adapted to may cause long-term damage to these ecosystems. This study has identified several broad-scale ecological trends that warrant further examination, however the threshold values for the various biological components of these biodiverse coral reef ecosystems are still largely unknown. To effectively manage the impact of anthropogenic activities that elevate suspended sediment levels (such as dredging), local exposure thresholds for both intensity and duration of suspended sediment elevation must be identified for key functional groups.

11.4.5 ACKNOWLEDGEMENTS

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11.4.6 REFERENCES

Abdul Wahab MA, Fromont J, Gomez O, Fisher R, Jones R (2017) Comparisons of benthic filter feeder communities before and after a large-scale capital dredging program. Marine Pollution Bulletin. doi: 10.1016/j.marpolbul.2017.06.041

Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory, Connectivity, and Ecosystem Resilience: Response of a Coral Reef to a Large-Scale Perturbation. PLoS ONE 6:e23717–8. doi: 10.1371/journal.pone.0023717

Akaike H (1973) Information theory and an extension of the maximum likelihood principal. In: Proceedings of the Second International Symposium on Information Theory. Akademiai Kiado, Budapest, pp 267-281

Althaus F, Hill N, Edwards L, Ferrari R (2013) CATAMI Classification Scheme for Scoring Marine Biota and Substrata in Underwater Imagery - A Pictorial Guide to the Collaborative and Annotation Tools for Analysis of Marine Imagery and Video (CATAMI) Classification Scheme. Version 1. http://catami.org/ classification

Amante C, Eakins BW (2009) ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA. doi:10.7289/V5C8276M

Bejarano I, Appeldoorn RS (2013) Seawater turbidity and fish communities on coral reefs of Puerto Rico. Mar Ecol Prog Ser 474:217–226. doi: http://dx.doi.org/10.3354/meps10051

Bellwood DR, Fulton CJ (2008) Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea-levels and climate change? Limnol Oceanogr 53:2695–2701. doi: 10.4319/lo.2008.53.6.2695

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc R Soc B 279:1621–1629. doi: 10.1098/rspb.2011.1906

Bennett K, Wilson SK, Shedrawi G, McLean DL, Langlois TJ (2016) Can diver operated stereo-video surveys for fish be used to collect meaningful data on benthic coral reef communities? Limnol Oceanogr Methods 14(12):874-885. doi: 10.1002/lom3.10141

Best RJ, Stone MN, Stachowicz JJ (2015) Predicting consequences of climate change for ecosystem functioning: variation across trophic levels, species and individuals (L Beaumont, Ed.). Diversity Distrib 21:1364–1374. doi: 10.1111/ddi.12367

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360:237–244. doi: http://dx.doi.org/10.3354/meps07413

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer, New York.

Cheal AJ, Emslie M, MacNeil A, Miller I, Sweatman H (2013) Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. Ecol Appl 23:174–188. doi: 10.1890/11-2253.1

Chevron (2012) Wheatstone Project: Dredging and Dredge Spoil Placement Environmental Monitoring and Management Plan. Chevron Australia Pty Ltd

Clausing RJ, Bittick SJ, Fong CR, Fong P (2016) Sediments influence accumulation of two macroalgal species through novel but differing interactions with nutrients and herbivory. Coral Reefs 35(4):1297–1309. doi: 10.1007/s00338-016-1477-1

Collin SP, Hart NS (2015) Vision and photoentrainment in fishes: The effects of natural and anthropogenic perturbation. Integr Zool 10:15–28. doi: 10.1111/1749-4877.12093

Cooper TF, Uthicke S, Humphrey C, Fabricius KE (2007) Gradients in water column nutrients, sediment parameters, irradiance and coral reef development in the Whitsunday Region, central Great Barrier Reef. Estuar Coastal Shelf Sci 74(3):458-470. doi: 10.1016/j.ecss.2007.05.020

Crain CM, Halpern BS, Beck MW, Kappel CV (2009) Understanding and Managing Human Threats to the Coastal Marine Environment. Ann N Y Acad Sci 1162:39–62. doi: 10.1016/j.ecss.2007.05.020

De'ath G, Fabricius K (2010) Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecol Appl 20:840–850. doi: 10.1890/08-2023.1

Dorji P, Fearns P (2016) A Quantitative Comparison of Total Suspended

Sediment Algorithms: A Case Study of the Last Decade for MODIS and Landsat-Based Sensors. Remote Sens Environ 8(10): 810. doi: 10.3390/rs8100810

Dorji P, Fearns P, Broomhall M (2016) A Semi-Analytic Model for Estimating Total Suspended Sediment Concentration in Turbid Coastal Waters of Northern Western Australia Using MODIS-Aqua 250 m Data. Remote Sens 8:55e6–24. doi: 10.3390/rs8070556

Erftemeijer PLA, Hagedorn M, Laterveer M, Craggs J, Guest JR (2012) Effects of suspended sediment on fertilization success in the scleractinian coral Pectinia lactuca. J Mar Biol Assoc U.K. 92(4):741-745. doi: 10.1017/S0025315411000944

Evans RD, Russ GR (2004) Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. Aquatic Conserv: Mar Freshw Ecosyst 14:505–519. doi: 10.1002/aqc.631

Fabricius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Mar Pollut Bull 51:384–398. doi: 10.1016/j.marpolbul.2004.10.041

Folke C (2006) Resilience: The emergence of a perspective for social–ecological systems analyses. Glob Environ Change 16:253–267. doi: 10.1016/j.gloenvcha.2006.04.002

Froese R, D Pauly (Eds) (2016) FishBase. www.fishbase.org

Gil MA, Goldenberg SU, Bach ALT, Mills SC, Claudet J (2016). Interactive effects of three pervasive marine stressors in a post-disturbance coral reef. Coral Reefs 35(4):1281–1293. doi: 10.1007/s00338-016-1489-x

Gilby BL, Tibbetts IR, Olds AD, Maxwell PS, Stevens T (2016) Seascape context and predators override water quality effects on inshore coral reef fish communities. Coral Reefs 35:977–988. doi: 10.1007/s00338-016-1449-5

Gilmour JP, Cooper T, Fabricius KE, Smith LD (2006) Early warning indicators of change in the condition of corals and coral communities in response to key anthropogenic stressors in the Pilbara, Western Australia. Australian Institute of Marine Science

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an Isolated Coral Reef System Following Severe Disturbance. Science 340:69–71. doi: 10.1126/science.1232310

Goatley CHR, Bellwood DR (2012) Sediment suppresses herbivory across a coral reef depth gradient. Biol Lett 8:1016–1018. doi: 10.1098/rsbl.2012.0770

Goatley CHR, Bonaldo RM, Fox RJ, Bellwood DR (2016) Sediments and herbivory as sensitive indicators of coral reef degradation. Ecol Soc 21(1):29. doi: 10.5751/ES-08334-210129

Gordon SE, Goatley CHR, Bellwood DR (2016) Low-quality sediments deter grazing by the parrotfish Scarus rivulatus on inner-shelf reefs. Coral Reefs 35:285-291. doi: 10.1007/s00338-015-1374-z

Graham NAJ, Nash KL (2012) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326. doi: 10.1007/s00338-012-0984-y

Graham N, Dulvy NK, Jennings S, Polunin N (2005) Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. Coral Reefs 24:118–124. doi: 10.1007/s00338-004-0466-y

Grober-Dunsmore R, Frazer TK, Lindberg WJ, Beets J (2007) Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. Coral Reefs 26:201–216. doi: 10.1007/s00338-006-0180-z

Hamner WM, Colin PL, Hamner PP (2007) Export-import dynamics of zooplankton on a coral reef in Palau. Mar Ecol Prog Ser 334:84–92. doi: http://dx.doi.org/10.3354/meps334083

Han X, Adam TC, Schmitt RJ, Brooks AJ, Holbrook SJ (2016) Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. Coral Reefs 35:997–1007. doi: 10.1007/s00338-016-1423-2

Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616. doi: 10.7717/peerj.616

Hess S, Wenger AS, Ainsworth TD, Rummer JL (2015). Exposure of clownfish larvae to suspended sediment levels found on the Great Barrier Reef: Impacts on gill structure and microbiome. Scientific Reports 5. doi: 10.1038/srep10561

Hutchins JB (2001) Biodiversity of shallow reef fish assemblages in Western Australia using a rapid censusing technique. Rec West Aust Museum 20:247–270

Johansen JL, Jones GP (2013) Sediment-induced turbidity impairs foraging performance and prey choice of planktivorous coral reef fishes. Ecol Appl 23:1504–1517. doi: 10.1890/12-0704.1

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci U S A 101:8251–8253

Jones R, Bessell-Browne P, Fisher R, Klonowski W, Slivkoff M (2016) Assessing the impacts of sediments from dredging on corals. Mar Pollut Bull 102:9–29. doi: 10.1016/j.marpolbul.2015.10.049

Kemp P, Sear D, Collins A, Naden P, Jones I (2011) The impacts of fine sediment on riverine fish. Hydrol Process 25:1800–1821. doi: http://dx.doi.org/10.1002/hyp.7940

Kroon FJ (2009) Integrated research to improve water quality in the Great Barrier Reef region. Mar Freshwater Res 60(11):1-4. doi: 10.1071/MF09216

Lafratta A, Fromont J, Speare P, Schönberg CHL (2016) Coral bleaching in turbid waters of north-western Australia. Mar Freshwater Res 68(1):65-75. doi: 10.1071/MF15314

Langlois TJ, Newman SJ, Cappo M, Harvey ES, Ben M Rome, Skepper CL, Wakefield CB (2015) Length selectivity of commercial fish traps assessed from in situ comparisons with stereo-video: Is there evidence of sampling bias? Fish Res 161:145–155. doi: 10.1016/j.fishres.2014.06.008

Lowry M, Folpp H, Gregson M, Suthers I (2012) Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries. J Exp Mar Biol Ecol 416-417:243–253. doi: 10.1016/j.jembe.2012.01.013

Madin EMP, Gaines SD, Madin JS, Warner RR (2010) Fishing Indirectly Structures Macroalgal Assemblages by Altering Herbivore Behaviour. Am Nat 176:785–801. doi: 10.1086/657039

Malcolm HA, Jordan A, Smith SDA (2010) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. Mar Biodiv 40:181–193. doi: 10.1007/s12526-010-0042-3

McLean DL, Langlois TJ, Newman SJ, Holmes TH, Birt MJ, Bornt KR, Bond T, Collins DL, Evans SN, Travers MJ, Wakefield CB, Babcock RC, Fisher R (2016) Distribution, abundance, diversity and habitat associations of fishes across a bioregion experiencing rapid coastal development. Estuar Coast Shelf Sci 178:36–47. doi: 10.1016/j.ecss.2016.05.026

Messmer V, Blowes SA, Jones GP, Munday PL (2014) Experimental evaluation of diversity–productivity relationships in a coral reef fish assemblage. Oecologia 176:237–249. doi: 10.1007/s00442-014-2992-9

Moore JAY, Bellchambers LM, Depczynski MR, Evans RD, Evans SN, Field SN, Friedman KJ, Gilmour JP, Holmes TH, Middlebrook R, Radford BT, Ridgway T, Shedrawi G, Taylor H, Thomson DP, Wilson SK (2012) Unprecedented Mass Bleaching and Loss of Coral across 12° of Latitude in Western Australia in 2010–11 (I Álvarez, Ed.). PLoS ONE 7:e51807–12. doi: 10.1371/journal.pone.0051807

Nash KL, Abesamis RA, Graham N, McClure EC, Moland E (2016) Drivers of herbivory on coral reefs: species, habitat and management effects. Mar Ecol Prog Ser 554:129–140. doi: http://dx.doi.org/10.3354/meps11795

O'Connor JJ, Lecchini D, Beck HJ, Cadiou G, Lecellier G, Booth DJ, Nakamura Y (2015) Sediment pollution impacts sensory ability and performance of settling coral-reef fish. Oecologia 180:11–21. doi: 10.1007/s00442-015-3367-6

Pittman SJ, Brown KA (2011) Multi-Scale Approach for Predicting Fish Species Distributions across Coral Reef Seascapes (B Gratwicke, Ed.). PLoS ONE 6:e20583–13. doi: 10.1371/journal.pone.0020583

R Core Team (2017) R: A Language and Environment for Statistical Computing. https://www.r-project.org [Accessed 01 June 2016]

SeaGIS Pty Ltd (2014) SeaGISCAL. SeaGIS Pty Ltd, Bacchus Marsh http://www.seaGIS.com.au

SeaGIS Pty Ltd (2016) TransectMeasure. SeaGIS Pty Ltd, Bacchus Marsh http://www.seaGIS.com.au

Shono H (2008) Application of the Tweedie distribution to zero-catch data in CPUE analysis. Fish Res 93:154–162. doi: 10.1016/j.fishres.2008.03.006

Suedel BC, Kim J, Clarke DG, Linkov I (2008) A risk-informed decision framework for setting environmental windows for dredging projects. Scie Total Environ 403:1-11. doi: 10.1016/j.scitotenv.2008.04.055

Wenger AS, McCormick MI (2013) Determining trigger values of suspended sediment for behavioral changes in a coral reef fish. Mar Pollut Bull 70:73–80. doi: 10.1016/j.marpolbul.2013.02.014

Wenger AS, Johansen JL, Jones GP (2011) Suspended sediment impairs habitat choice and chemosensory discrimination in two coral reef fishes. Coral Reefs 30:879–887. doi: 10.1007/s00338-011-0773-z

Wenger AS, Johansen JL, Jones GP (2012) Increasing suspended sediment reduces foraging, growth and condition of a planktivorous damselfish. J Exp Mar Biol Ecol 428:43–48. doi: 10.1016/j.jembe.2012.06.004

Wenger AS, Harvey E, Wilson S, Rawson C, Newman, SJ, Clarke D, Saunders BJ, Browne N, Travers MJ, Mcilwain JL, Erftemeijer PLA, Hobbs JA, McLean D, Depczynski M, Evans RD (2017) A critical analysis of the direct effects of dredging on fish. Fish and Fisheries. doi: 10.1111/faf.12218

Wilber DH, Clarke DG (2001) Biological Effects of Suspended Sediments: A Review of Suspended Sediment Impacts on Fish and Shellfish with Relation to Dredging Activities in Estuaries. N Am J Fish Management 21:855–875. doi: 10.1577/1548-8675(2001)021<0855:BEOSSA>2.0.CO

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Glo Change Biol 12:2220–2234. doi: 10.1111/j.1365-2486.2006.01252.x

Wood S, Scheipl F (2015) Package ‘gamm4’ (Version 0.2-3). Generalized Additive Mixed Models Using mgcv and lme4 https://cran.r-project.org/web/packages/ gamm4/gamm4.pdf

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science 314:787–790.

11.4.7 SUPPLEMENTARY MATERIAL

TSS concentration data was derived from daily MODIS observation from 05/11/2000 – 13/02/2016 for each site using an average 9 x 9 (250 m-pixel) grid over a GPS point located as close to the sampling site as possible, without overlapping any land or shallow reef. On occasion cloud cover, poor atmospheric correction or issues with satellite view geometry lead to TSS algorithm failure. Where fewer than 5 of the 9 pixels could be processed successfully, the corresponding TSS data was excluded prior to analysis. Useable data was retrieved on an average of 73.6% of total sampling days across all sites. Anomalous TSS values were investigated to ensure they correlated with extreme weather events, dredging activity, or satellite imagery (Chevron 2012; BOM 2016; NASA 2016).

Two principal coordinate analyses were performed on the TSS data, one based on the longterm data (05-Nov-2000 – 22-May-2013) and one on the short-term data (23-May-2013 – 13- Feb-2016). The short-term time frame was selected based on the date of installation of the Chevron water quality loggers for their dredge operations, as the loggers had more power to detect fine-scale changes in turbidity. Turbidity data recorded by the water quality loggers during the pre-dredge period (19-May-2011 – 22-May-2013) was excluded from analysis due to the relocation of the Fly Island logger (resulting in a non-uniform dataset) at the commencement of dredging, therefore the short-term data is restricted to the dredging period only. As a result, TSS data from this pre-dredge period was included in the long-term PCoA, and a separate short-term PCoA. The PCoA was based on a dataset consisting of the 50th, 80th, 90th, 95th, and 100th percentile TSS values, across both the long-term and short-term, of a sequence of running means from 1 day up to 365 days (Figure S11.4.1, Figure S11.4.2; after Jones et al. 2015). Due to the skewed nature of turbidity data, PCoAs were performed on log10 (TSS + 1) transformed data. This process was repeated for the Chevron water quality logger turbidity (reported in nephelometric turbidity units [NTU]) data, however due to the shorter time span of data collection, only a short-term PCoA was conducted (Figure S11.4.3). The first axis (PC1) accounted for 90.2%, and 93.3%, of the variability for the long-term TSS and short-term TSS respectively, and in both cases this was strongly positively correlated with high values of turbidity across all time scales and percentile summaries (Figure S11.4.1, Figure S11.4.2). As such, the PC1 axes for TSS characterise the differences in the general suspended sediment regime between sites, with higher positive scores indicating high turbidity. The second axes (PC2) accounted for 6.6%, and 4.1% of the variability for the long-term TSS and short-term TSS, respectively (Figure S11.4.1, Figure S11.4.2), and in both cases was strongly negatively correlated with high values of TSS across short time frames, but only for the extreme percentiles (Figure S11.4.1, Figure S11.4.2). Therefore, low values of PC2 indicate the occurrence of extreme, discrete turbidity events. The first axis (PC1) for short-term in situ turbidity (NTU) represented 90.3% of variability and was strongly negatively correlated with high values of turbidity across all time scales and percentile summaries (Figure S11.4.3). Therefore, for short-term in situ turbidity (NTU), high values of PC1 indicate less turbid water quality conditions. The second axis (PC2) for short-term in situ turbidity represented 5.9% of the remaining variation, with positive values indicating greater frequency or intensity of discrete spikes in turbidity (Figure 11.4.3C). Therefore, the principal coordinate axes for both short-term TSS and short-term in situ turbidity (NTU) characterise the combined turbidity profile of both natural and anthropogenic stressors.

Sponges were removed from the fine-scale habitat categories due to limited coverage and unconsolidated substrate was removed due to its collinearity (>0.9) with reef. The first turbidity principal component axis from the logger water quality data (finescale NTU PCO1) was not included in full subsets analyses due to its high correlation (>0.9) with the principal coordinate axes derived from the TSS data. In addition, prior to each model being run, the distribution of predictor variables was visually inspected and appropriate data transformations applied where necessary. UVC data was transformed as follows: for all models (except UVC biomass at taxa level), mean relief and reef were cubed, macroalgae was log(x+1) transformed, and a SQRT transformation was applied to stony coral.

For the UVC biomass taxa level model, the same transformations were applied, with the addition of a SQRT transformation being applied to pre-dredge TSS PC1.

Supplementary Material References

Brewin RJW, Sathyendranath S, Müller D, Brockman C, Deschamps PY, Devred E, White III GN (2015) The Ocean Colour Climate Change Initiative: III. A round-robin comparison on in-water bio-optical algorithms. Remote Sens Environ 162: 271-294. doi: 10.1016/j.rse.2013.09.016

Bureau of Meteorology (2016) Climate Data Online. Australian Government. http://www.bom.gov.au/climate/data/

National Aeronautics and Space Administration (2016) The Earth Observing System Data and Information System. United States Government https://worldview.earthdata.nasa.gov

Supplementary Material Figures and Tables

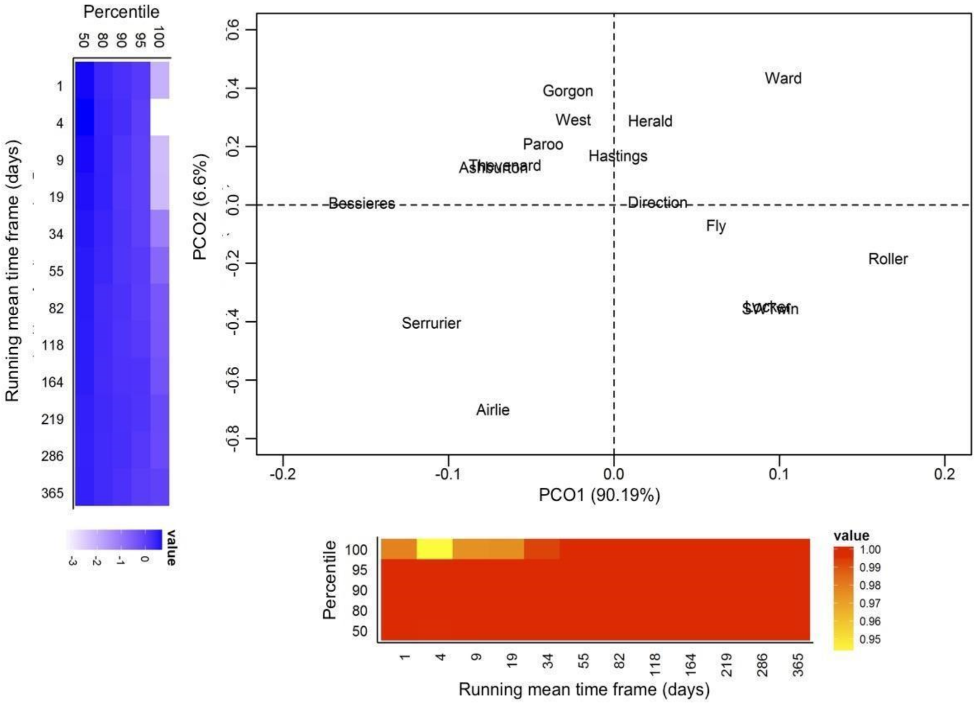

Figure S11.4.1 Principle coordinate analysis (PCoA) plot and axes correlations for long-term remotely-sensed total suspended solids (TSS) at the 16 study sites in the Pilbara, Western Australia.

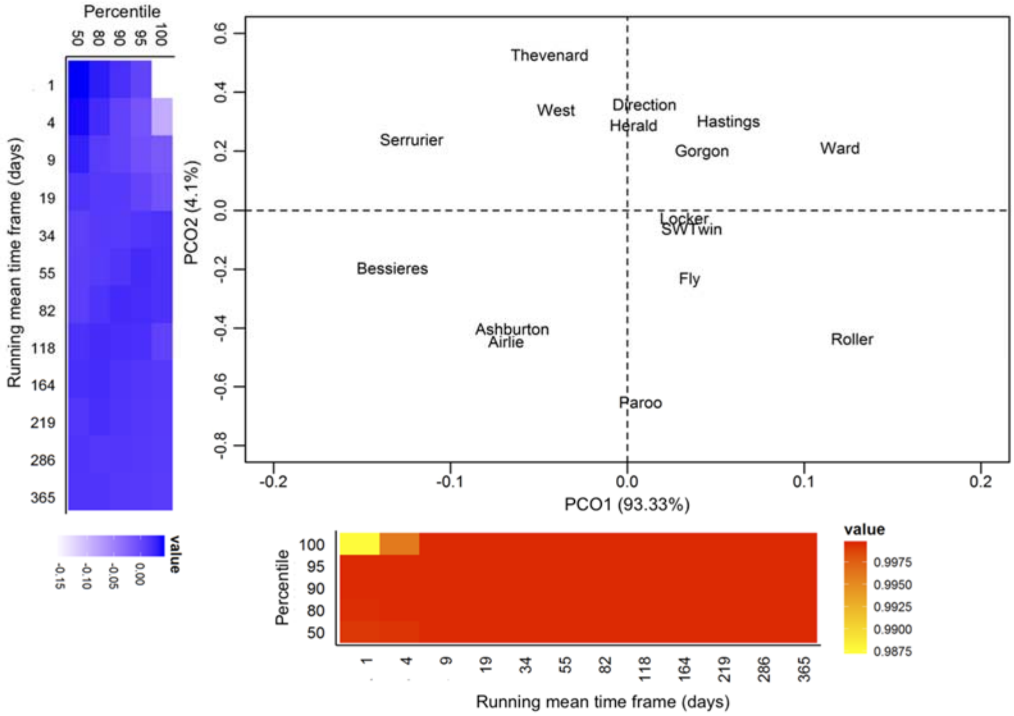

Figure S11.4.2 Principle coordinate analysis (PCoA) plot and axes correlations for short-term remotely-sensed total suspended solids (TSS) at the 16 study sites in the Pilbara, Western Australia.

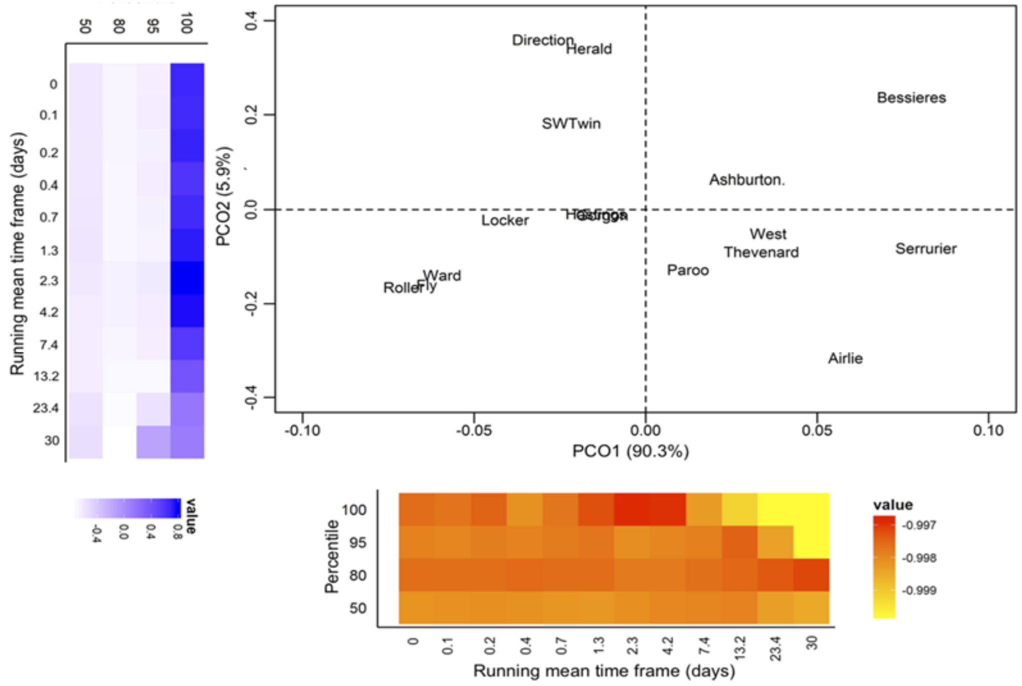

Figure S11.4.3 Principle coordinate analysis (PCoA) plot and axes correlations for short-term *in situ* turbidity (NTU) at the 16 study sites in the Pilbara, Western Australia.

Table S11.4.1 All generalised additive mixed models (GAMMs) within two units of the lowest Akaike Information Criterion (AICc) for predicting the relief of substrate (mean and standard deviation [SD]) and percent cover of fine-scale habitat types in the Pilbara. The Akaike information criterion (corrected for finite sample sizes; AICc), Bayesian information criterion (BIC), delta AIC (AIC differences), model weight (wi.AICc), the coefficient of determination (R^2), and model size (edf) were also reported. Best models are indicated in bold.

DEPENDENT VARIABLE	AICc	BIC	ΔAICc	wi.AICc	R²	EDF	BEST MODEL
Mean habitat relief	108.16	138.61	0	0.13	0.33	9.96	**Depth**
	109.36	141.21	1.19	0.07	0.34	10.82	Depth, Short-term NTU PC2
	109.46	141.39	1.3	0.07	0.34	10.92	Depth, Short-term TSS PC2
	109.47	141.41	1.31	0.07	0.34	10.93	Depth, Short-term TSS PC1
	109.48	141.3	1.31	0.07	0.34	10.84	Depth, Distance to 30 m
SD habitat relief	-20.32	5.39	0	0.84	0.4	8.63	**Depth, Long-term TSS PC1, Short-term NTU PC2**
Consolidated	-79.4	-51.59	0	0.06	0.37	11.42	Long-term TSS PC2
	-78.7	-50.04	0.7	0.04	0.95	11.87	**Null**
	-78.68	-50.01	0.72	0.04	0.37	11.88	Long-term TSS PC2, Short-term TSS PC1
	-78.61	-49.86	0.79	0.04	0.37	11.92	Long-term TSS PC2, Short-term NTU PC2
	-78.48	-49.57	0.92	0.04	0.38	12.01	Long-term TSS PC1, Long-term TSS PC2
	-78.43	-49.45	0.97	0.04	0.38	12.04	Short-term TSS PC1
	-78.24	-49.07	1.16	0.03	0.38	12.14	Depth
	-78.09	-48.72	1.31	0.03	0.38	12.26	Short-term TSS PC2
	-77.9	-48.32	1.5	0.03	0.38	12.37	Long-term TSS PC1
	-77.9	-48.36	1.5	0.03	0.38	12.35	Depth, Short-term TSS PC1
	-77.87	-48.27	1.53	0.03	0.38	12.38	Distance to 30 m
	-77.87	-48.24	1.53	0.03	0.38	12.4	Short-term NTU PC2
	-77.86	-48.23	1.54	0.03	0.38	12.4	Short-term TSS PC1, Short-term TSS PC2
	-77.86	-47.31	1.54	0.03	0.39	12.9	Long-term TSS PC2, Short-term NTU PC2, Distance to 30 m
	-77.85	-47.16	1.55	0.03	0.39	12.99	Long-term TSS PC2, Distance to 30 m
	-77.82	-48.14	1.58	0.03	0.38	12.43	Long-term TSS PC2, Short-term TSS PC1, Short-term NTU PC2
	-77.71	-47.9	1.69	0.02	0.38	12.5	Long-term TSS PC1, Long-term TSS PC2, Short-term NTU PC2
	-77.59	-47.66	1.81	0.02	0.38	12.56	Short-term TSS PC1, Distance to 30 m
	-77.56	-47.59	1.84	0.02	0.38	12.59	Short-term TSS PC1, Short-term NTU PC2
	-77.53	-47.51	1.87	0.02	0.38	12.61	Depth, Short-term TSS PC2
	-77.49	-46.69	1.9	0.02	0.39	13.05	Long-term TSS PC2, Short-term TSS PC1, Distance to 30 m
	-77.49	-47.43	1.91	0.02	0.38	12.63	Depth, Long-term TSS PC1
	-77.46	-47.12	1.94	0.02	0.38	12.79	Long-term TSS PC1, Long-term TSS PC2, Distance to 30 m
Macroalgae	-187.27	-154.98	0	0.03	0.67	13.9	**Null**

DEPENDENT VARIABLE	AICc	BIC	ΔAICc	wi.AICc	R²	EDF	BEST MODEL
	-187.21	-153.33	0.05	0.03	0.57	14.84	Depth, Long-term TSS PC1
	-187.07	-154.58	0.2	0.03	0.56	14.01	Long-term TSS PC1
	-186.98	-154.4	0.29	0.03	0.56	14.07	Short-term TSS PC1
	-186.97	-154.38	0.3	0.03	0.56	14.07	Long-term TSS PC2
	-186.95	-154.35	0.31	0.03	0.56	14.08	Short-term TSS PC2
	-186.93	-153	0.34	0.03	0.57	14.87	Depth
	-186.86	-154.18	0.41	0.03	0.56	14.12	Distance to 30 m
	-186.82	-154.07	0.45	0.03	0.56	14.16	Long-term TSS PC2, Short-term TSS PC1
	-186.81	-154.06	0.45	0.03	0.56	14.17	Short-term NTU PC2
	-186.79	-152.61	0.48	0.03	0.57	15.02	Depth, Short-term TSS PC1
	-186.77	-153.97	0.5	0.03	0.56	14.19	Long-term TSS PC1, Long-term TSS PC2
	-186.76	-152.46	0.5	0.03	0.57	15.1	Depth, Long-term TSS PC1, Short-term TSS PC2
	-186.76	-153.96	0.5	0.03	0.56	14.2	Long-term TSS PC1, Short-term TSS PC2
	-186.74	-153.17	0.53	0.03	0.57	14.65	Depth, Short-term TSS PC2
	-186.67	-152.35	0.59	0.02	0.57	15.11	Depth, Long-term TSS PC1, Short-term NTU PC2
	-186.67	-153.78	0.6	0.02	0.56	14.25	Short-term TSS PC1, Short-term TSS PC2
	-186.65	-153.72	0.62	0.02	0.56	14.28	Long-term TSS PC1, Distance to 30 m
	-186.64	-153.86	0.63	0.02	0.56	14.18	Short-term TSS PC2, Distance to 30 m
	-186.61	-153.65	0.66	0.02	0.56	14.29	Long-term TSS PC1, Short-term NTU PC2
	-186.58	-153.65	0.68	0.02	0.56	14.28	Long-term TSS PC2, Distance to 30 m
	-186.55	-153.52	0.72	0.02	0.56	14.33	Short-term TSS PC1, Distance to 30 m
	-186.53	-153.5	0.74	0.02	0.56	14.33	Short-term TSS PC1, Short-term NTU PC2
	-186.52	-153.49	0.74	0.02	0.56	14.34	Long-term TSS PC2, Short-term NTU PC2
	-186.46	-152.14	0.81	0.02	0.57	15.1	Depth, Short-term NTU PC2
	-186.44	-152	0.83	0.02	0.57	15.18	Depth, Distance to 30 m
	-186.42	-153.27	0.85	0.02	0.56	14.4	Short-term NTU PC2, Distance to 30 m
	-186.4	-153.23	0.87	0.02	0.56	14.41	Long-term TSS PC2, Short-term TSS PC1, Short-term NTU PC2
	-186.38	-153.19	0.88	0.02	0.56	14.43	Long-term TSS PC2, Short-term TSS PC1, Distance to 30 m
	-186.37	-153.15	0.9	0.02	0.56	14.44	Long-term TSS PC1, Long-term TSS PC2, Distance to 30 m
	-186.34	-151.74	0.93	0.02	0.57	15.28	Depth, Short-term TSS PC1, Short-term TSS PC2
	-186.33	-153.09	0.93	0.02	0.56	14.46	Long-term TSS PC1, Short-term TSS PC2, Distance to 30 m
	-186.32	-153.09	0.94	0.02	0.56	14.45	Long-term TSS PC1, Long-term TSS PC2, Short-term NTU PC2

DEPENDENT VARIABLE	AICc	BIC	ΔAICc	wi.AICc	R²	EDF	BEST MODEL
	-186.28	-151.69	0.99	0.02	0.57	15.28	Depth, Short-term TSS PC1, Short-term NTU PC2
	-186.24	-152.95	1.02	0.02	0.56	14.49	Short-term TSS PC1, Short-term TSS PC2, Distance to 30 m
	-186.22	-152.86	1.05	0.02	0.56	14.53	Long-term TSS PC1, Short-term NTU PC2, Distance to 30 m
	-186.21	-152.16	1.06	0.02	0.57	14.94	Depth, Short-term TSS PC1, Distance to 30 m
	-186.13	-152.69	1.14	0.02	0.56	14.57	Long-term TSS PC2, Short-term NTU PC2, Distance to 30 m
	-186.13	-152.68	1.14	0.02	0.56	14.58	Short-term TSS PC1, Short-term NTU PC2, Distance to 30 m
	-186.04	-151.21	1.23	0.02	0.58	15.42	Depth, Short-term TSS PC2, Distance to 30 m
	-185.91	-151.03	1.36	0.02	0.57	15.45	Depth, Short-term NTU PC2, Distance to 30 m
	-185.88	-147.87	1.39	0.02	0.6	17.5	Depth, Long-term TSS PC1, Distance to 30 m
Stony corals	-166.92	-135.33	0	0.06	0.59	13.49	Short-term TSS PC1, Short-term TSS PC2, Distance to 30 m
	-166.69	-134.91	0.23	0.05	0.59	13.6	Short-term TSS PC2, Distance to 30 m
	-166.65	-134.94	0.27	0.05	0.59	13.56	Long-term TSS PC1, Short-term TSS PC2, Distance to 30 m
	-166.38	-134.49	0.54	0.04	0.59	13.67	Short-term TSS PC1, Distance to 30 m
	-166.28	-134.71	0.64	0.04	0.59	13.48	Long-term TSS PC1, Distance to 30 m
	-165.94	-134.42	0.98	0.03	0.58	13.45	Depth, Short-term TSS PC2, Distance to 30 m
	-165.82	-133.26	1.1	0.03	0.59	14.05	Long-term TSS PC2, Distance to 30 m
	-165.76	-133.17	1.15	0.03	0.59	14.08	Short-term TSS PC1, Short-term NTU PC2, Distance to 30 m
	-165.68	-133.08	1.24	0.03	0.59	14.08	Short-term NTU PC2, Distance to 30 m
	-165.65	-132.92	1.27	0.03	0.59	14.15	Long-term TSS PC2, Short-term TSS PC1, Distance to 30 m
	-165.58	-132.91	1.34	0.03	0.59	14.12	Long-term TSS PC1, Long-term TSS PC2, Distance to 30 m
	-165.5	-132.91	1.42	0.03	0.59	14.07	Long-term TSS PC1, Short-term NTU PC2, Distance to 30 m
	-165.28	-131.72	1.64	0.02	0.6	14.65	**Distance to 30 m**
	-165.21	-133.04	1.71	0.02	0.59	13.83	Depth, Long-term TSS PC1, Distance to 30 m
	-165.2	-132.63	1.72	0.02	0.59	14.06	Depth, Short-term TSS PC1, Distance to 30 m
	-165.17	-131.92	1.75	0.02	0.59	14.46	Long-term TSS PC2, Short-term NTU PC2, Distance to 30 m
	-165.16	-132.39	1.76	0.02	0.59	14.18	Depth, Distance to 30 m
	-165.15	-132.84	1.77	0.02	0.59	13.91	**Long-term TSS PC1**

DEPENDENT VARIABLE	AICc	BIC	ΔAICc	wi.AICc	R²	EDF	BEST MODEL
	-165.04	-132.44	1.88	0.02	0.59	14.08	Long-term TSS PC2, Short-term TSS PC1, Short-term NTU PC2
	-165.02	-132.79	1.9	0.02	0.59	13.87	**Short-term TSS PC1**
Reef	-114.16	-86.49	0	0.06	0.42	11.34	Short-term NTU PC2, Distance to 30 m
	-114.02	-86.18	0.14	0.06	0.42	11.43	Long-term TSS PC2, Short-term NTU PC2, Distance to 30 m
	-113.65	-83.81	0.51	0.05	0.44	12.51	Depth, Distance to 30 m
	-113.48	-84.95	0.68	0.05	0.43	11.8	Short-term TSS PC1, Short-term NTU PC2, Distance to 30 m
	-113.17	-82.68	0.99	0.04	0.44	12.87	Depth, Short-term TSS PC1, Distance to 30 m
	-113.11	-83.45	1.04	0.04	0.43	12.42	Depth, Short-term NTU PC2, Distance to 30 m
	-112.96	-83.85	1.2	0.04	0.43	12.11	Long-term TSS PC1, Short-term NTU PC2, Distance to 30 m
	-112.82	-81.93	1.34	0.03	0.44	13.1	Depth, Long-term TSS PC1, Distance to 30 m
	-112.8	-83.6	1.36	0.03	0.43	12.16	Long-term TSS PC2, Distance to 30 m
	-112.67	-81.23	1.49	0.03	0.45	13.41	Depth, Short-term TSS PC2, Distance to 30 m
	-112.2	-82.58	1.96	0.02	0.43	12.39	**Long-term TSS PC2**
	-112.18	-82.22	1.98	0.02	0.43	12.58	**Distance to 30 m**

Table S11.4.2 Total number and commonality of all fish species (alphabetical by family and then genus) observed in the nearshore Pilbara region of north-west Australia.

FAMILY	TAXA	SUM ABUNDANCE	% SAMPLES
Acanthuridae	*Acanthurus dussumieri*	41	18.75
	Acanthurus grammoptilus	139	42.71
	Acanthurus triostegus	89	13.54
	Ctenochaetus striatus	13	10.42
	Naso annulatus	12	4.17
	Naso lituratus	2	2.08
	Naso unicornis	5	3.13
	Naso fageni	15	3.13
Apogonidae	*Cheilodipterus intermedius*	2	2.08
	Taeniamiav melasma	1037	10.42
Blenniidae	*Meiacanthus grammistes*	15	12.5
	Plagiotremus rhinorhynchos	7	7.29
Caesionidae	*Caesio cuning*	498	21.88
	Caesio teres	132	12.5
	Pterocaesio digramma	289	8.33
	Pterocaesio tile	48	4.17
Carangidae	*Carangoides fulvoguttatus*	62	4.17
	Gnathanodon speciosus	4	2.08
	Scomberoides commersonnianus	5	2.08
Carcharhinidae	*Carcharhinus amblyrhynchos*	1	1.04
Chaetodontidae	*Chaetodon aureofasciatus*	7	7.29
	Chaetodon auriga	6	4.17
	Chaetodon citrinellus	2	1.04
	Chaetodon lineolatus	3	2.08
	Chaetodon lunula	7	5.21
	Chaetodon trifascialis	2	2.08
	Chelmon marginalis	10	9.38
	Heniochus acuminatus	21	13.54
	Heniochus singularius	1	1.04
Echeneidae	*Platax teira*	1	1.04
Glaucosomatidae	*Glaucosoma magnificum*	8	3.13
Gobiidae	*Amblygobius phalaena*	2	1.04
	Valenciennea muralis	10	4.17
Grammistidae	*Diploprion bifasciatum*	8	4.17
Haemulidae	*Plectorhinchus multivittatus*	12	9.38
	Plectorhinchus polytaenia	1	1.04
Holocentridae	*Sargocentron spiniferum*	1	1.04
Labridae	*Anampses lennardi*	10	6.25
	Cheilinus chlorourus	15	12.5
	Cheilinus trilobatus	2	2.08
	Choerodon cyanodus	59	44.79
	Choerodon schoenleinii	59	36.46

FAMILY	TAXA	SUM ABUNDANCE	% SAMPLES
	Coris aygula	3	2.08
	Gomphosus varius	5	5.21
	Halichoeres hortulanus	1	1.04
	Halichoeres melanochir	145	65.63
	Halichoeres nebulosus	31	20.83
	Hemigymnus fasciatus	3	3.13
	Hemigymnus melapterus	18	16.67
	Hologymnosus doliatus	5	5.21
	Labroides dimidiatus	68	38.54
	Stethojulis bandanensis	15	11.46
	Stethojulis interrupta	114	26.04
	Thalassoma amblycephalum	4	2.08
	Thalassoma hardwicke	3	3.13
	Thalassoma lunare	63	34.38
	Thalassoma lutescens	29	14.58
	Anampses caeruleopunctatus	1	1.04
	Anampses geographicus	5	2.08
	Coris gaimard	9	7.29
	Halichoeres nigrescens	3	2.08
	Macropharyngodon meleagris	1	1.04
	Macropharyngodon negrosensis	2	2.08
	Pseudodax moluccanus	7	3.13
Latidae	*Psammoperca waigiensis*	4	4.17
Lethrinidae	*Lethrinus atkinsoni*	5	4.17
	Lethrinus genivittatus	1	1.04
	Lethrinus nebulosus	10	5.21
Lutjanidae	*Lutjanus carponotatus*	104	58.33
	Lutjanus fulviflamma	27	3.13
	Lutjanus lemniscatus	88	51.04
	Lutjanus rivulatus	1	1.04
	Symphorus nematophorus	1	1.04
Monacanthidae	*Cantherhines pardalis*	3	2.08
Mullidae	*Parupeneus barberinoides*	4	4.17
	Parupeneus indicus	30	16.67
Nemipteridae	*Pentapodus emeryii*	3	2.08
	Scolopsis bilineata	26	17.71
	Scolopsis monogramma	12	12.5
Ostraciidae	*Ostracion cubicus*	2	2.08
Plotosidae	*Paraplotosus butleri*	1	1.04
Pomacanthidae	*Chaetodontoplus duboulayi*	11	9.38
	Pomacanthus semicirculatus	1	1.04
	Pomacanthus sexstriatus	17	12.5
Pomacentridae	*Abudefduf bengalensis*	112	63.54
	Abudefduf sexfasciatus	106	22.92

FAMILY	TAXA	SUM ABUNDANCE	% SAMPLES
	Chromis cinerascens	11	4.17
	Neoglyphidodon nigroris	23	7.29
	Neopomacentrus azysron	588	22.92
	Neopomacentrus filamentosus	2047	57.29
	Pomacentrus coelestis	196	18.75
	Pomacentrus milleri	554	87.5
	Pomacentrus nagasakiensis	59	11.46
	Stegastes obreptus	111	53.13
	Abudefduf vaigiensis	2	2.08
	Chromis viridis	76	3.13
	Dischistodus prosopotaenia	3	2.08
	Neopomacentrus cyanomos	2	2.08
	Plectroglyphidodon lacrymatus	4	4.17
	Pomacentrus moluccensis	16	4.17
Pseudochromidae	*Labracinus lineatus*	17	15.63
Pteroidae	*Pterois volitans*	3	2.08
Scaridae	*Chlorurus sordidus*	17	7.29
	Scarus frenatus	4	2.08
	Scarus ghobban	69	19.79
	Scarus prasiognathos	17	7.29
	Scarus rivulatus	123	27.08
	Scarus rubroviolaceus	4	3.13
	Scarus schlegeli	78	12.5
	Scarus sp3	51	26.04
	Chlorurus rhakoura	2	1.04
	Hipposcarus longiceps	1	1.04
	Scarus chameleon	1	1.04
Serranidae	*Cephalopholis boenak*	3	3.13
	Cephalopholis miniata	1	1.04
	Epinephelus bilobatus	13	12.5
	Epinephelus fasciatus	12	11.46
	Epinephelus malabaricus	0	0
	Epinephelus polyphekadion	0	0
	Epinephelus quoyanus	1	1.04
	Plectropomus spp	38	23.96
	Cephalopholis argus	3	3.13
	Chromileptes altivelis	1	1.04
Siganidae	*Siganus doliatus*	97	22.92
	Siganus fuscescens	23	6.25
	Siganus lineatus	2	2.08
Sphyraenidae	*Sphyraena obtusata*	6	1.04
Zanclidae	*Zanclus cornutus*	3	2.08

Table S11.4.3 All generalised additive mixed models (GAMMs) within two units of the lowest Akaike Information Criterion (AICc) for predicting the species richness, abundance, and biomass of fish assemblages and feeding guilds (planktivorous omnivores [PO] and herbivorous scraper in the Pilbara. The Akaike information criterion (corrected for finite sample sizes; AICc), Bayesian information criterion (BIC), delta AIC (AIC differences), model weight (wi.AICc), the coefficient of determination (R^2), and model size (edf) were also reported. Best models are indicated in bold.

DEPENDENT VARIABLE	AICc	BIC	ΔAICc	wi.AICc	R²	EDF	BEST MODEL
Species richness	546.03	581.01	0	0.1	0.57	13.91	Consolidated, Long-term TSS PC1, Short-term NTU PC2
	546.95	582.43	0.92	0.06	0.57	14.37	**Consolidated, Long-term TSS PC1***
	547.67	583.52	1.63	0.04	0.58	14.53	Consolidated, Short-term NTU PC2, Distance to 30 m
	547.71	582.28	1.68	0.04	0.56	13.65	Stony corals (sqrt), Short-term NTU PC2, Distance to 30 m
	547.74	583.29	1.71	0.04	0.56	14.43	**Stony corals (sqrt), Distance to 30 m***
	547.9	583.92	1.87	0.04	0.58	14.73	Consolidated, Long-term TSS PC1, Distance to 30 m
	548.01	582.88	1.98	0.04	0.56	13.85	Stony corals (sqrt), Depth, Short-term NTU PC2
Total abundance	996.16	1,029.57	0	0.02	0.52	13.04	Distance to 30 m
	996.67	1,030.56	0.51	0.02	0.52	13.35	Long-term TSS PC2, Distance to 30 m
	996.7	1,030.65	0.54	0.02	0.52	13.39	Short-term TSS PC1, Distance to 30 m
	996.73	1,030.68	0.57	0.02	0.52	13.47	**Null***
	996.74	1,030.72	0.59	0.02	0.52	13.41	Long-term TSS PC1, Distance to 30 m
	996.77	1,030.73	0.61	0.02	0.52	13.38	Short-term TSS PC2, Distance to 30 m
	996.85	1,030.87	0.69	0.02	0.52	13.41	Short-term NTU PC2, Distance to 30 m
	997.11	1,031.44	0.95	0.02	0.52	13.71	Long-term TSS PC2
	997.14	1,031.57	0.98	0.02	0.52	13.68	Depth
	997.19	1,031.57	1.03	0.01	0.52	13.75	Short-term TSS PC1
	997.23	1,031.66	1.07	0.01	0.52	13.7	Long-term TSS PC1, Long-term TSS PC2, Distance to 30 m
	997.23	1,031.67	1.07	0.01	0.52	13.71	Long-term TSS PC2, Short-term TSS PC1, Distance to 30 m
	997.25	1,031.70	1.1	0.01	0.52	13.79	Short-term NTU PC2
	997.26	1,031.67	1.1	0.01	0.52	13.67	Long-term TSS PC2, Short-term NTU PC2, Distance to 30 m
	997.26	1,031.71	1.1	0.01	0.52	13.79	Long-term TSS PC1
	997.28	1,031.75	1.12	0.01	0.52	13.71	Short-term TSS PC1, Short-term TSS PC2, Distance to 30 m
	997.35	1,031.97	1.2	0.01	0.52	13.8	Depth, Short-term TSS PC1, Distance to 30 m
	997.36	1,031.89	1.2	0.01	0.52	13.75	Short-term TSS PC1, Short-term NTU PC2, Distance to 30 m
	997.41	1,031.96	1.25	0.01	0.52	13.76	Long-term TSS PC1, Short-term NTU PC2, Distance to 30

DEPENDENT VARIABLE	AICc	BIC	ΔAICc	wi.AICc	R^2	EDF	BEST MODEL
							m
	997.42	1,031.96	1.26	0.01	0.52	13.73	Long-term TSS PC1, Short-term TSS PC2, Distance to 30 m
	997.44	1,032.11	1.28	0.01	0.52	13.81	Depth, Short-term NTU PC2, Distance to 30 m
	997.59	1,032.37	1.43	0.01	0.52	14.01	Long-term TSS PC2, Short-term TSS PC1
	997.62	1,032.42	1.46	0.01	0.52	14.02	Long-term TSS PC1, Long-term TSS PC2
	997.63	1,032.43	1.47	0.01	0.52	14.02	Long-term TSS PC2, Short-term NTU PC2
	997.68	1,032.53	1.52	0.01	0.52	14.05	Short-term TSS PC1, Short-term NTU PC2
	997.76	1,032.67	1.6	0.01	0.52	14.09	Long-term TSS PC1, Short-term NTU PC2
	997.79	1,032.89	1.63	0.01	0.52	14.1	Consolidated, Distance to 30 m
	997.79	1,032.15	1.63	0.01	0.52	13.18	Short-term TSS PC2
	997.79	1,032.77	1.63	0.01	0.52	14	Depth, Short-term TSS PC1
	998.07	1,033.29	1.91	0.01	0.52	14.3	Long-term TSS PC2, Short-term TSS PC1, Short-term NTU PC2
	998.1	1,033.34	1.94	0.01	0.52	14.31	Long-term TSS PC1, Long-term TSS PC2, Short-term NTU PC2
	998.14	1,032.92	1.98	0.01	0.52	13.88	Stony corals (sqrt), Distance to 30 m
Total biomass	225.09	237.89	0	0.18	0.66	8.18	SD habitat relief, Long-term TSS PC2, Short-term TSS PC1
	225.53	236.24	0.44	0.15	0.6	5.06	**Long-term TSS PC2, Short-term TSS PC1 ***
	226.12	237.49	1.02	0.11	0.61	6.55	Stony corals (sqrt), Long-term TSS PC2, Short-term TSS PC1
PO abundance	617.83	656.04	0	0.04	0.61	15.12	**Macroalgae (log+1), Long-term TSS PC1***
	617.88	655.93	0.05	0.04	0.61	14.97	**Macroalgae (log+1), Short-term TSS PC1***
	618.17	650.8	0.33	0.03	0.56	12.14	SD habitat relief, Long-term TSS PC1, Distance to 30 m
	618.47	651.49	0.63	0.03	0.56	12.43	Reef (cube), Long-term TSS PC1, Distance to 30 m
	618.88	657.04	1.05	0.02	0.6	14.69	Macroalgae (log+1), Long-term TSS PC1, Distance to 30 m
	618.9	657.41	1.06	0.02	0.61	15.18	Macroalgae (log+1), Short-term TSS PC1, Distance to 30 m
	619.04	659.03	1.21	0.02	0.62	15.83	Mean habitat relief (cube), Macroalgae (log+1), Long-term TSS PC1
	619.06	652.22	1.22	0.02	0.56	12.42	Reef (cube), Short-term TSS PC1, Distance to 30 m
	619.06	657.79	1.23	0.02	0.61	15.48	Macroalgae (log+1), Depth, Long-term TSS PC1
	619.31	652.23	1.48	0.02	0.56	12.14	SD habitat relief, Short-term TSS PC1, Distance to 30 m

DEPENDENT VARIABLE	AICc	BIC	ΔAICc	wi.AICc	R^2	EDF	BEST MODEL
	619.42	652.74	1.58	0.02	0.56	11.89	Mean habitat relief (cube), Short-term TSS PC1, Short-term NTU PC2
	619.7	650.96	1.87	0.02	0.54	11.42	**Long-term TSS PC1, Distance to 30 m***
	619.79	653.71	1.96	0.01	0.56	12.94	Mean habitat relief (cube), Short-term TSS PC1, Distance to 30 m
PO biomass	-171.1	-148.28	0	0.04	0.12	5.73	Depth, Short-term NTU PC2
	-170.39	-143.55	0.71	0.03	0.15	8.2	Short-term TSS PC2
	-170.22	-142.94	0.88	0.03	0.15	8.53	Long-term TSS PC2
	-169.98	-147.17	1.12	0.02	0.11	6.12	Mean habitat relief (cube), Depth, Short-term NTU PC2
	-169.88	-143.61	1.22	0.02	0.14	7.61	**Null***
	-169.76	-143.84	1.34	0.02	0.13	7.16	Depth, Short-term TSS PC2
	-169.66	-143.16	1.44	0.02	0.14	7.59	Short-term NTU PC2
	-169.53	-145.57	1.57	0.02	0.11	6.44	Reef (cube), Depth, Short-term NTU PC2
	-169.46	-141.45	1.64	0.02	0.15	8.82	Long-term TSS PC2, Short-term NTU PC2
	-169.21	-140.73	1.89	0.02	0.16	9.23	Short-term TSS PC2, DistanceTo30m
	-169.14	-140.65	1.96	0.02	0.15	9.2	Short-term TSS PC1, Short-term TSS PC2
HS abundance	388.71	426.81	0	0.09	0.62	15.79	SD habitat relief, Stony corals (sqrt), Short-term NTU PC2
	388.99	425.23	0.27	0.08	0.6	14.53	SD habitat relief, Long-term TSS PC1, Short-term NTU PC2
	389.66	427.9	0.95	0.06	0.62	15.84	**SD habitat relief, Stony corals (sqrt)***
	389.83	426.26	1.11	0.05	0.6	14.71	**SD habitat relief, Long-term TSS PC1***
	390.14	428.74	1.43	0.04	0.62	16.03	SD habitat relief, Stony corals (sqrt), Short-term TSS PC2
	390.28	430.81	1.57	0.04	0.64	16.58	Mean habitat relief (cube), Consolidated, Short-term TSS PC1
	390.34	427.26	1.63	0.04	0.6	14.98	SD habitat relief, Long-term TSS PC1, Distance to 30 m
	390.53	427.43	1.81	0.04	0.6	14.91	SD habitat relief, Long-term TSS PC1, Short-term TSS PC2
HS biomass	228.27	248.71	0	0.46	0.37	7.34	**Stony Corals (sqrt), Depth, Short-term TSS PC2***

12. Management effectiveness

12.1 Baited video, but not diver video, detects a greater abundance of legal size target species within no-take areas

Authors: Haberstroh J**,** McLean D, Holmes T, Langlois T.

ABSTRACT

The inherent differences between baited video versus diver video survey methodologies may influence their ability to detect effects of fishing. Here the ability of no-take areas (NTAs) to provide detectable protection for legal sized individuals 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, *Lethrinus nebulosus*, *Epinephelus rivulatus* and *Carangoides fulvoguttatus*, were examined using both methodologies inside and outside no-take areas across the NMP. Stereo-BRUVs found positive effects of protection on the relative abundance of legal sized *C. fulvoguttatus* and *L. nebulosus* and larger sized *L. nebulosus* in no-take areas. Stereo-DOVs however did not detect any differences in relative abundance and size between areas open and closed to fishing. These contrasting results suggest that choice of sampling methodology can influence interpretations of the ability of no-take areas to provide adequate levels of protection for target species.

12.1.1 INTRODUCTION

No-take areas are used worldwide as a spatial management tool for conservation purposes (Edgar et al. 2014). No-take areas were initially used to provide unimpacted reference sites for scientific purposes, but many studies have subsequently shown that no-take areas are a useful tool to investigate the effects of extractive fishing on fish assemblages when contrasted with comparable unprotected areas (Gell and Roberts 2003, Westera et al. 2003, Denny et al. 2004, Watson et al. 2007). Increases in fish abundance (Buxton and Smale 1989, Alcala and Russ 1990, Pande et al. 2008), biomass (Russ and Alcala 1996, Roberts et al. 2001), length (Bornt et al. 2015) and species richness (Edgar and Barrett 1999, I. M. Cote 2001, Rife et al. 2013) have been observed within no-take areas in cases where stock depletion or ecosystem degradation existed prior to establishment. Additionally, no-take areas may act as an insurance measure against wider fisheries stock depletion (Roberts et al. 2001, Sale et al. 2005, Russ et al. 2008). Certainly evidence that no-take areas can mitigate the influences of extractive fishing in surrounding areas has been demonstrated worldwide (Claudet et al. 2008, Lester et al. 2009).

Appropriate tests of no-take area effectiveness require the use of methodologies that sample fish communities with a minimum of bias and selectivity (both species abundance and size composition). A range of sampling methodologies have been used to do so in marine ecosystems (e.g. Priede et al. 1994, Willis and Babcock 2000, Bornt et al. 2015). 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; Watson et al. 2007, Fitzpatrick et al. 2015) and diver operated stereo-video (stereo-DOV; 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 rapidly advancing technologies, decreasing costs, the benefits of maintaining a permanent record that can be revisited if required, and the ability to obtain accurate length measurements of a large proportion of the observed fish community (Watson et al. 2010, Holmes et al. 2013, Goetze et al. 2015). While there are a number of associated advantages, both methods however have limitations and can also introduce sources of bias which may influence the fish communities recorded (Langlois et al. 2010, Watson et al. 2010, Holmes et al. 2013, Goetze et al. 2015, Langlois et al. 2015). The presence of SCUBA divers as a part of the stereo-DOV method is a frequently considered bias in terms of fish behaviour (Lowry et al. 2012, Mallet and Pelletier 2014). SCUBA divers can have negative effects in causing avoidance behaviours in fishes, especially on larger mobile species that may be less likely to approach within the transect area or camera field of view (Cole et al. 2007, Watson et al. 2010, Goetze et al. 2015). Additionally, learned avoidance responses to divers or in-water disturbance as a result of fishing activity may create bias within datasets when comparing between fished and unfished areas (Gotanda et al. 2009, Januchowski-Hartley et al. 2012). In the case of the stereo-BRUV methodology, there has been considerable debate about the attractant effects that the use of bait has on the composition of the fish community and fish sizes sampled, particularly in the case of predatory species most likely to be targeted by extractive fishing (Harvey et al. 2007, Dorman et al. 2012). However, several studies have shown that a representative sample of the fish assemblage can still be observed when bait is used (Cappo et al. 2006, Harvey et al. 2007) and in addition, that bigger and rarer predators may be more effectively sampled than with diver-based techniques (Watson et al. 2005).

Comparisons of the assemblage structures recorded by different stereo-video sampling methods are ample (e.g. Watson et al. 2005, 2010, Langlois et al. 2010, Goetze et al. 2015). Stereo-BRUVs have previously been found to record higher overall abundances and species richness, while stereo-DOVs record some small-bodied species in higher abundance (Watson et al. 2010). The diversity and abundance of carnivorous (Langlois et al. 2010) and large-bodied species most likely to be targeted by extractive fishing (Watson et al. 2010) have also been observed to be greater using the stereo-BRUV method than with stereo-DOVs (Langlois et al. 2010). As the abundance and size structure of these groups are considered sensitive indicators of extractive fishing activity, it is essential to determine how these methodological biases may influence the ability to detect change between fish communities inside and outside of no-take areas. Such information is of high value to long term monitoring programs that aim to continually assess the effectiveness of spatial zoning as a key strategy in marine protected area management.

This study used both stereo-BRUV and stereo-DOV methodologies to assess the abundance and size structure of recreationally targeted fish species between fished and no-take areas (NTAs) within the Ningaloo Marine Park (NMP). The NMP is a large sub-tropical Marine Protected Area (MPA) situated on the mid-west coast of Australia, which is a popular recreational fishing location (CALM and MPRA 2005). The abundance of species targeted by fishers, and in particular those greater than legal size, are expected to be sensitive indicators of protection from fishing within no-take areas (Russ and Alcala 2004). It was hypothesised that the abundance of legal sized individuals and the length of targeted species is larger in no-take than in fished areas. Further, it was hypothesised that stereo-BRUVs identify differences between no-take and fished areas more clearly, due to their typically greater rates of detection of targeted fish species (Watson et al. 2010).

12.1.2 METHODS

Study Site

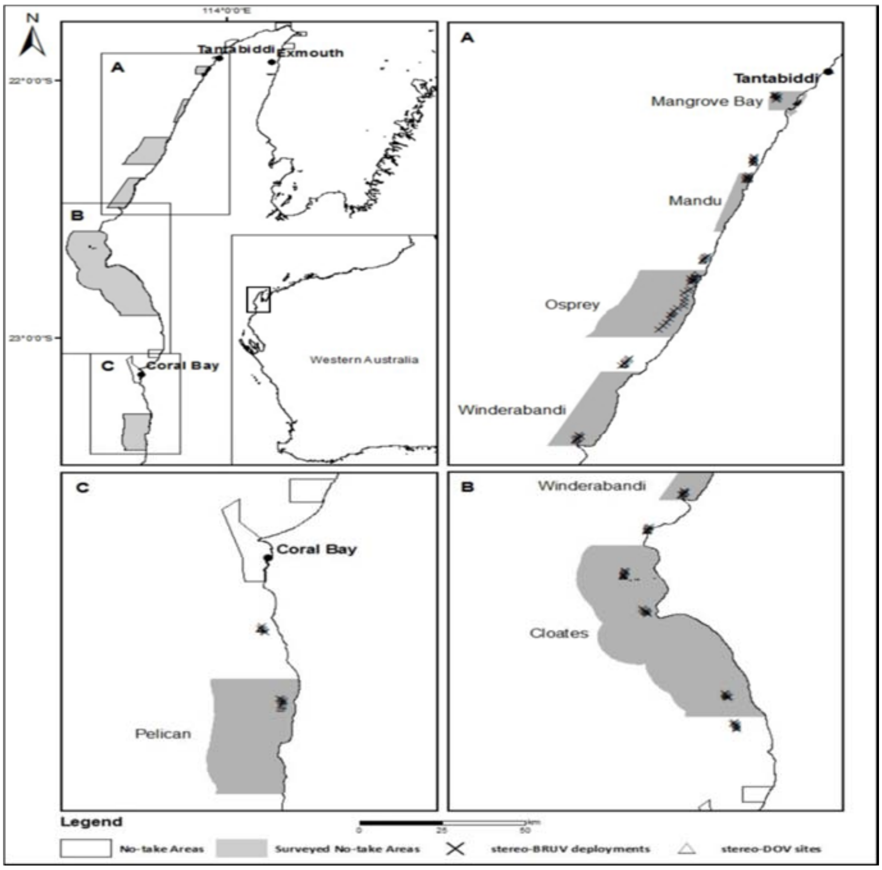

Figure 12.1.1 Overview and detailed maps (A, B and C) of the survey sites within the lagoon of the Ningaloo Marine Park, showing the baited remote underwater stereo-video deployments (cross) and the diver operated stereo-video sites (triangle) within the surveyed Sanctuary Zones (grey areas), Sanctuary Zones not surveyed are shown in white.

The Ningaloo Marine Park (NMP) is located adjacent to the North West Cape of Western Australia and covers a total area of 2633.43 km^2. It stretches along approximately 300 km of coastline from 23˚48'S to 21˚48'S (Figure 12.1.1; CALM and MPRA 2005, Smallwood et al. 2011). The NMP was first established in 1987 and was revised and extended in 2004 to incorporate the full length of the fringing coral reef (CALM and MPRA 2005, Watson et al. 2010). In 2011 the area was also listed as a World Heritage Site (Catlin et al. 2011). The NMP is divided into four different management zones, with the two major zones being the General Use Zone and the no-take areas (NTA; locally referred to as Sanctuary Zones), comprising 50% and 34% of the whole marine park respectively (CALM and MPRA 2005). The 18 separate NTAs in the NMP vary greatly in size, but together equate to a total area of 883.65 km^2 (CALM and MPRA 2005).

The focus of this research project was on the shallow lagoonal waters (depth ~0.5 – 8 m), inside and outside of six of the no-take areas within the NMP, in the area between Exmouth and Pelican Point (Figure 12.1.1). The six surveyed no-take areas were: Mangrove Bay (11.35 km^2), Mandu (13.49 km^2), Osprey (95.13 km^2), Winderabandi (55.26 km^2), Cloates (447.52 km^2) and Pelican (108.64 km^2; Figure 1C). Although any boat-based extractive uses are prohibited in the no-take areas surveyed here, shore-based recreational line fishing is permitted adjacent to the landward borders of no-take areas in some locations within the Osprey, Winderabandi, Cloates and Pelican no-take areas (CALM and MPRA 2005).

Experimental Design

The current study used stereo-DOV surveys collected as part of the existing long-term monitoring program (LTMP) conducted by the Department of Biodiversity, Conservation and Attractions (DBCA) of fish assemblages within the NMP. The survey areas are known to support a relatively high fish species richness and to encompass a range of site attached and mobile species, including common recreationally targeted species (CALM and MPRA 2005, Cassata and Collins 2008). Deployments followed a depth gradient and habitat which contains contiguous reef structure or broken up coral or rubble bordering the lagoon. Stereo-BRUV surveys were generally conducted at the same sites, with replicate deployments targeted towards comparable habitat during a subsequent collaborative sampling program conducted by The University of Western Australia and DBCA. The one exception to this occurred within the Osprey no-take area, 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. 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 no formal statistical comparison between the two sampling methods has been conducted. Instead simultaneous analyses of the effect of no-take areas and habitat covariates for both sampling methods were conducted. The design of the LTMP for the NMP is also established to provide information at the level of the marine park and is also lacking adequate replication to investigate the generality of any patterns in the fish assemblage for each no-take area surveyed.

The replicates of the stereo-BRUV deployments and stereo-DOV transects totalled 55 and 66 within no-take areas and 34 and 36 within the adjacent fished areas respectively. These replicates were summed into a total of 17 sites, which comprised either three to five independent replicate stereo-BRUV deployments or six replicate stereo-DOV belt transects (Figure 12.1.1).

Sampling Methods

BAITED REMOTE UNDERWATER STEREO-VIDEO (STEREO-BRUV)

Stereo-BRUV deployments were conducted by the Marine Ecology Group of The University of Western Australia, in a collaborative project with DBCA, over a ten day period in August 2015. A total of 109 deployments were conducted, of which some had to be excluded due to differing reasons. The minimum distance of ~250 m was maintained between deployments to minimise the likelihood of fish travelling between neighbouring deployments within the 60-minute deployment duration (see Cappo et al. 2004). This study used a stereo-BRUV system consisting of two paired GoPro HERO3+ cameras (Figure 12.1.2A). 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 1996, Langlois et al. 2010, Watson et al. 2010). To guarantee the accuracy of length measurements the cameras were calibrated prior to field work using the software CAL (Shortis and Harvey 1998, SeaGIS Pty Ltd 2014). 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. 2007, 2010). Approximately 1 kg of crushed pilchards (*Sardinops* spp) were used as bait, crushing is done to maximise the amount of fish oil and flesh released (Harvey et al. 2007, Langlois, Harvey, et al. 2012). The stereo-BRUV system was deployed on the seafloor by boat and set to automatically film for a period of 60 minutes.

DIVER-OPERATED STEREO-VIDEO (STEREO-DOV)

A total of 102 stereo-DOV transects were conducted by DBCA over a ten day period in August 2014. The stereo-DOV system consisted of two paired Canon Legria HF G25 cameras, following the same design as the stereo-BRUV system (Figure 12.1.2B). 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 were conducted at each site, with each transect being 50 m long and 5 m wide. A minimum distance of 10 m was maintained between each replicate transect, to avoid overlapping. SCUBA divers swam at an approximate speed of 1 m per 3 seconds staying circa 0.5 - 0.7 m above the substrate. The system was held at a slight downwards facing angle in order to keep the horizon line in the middle third of the video frame.

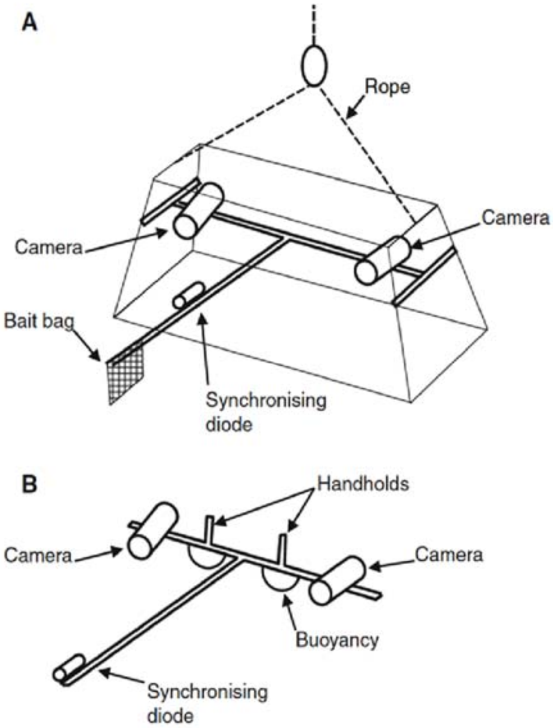

Figure 12.1.2 Stereo-video systems for surveying the fish assemblage, showing the setup of the baited remote underwater stereo-video system (A) and the diver operated stereo-video system (B). Source: Langlois et al. 2010.

Video Analysis

BAITED REMOTE UNDERWATER STEREO-VIDEO SYSTEM (STEREO-BRUV)

Prior to analysis, videos were converted into high definition AVI format using the software Xilisoft©. EventMeasure Stereo^{TM} was then used to accurately 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,* which could not be reliably distinguished from morphologically similar species from video imagery, these are herein referred to as *Scomberomorus* spp. The stereo-enabled capacity was used to measure distance and identify whether individuals were within the 7 m survey boundary. MaxN was used as the relative abundance of a species (herein referred to as abundance), which is defined as the maximum number of individuals from the same species present at any one time within the 60 minute video period (Priede et al. 1994). Using MaxN as a conservative measure of abundance prevents double counting of individuals which, might leave and re-enter the field of view throughout the video. 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 by recreational fishers at Ningaloo (Table S12.1.1; Pers. Com. T. Holmes). After identification, and at the time of MaxN for each species, the length of each individual fish was measured from the snout to the caudal fork (fork length; FL). The stereo-configuration in combination with the calibration of the video system provides accuracy and precision during the length measurement of fish using EventMeasure Stereo^{TM} (SeaGIS Pty Ltd 2014). Length data obtained was then used to identify which individuals of the targeted species were either equal to or greater than the minimum legal length (MLL) for retention, hereafter referred to as 'Legal sized' (see Table S12.1.1). Subsequently only these legal sized individuals were examined. For further information on additional species that were identified, 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 (Table S12.1.2).

For each deployment, the characteristic habitat type and percentage cover was determined using TransectMeasure^{TM} (SeaGIS Pty Ltd 2014). A freeze-frame of each video was overlaid with a 5 x 4 grid and the major habitat type of each grid was classified following the CATAMI classification scheme (Althaus et al. 2013), with some modifications. This resulted in the selection 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 building broad habitat types, rubble, macroalgae and black octocoral. The percent cover of each habitat type per freeze-frame was calculated with grids placed over open water excluded from this calculation. Additional to the habitat variables, vertical relief was classified on a scale from flat (0) to high structural complexity (5). With measures from every grid cell, the mean and standard deviation (SD) of relief could be calculated for each deployment and subsequently used in the analyses.

DIVER-OPERATED STEREO-VIDEO SYSTEMS (STEREO-DOV)

Videos from each transect were analysed using the same software as for stereo-BRUVs. Each individual recorded within the transect boundaries (i.e. 2.5 m to either side of the centerpoint of the cameras and 7 m distance) was identified to species level where possible and their FLs measured simultaneously. All identified fish were also assigned to either targeted or non-targeted species (Table S12.1.1). Length measurements obtained from the stereo-DOV transects were also used to identify legal sized individuals (see Table S12.1.1). The stereo-enabled capacity to measure distance was used here to restrain identifications to the sample boundaries of 7 m distance and 5 m width. Abundance was obtained by summing the individuals of each species within a transect.

Habitat classification followed the same procedure as described for the stereo-BRUV data. However, habitat and relief was estimated from five separate freeze-frames, which were evenly spaced over the length of each transect. This was followed by the calculation of the average percent habitat cover and relief per transect.

Statistical Analysis

Prior to analysis, the EventMeasure Stereo^{TM} outputs were checked and formatted using the R language for statistical computing (R Core Team 2015) and the packages 'dplyr' (Wickham and Francois 2016) and 'tidyr' (Wickham 2016) following scripts provided in Langlois et al. (2015). Additional information about data checking and formatting including examples and R scripts can be found at http://github.com/TimLanglois/Stereo-or-mono-video-annotation-workflows.

Relative abundance analysis 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: no-take areas, fished areas) and Site (random, nested within Status). Full-subset generalised additive mixed models (GAMMs; Lin and Zhang 1999) were used to identify the correlation between the abundance of each species of interest and the Status and habitat variables, and the interaction between Status and habitat. GAMMs are an extension of generalised additive models (GAMs; Hastie and Tibshirani 1986), which in contrast to GAMs, use a sum of smooth functions to model covariate effects instead of a linear form. Models were fitted to untransformed abundance data, as GAMMs can account for nonnormal distribution of the data, using a Tweedie error distribution (Tweedie 1984). GAMMs were performed using the package 'mgcv' in the R language for statistical computing (R Core Team 2015). Habitat variables were tested for correlation with each other ($|R| > 0.9$ led to exclusion) and their distributions examined, transformations were applied where necessary to reduce the influence of outliers. This resulted in the utilisation of the variables mean relief, SD relief, sand, stony coral and reef.

The corrected Akaike Information Criterion (AICc; Akaike 1973, Hurvich and Tsai 1989) was used for model selection. The best model was one within two AICc units of the lowest AICc (Burnham and Anderson 2002) and with the fewest variables (most parsimonious). This model selection was based on the weak evidence shown to favour one model over another within AICc values that differ by less than two units (Raftery 1995, Burnham and Anderson 2002).

12.1.3 RESULTS

In total 13 recreationally targeted fish species were recorded from the 89 stereo-BRUV deployments and 102 stereo-DOV transects (Table S12.1.1). Stereo-BRUVs recorded 12 different targeted species, while only eight species were recorded by stereo-DOVs. The targeted species *Lethrinus laticaudis* (grass emperor) was unique to stereo-DOVs, while five species (*Gymnocranius grandoculis* (Robinson's seabream), *Scomberomorus* spp (mackerel), *Cephalopholis sonnerati* (tomato rockcod), *Epinephelus coioides* (estuary cod) and *Variola louti* (yellow-edged coronation trout) were only recorded on stereo-BRUVs (Table S12.1.1). Both methods only recorded legal sized individuals from three species (*Carangoides fulvoguttatus* (goldspotted trevally), *Epinephelus rivulatus* (chinaman rockcod) and *Lethrinus nebulosus* (spangled emperor), individuals from the remaining ten species recorded by both methods were either below legal size or the sample size was too small to allow for analysis (Table S12.1.1).

The two methods recorded rather varying numbers of the highly targeted species *L. nebulosus*, while stereo-BRUVs recorded only 109 individuals, 429 individuals were recorded on stereo-DOVs (Table

S12.1.1). However, ~35% of the measured individuals recorded on stereo-BRUVs were of legal size, opposed to only ~5.5% on stereo-DOVs (Table S12.1.1). Additionally, the percent of transects in which *L. nebulosus* were recorded on stereo-DOVs was ~28% compared to ~66% of the stereo-BRUV deployments (Table S12.1.1).

Distribution patterns

The best model from the GAMM analysis for the abundance of *L. nebulosus* in the stereo-BRUV data included an interaction between the fishing status and the mean and the SD of relief, which explained 45% of the variation in their distribution (Table 12.1.1). Both of these interactions indicated that the abundance of *L. nebulosus* was higher in no-take areas, however with increased levels of mean relief the abundance in protected areas decreased, while increased levels of the SD of relief in protected areas correlated with a higher abundance of *L. nebulosus* (Figure 12.1.3; Figure 12.1.4). However, the only significant correlation detected for *L. nebulosus* in stereo-DOV transects was a negative correlation of their abundance with the percent cover of reef, explaining 31% of the distribution (Table 12.1.1; Figure 12.1.3; Figure 12.1.4).

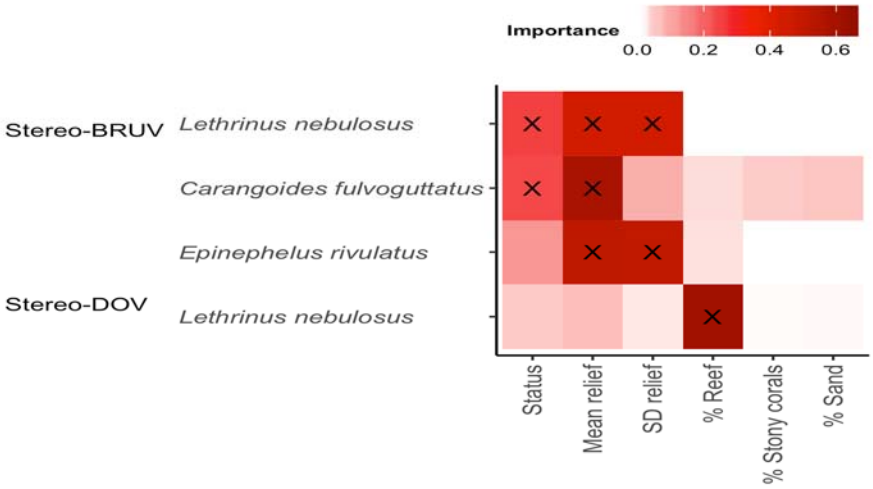

Figure 12.1.3 Variable importance scores from full-subset generalised additive mixed models analyses to predict the abundance distribution of *Lethrinus nebulosus*, *Carangoides fulvoguttatus* and *Epinephelus rivulatus* on stereo-BRUVs and stereo-DOVs, inside and outside the no-take areas across the Ningaloo Marine Park, predictor variables within the most parsimonious model for each response variable are indicated (P, see Table 12.1.1).

The best model for the abundance of *C. fulvoguttatus* in the stereo-BRUV deployments explained 39% of the variation in their distribution (Table 12.1.1). Overall abundance of *C. fulvoguttatus* in stereo-BRUVs was higher in no-take areas than fished areas (Figure 12.1.3; Figure 12.1.4). Additionally, the abundance of *C. fulvoguttatus* in the stereo-BRUV data, was correlated with intermediate levels of mean relief (Table 12.1.1; Figure 12.1.3; Figure 4).

The abundance of the targeted species *E. rivulatus* was correlated with intermediate levels of both mean and SD of relief, which explained 51% of the variation in the distribution, when recorded on stereo-BRUVs (Table 12.1.1; Figure 12.1.3; Figure 12.1.4). The occurrence of *C. fulvoguttatus* and *E. rivulatus* was too low (<10% of the transects) to allow for statistical analysis from stereo-DOV transects.

Table 12.1.1 Best models for the prediction of the abundance distribution of legal sized targeted species recorded on stereo-BRUVs and stereo-DOVs, inside and outside the no-take areas across the Ningaloo Marine Park from the full-subset generalised additive mixed models. Difference between lowest reported corrected Akaike Information Criterion (ΔAICc), AICc weights (ωAICc), variance explained (R^2) 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	ΔAICC	ΩAICC	R^2	EDF
Ningaloo Marine Park						
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
		Mean Relief	0.34	0.28	0.38	12.53
	Epinephelus rivulatus	Mean Relief + SD Relief	0	0.58	0.51	17.43
		Mean Relief + SD Relief + Status	0.97	0.36	0.51	17.80
stereo-DOV	*Lethrinus nebulosus*	Reef	0	0.80	0.31	7.42

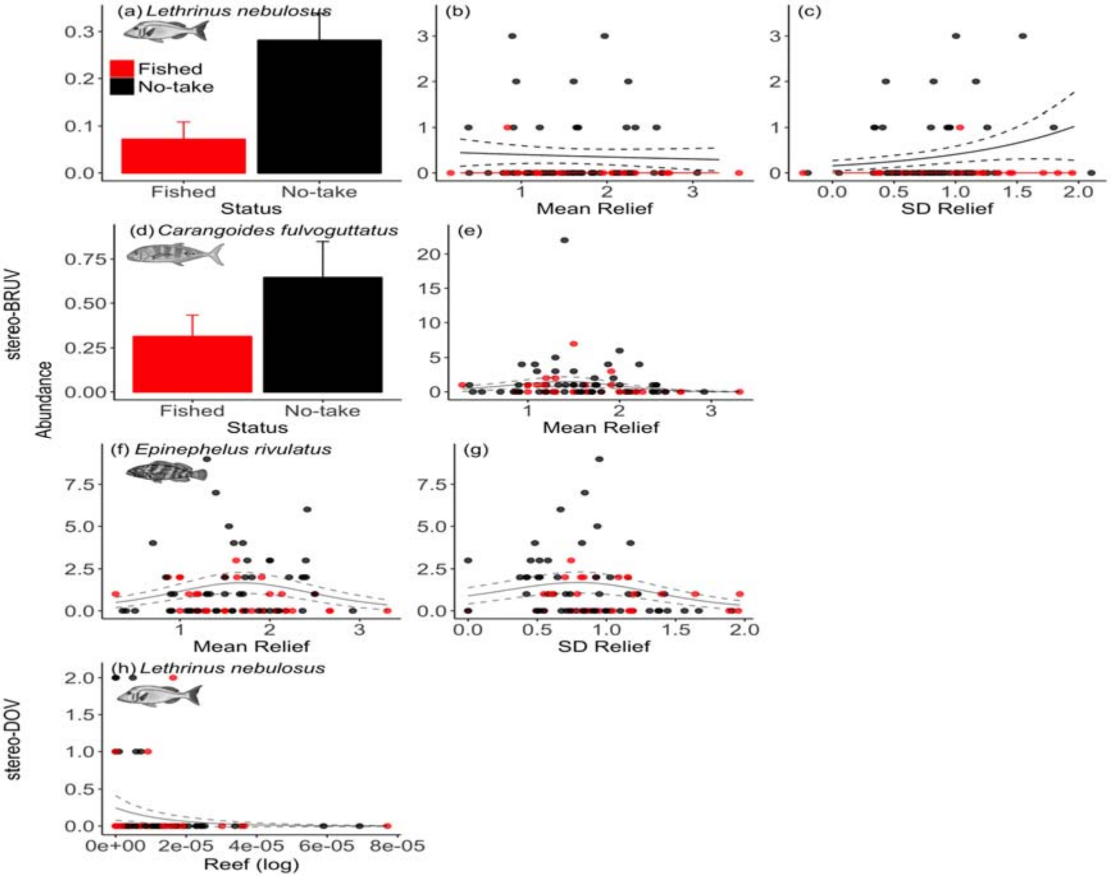

Figure 12.1.4 Important variables for each species recorded with stereo-BRUVs and stereo-DOVs, retrieved from the best model fitted using full-subset generalised additive mixed models; the correlation between the mean abundance +/- SE and the fishing status (a, d) and the residual abundance with the habitat variables (b, c, e - h) is shown; solid lines show the estimated smoothing curve, dashed lines show +/- 2SE of the estimated smoothing curve, interactions of variables are indicated with a red line for fished and a black line no-take locations.

Length patterns

Of the *L. nebulosus* measured from stereo-BRUV records in no-take areas 44% were larger than the minimum legal size of 410 mm as opposed to only 6.25% in fished areas. While 37% of the individuals measured on stereo-DOVs in no-take areas where larger than the minimum legal size and only 0.8% in fished areas. Length records of *C. fulvoguttatus* from stereo-BRUV deployments in no-take and fished areas did not show differences. However, the number of length measurements are more than three-fold higher in protected areas than fished areas (Figure 12.1.5). Stereo-BRUVs also observed higher abundance of *C. fulvoguttatus* inside no-take areas (Figure 12.1.4). Additionally, the number of *E. rivulatus* measured in no-take areas was three-fold higher than in fished areas, using stereo-BRUVs, with larger individuals in no-take than fished areas (Figure 12.1.5).

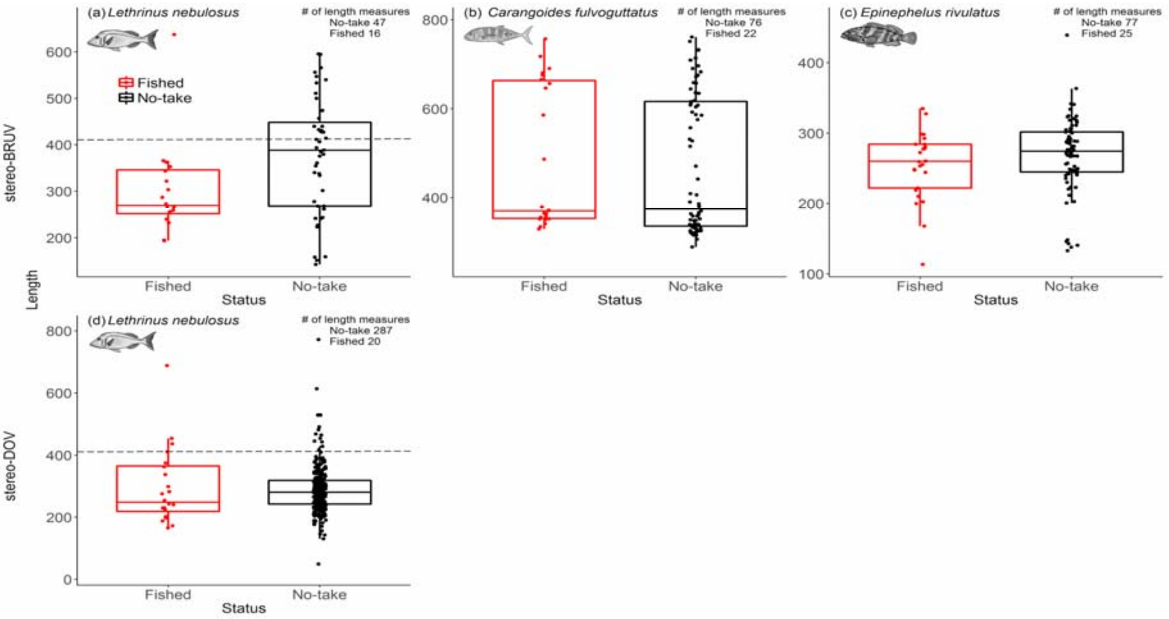

Figure 12.1.5 Correlation between the length and the fishing status for each species recorded with stereo-BRUVs and stereo-DOVs; dashed lines indicate the minimum legal length for retention if applicable.

12.1.4 DISCUSSION

Comparisons of fish assemblages between fished and no-take areas can use a variety of survey methods, despite studies showing that different methodologies can reveal different aspects of the assemblage (e.g. Goetze et al. 2015). Here, stereo-BRUVs were found to sample a greater abundance of legal size recreationally targeted species than stereo-DOVs, irrespective of the management zone. Further, stereo-BRUVs more frequently indicated differences in the abundance of legal sized recreationally target species between fished and no-take areas (Table 12.1.1; Figure 12.1.3; Figure 12.1.4). Overall these results suggest that stereo-BRUVs may be a more powerful and sensitive method to investigate differences in the abundance of legal size recreationally targeted species across the Ningaloo Marine Park. This is likely due to a combination of factors such as the use of bait (Willis and Babcock 2000, Watson et al. 2005, Harvey et al. 2007), responses of target species towards the presence of a SCUBA diver (Watson and Harvey 2007, Goetze et al. 2015) and other methodological differences (e.g. the sampling duration; Watson 2006).

The differences observed in the total number, the number of measured individuals and the percentages of legal sized individuals of *L. nebulosus* recorded with each method could be a result of different biases. The use of MaxN, as a measure of 'relative abundance' in the stereo-BRUV method, could for example introduce biases, as individuals of the same species but of varying sizes might be present at different times of the recording and thus larger individuals may displace small ones during the time of the deployment (Watson et al. 2010). This can additionally be enhanced by the use of bait in stereo-BRUV deployments, which might cause greater attraction of faster moving larger individuals which cover a greater distance than juveniles (Grüss et al. 2011). Further, larger schools of juvenile *L. nebulosus* were recorded on stereo-DOVs, but not on stereo-BRUVs, within several sites in no-take areas. This could explain why differences in the length patterns were observed by the stereo-BRUVs but not the stereo-DOVs. A further possible explanation for the reduced numbers of larger *L. nebulosus* recorded on stereo-DOVs might be that legal sized recreationally targeted species are avoiding the SCUBA divers present during the stereo-DOV sampling (Watson and Harvey 2007, Goetze et al 2015). Relationships between a larger body size and increased wariness, i.e. the approach distance of an individual towards a diver, have been reported for several different fish families and species (Kulbicki 1998, Januchowski-Hartley et al. 2011). Further, previous studies have observed that the flight-initiation distance of target species, due to the presence of SCUBA divers increases with increasing fishing pressure (Feary et al. 2011, Januchowski-Hartley et al. 2012). Although certain species are protected from spearfishing within the Ningaloo Marine Park, Lethrinidae and in particular *L. nebulosus* can be targeted by spearfishing (Pers. Com. T. Holmes). Even though protection from fishing within no-take areas or protected areas has previously been found to decrease the flight-initiation distance of targeted species (Januchowski-Hartley 2012), a study of the movement patterns of *L. nebulosus* within no-take areas at Ningaloo has suggested that their home-ranges frequently cross the boundaries of the no-take areas (Pillans et al. 2014). Thus, although the results from the stereo-BRUVs suggest *L. nebulosus* populations are provided with a certain level of protection within the no-take areas, the lack of a difference in the stereo-DOV results suggests they are still exposed to a certain level of fishing pressure. This might be possibly due to the movement between fished and no-take areas, which may influence their rate of detection by the diver based sampling method. Stereo-BRUVs, through the use of bait attracting these carnivorous target species, likely also had improved power to detect differences between no-take areas and fished locations (Willis and Babcock 2000, Watson et al. 2005, Harvey et al. 2007). These differing results between stereo-BRUVs and stereo-DOVs seem to indicate that stereo-BRUVs probably have a greater ability to detect the effects that the protection with no-take areas has on legal sized individuals from targeted species within the NMP. However, to identify if either method is more suitable for the long-term monitoring program at the NMP, additional comparisons that include further target and non-target species are needed.

Caution should be used when interpreting the positive results for highly mobile species within the current study. Several studies have indicated that protection from fishing might not affect highly mobile species (e.g. Walters et al. 2007, Le Quesne and Codling 2009, Grüss et al. 2011). Indeed, the higher abundance within no-take areas observed on stereo-BRUVs for the pelagic species *C. fulvoguttatus* should be viewed with caution. These species is easily capable of swimming between adjacent stereo-BRUV deployments (~250 m) during the 60 minutes of the video. An indication for this would be the consistent presence of schools of these species between adjacent stereo-BRUV deployments, however this was not observed. Therefore, the findings of the current study suggest that no-take areas within the NMP provide a certain level of protection for the most targeted species *L. nebulosus* and potentially for the highly mobile species *C. fulvoguttatus*.

Wilson et al. (2012) previously suggested that, within the NMP, the influence of habitat could potentially be greater or confound any evidence of protection from fishing within the no-take areas. The current study found that the distribution of the target species considered was partially influenced by habitat. Implementation of the original no-take areas within the NMP was focused on representative areas of high biological and structural diversity (CALM and MPRA 1989) which could potentially confound a comparison of the fish assemblage between fished and protected areas. The current study has attempted to account for the influence of habitat by including habitat composition and relief variables as covariates in the tests of the effect of the protection status. For example, separate interactions between the protection status and both mean and SD of relief were found to explain the distribution patterns of *L. nebulosus* when recorded with stereo-BRUVs. These interactions indicated that increased abundance of legal sized *L. nebulosus* were found in no-take areas where mean relief decreases and where the SD of relief increases. This pattern matches observations that found that *L. nebulosus* tend to be more abundant on sand adjacent to reef habitats (Ayling and Ayling 1987). However, stereo-DOVs only recorded a reduction in the abundance of legal sized *L. nebulosus* with increasing percent cover of reef. This contradicts with findings of McLean et al. (2016) who reported that the abundance of some targeted species was lowest in the Pilbara where the percent cover of reef was lowest. Reduced abundance of legal sized individuals on stereo-DOVs could be related to the biases introduced by the presence of SCUBA divers, as discussed previously. Increased reef cover could reduce the ability to detect and therefore count and measure individuals on transects. However, a negative correlation between the abundance of legal sized individuals on stereo-DOVs and the level of habitat complexity was not found here. Though, it could be argued that the percent cover of reef implies also an increased complexity, being composed of habitat variables with higher complexities. The effect of varying habitats on the ability of stereo-DOVs to reliably detect differences between fished and no-take areas should be investigated further by increasing the habitat variables (finer scale) and the fish species included in the analysis.

A study by Fitzpatrick (2012) partially supports the findings of the distribution patterns of *E. rivulatus* found in the current study. Fitzpatrick (2012) reported an association of *E. rivulatus* with inshore reef pavements and Porites coral bommie zones. However, sampling across a greater range of habitats, Fitzpatrick (2012) also observed a higher abundance and size of *E. rivulatus* in protected areas within the NMP, which was not observed here. An explanation for this could be that the sites surveyed were stratified for coral dominated habitats whereas *E. rivulatus* has previously been found to be strongly related to high algal cover (Ayling and Ayling 1987, Mackie and Black 1996). Additionally, the distribution of *C. fulvoguttatus* was also partially influenced by the level of mean relief (Table 12.1.1; Figure 12.1.3; Figure 12.1.4). It has been shown that the structural complexity of habitats positively influences fish abundance, diversity and distribution (Newman and Williams 2001, Willis and Anderson 2003, Wilson et al. 2012). This is likely related to an increased availability of food resources and refuges from predation. Both, *E. rivulatus* and *C. fulvoguttatus*, are generalist carnivores thus the utilisation of complex habitats as food resources is likely.

The results from this study show that the no-take areas within the NMP can provide protection for targeted species resulting in greater abundance of legal size individuals. However, as predicted stereo-BRUVs more frequently detected differences between fished and no-take areas than stereo-DOVs. Abundance of legal sized *C. fulvoguttatus* and the abundance and size of the highly targeted specie *L. nebulosus* was higher in no-take areas, but only on stereo-BRUV deployments. Thus stereo-BRUVs are likely to be a more suitable method for any long-term monitoring program aiming to observe changes in these indicator species and to evaluate the adequacy of the existing no-take marine areas. In addition, strong evidence of the influence of habitat on distribution patterns was observed, including a clear example of interacting effects of habitat and protection from fishing on abundance. Long-term monitoring of no-take areas is incredibly important not only to assess the impacts and recovery from fishing effects (Babcock et al. 2010) but also as an indicator of large-scale and long-term change (Wernberg et al. 2016). However, consistent sampling methods are required to allow the interpretation of these patterns and the current study indicates that the choice of sampling methods can have a large impact on conclusions that might be reached about the effectiveness of no-take areas or changes in the body-size distribution of targeted species.

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12.1.6 REFERENCES

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: International Symposium on Information Theory. 267–281

Alcala AC and Russ GR (1990) A direct test of the effects of protective management on a tropical marine reserve. J Cons int Explor 46:40–47

Althaus F, Hill N, Edwards L, Ferrari R, *et al* Others (2013) CATAMI Classification Scheme for scoring marine biota and substrata in underwater imagery – A pictorial guide to the Collaborative and Annotation Tools for Analysis of Marine Imagery and Video (CATAMI) classification scheme. Version 1.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Anderson MJ, Robinson J (2003) Generalized discriminant analysis based on distances. Aust New Zeal J Stat 45:301–318

Anderson MJ and Willis TJ (2003) Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. Ecology 84:511–525

Ayling AM and Ayling AL (1987) Ningaloo Marine Park: Preliminary Fish Density Assessment and Habitat Survey: With information on coral damage due to Drupella cornus grazing. Rep Prep Dep Conserv L Manag by Sea Res Daintree, Queensl:19

Babcock RC, Haywood M, Vanderklift MA, Clapin G, Dennis D, Skewes T, Milton D, Murphy N, Pillans RD and Limbourn A (2008) Ecosystem impacts of human usage and the effectiveness of zoning for biodiversity conservation: broad-scale fish census. Final analysis and recommendations 2007:100

Babcock RC, Kelly S, Shears NT, Walker JW and Willis TJ (1999) Changes in community structure in temperate marine reserves. Mar Ecol Prog Ser 189:125–134

Babcock RC, Shears NT, Alcala AC, Barrett NS, Edgar GJ, Lafferty KD, McClanahan TR and Russ GR (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proc Natl Acad Sci U S A 107:18256–61

Ballantine B (2014) Fifty years on: Lessons from marine reserves in New Zealand and principles for a worldwide network. Biol Conserv 176:297–307

Boersma PD and Parrish JK (1999) Limiting abuse: Marine protected areas, a limited solution. Ecol Econ 31:287–304

Bornt KR, McLean DL, Langlois TJ, Harvey ES, Bellchambers LM, Evans SN and Newman SJ (2015) Targeted demersal fish species exhibit variable responses to long-term protection from fishing at the Houtman Abrolhos Islands. Coral Reefs 34:1297–1312

Bowman AW and Azzalini A (1997) Applied Smoothing Techniques for Data Analysis: The Kernel Approach with S-Plus Illustrations. Oxford Univ Press Oxford

Burnham KP and Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach.

Buxton CD and Smale MJ (1989) Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape coast. J Appl Ecol 26:441–451

CALM, MPRA (1989) Ningaloo Marine Park Management Plan 1989 - 1999. Department of Conservation and Land Management, Perth, Western Australia.

CALM, MPRA (2005) Management Plan for the Ningaloo Marine Park and Muiron Islands Marine Management Area: 2005-2015. Management Plan No. 52. Perth, Western Australia

Cappo M, Harvey E and Shortis M (2006) Counting and measuring fish with baited video techniques - an overview. Cutting-Edge Technol Fish Sci:101–114

Cappo M, Speare P and De'Ath G (2004) Comparison of baited remote underwater video stations (BRUVs) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. J Exp Mar Bio Ecol 302:123–152

Cassata L and Collins LB (2008) Coral reef communities, habitats, and substrates in and near sanctuary zones of Ningaloo Marine Park. J Coast Res 241:139–151

Catlin J, Jones T and Jones R (2011) Balancing commercial and environmental needs: licensing as a means of managing whale shark tourism on Ningaloo reef. J Sustain Tour 20:163–178

Clarke K and Gorley R (2006) PRIMER v6, User Manual/Tutorial. PRIMER-E, Plymouth, 192pp.

Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, Garcia-Charton JA, Perez-Ruzafa A, Badalamenti F, Bayle-Sempere J, Brito A, Bulleri F, Culioli JM, Dimech M, Falcon JM, Guala I, Milazzo M, Sanchez-Meca J, Somerfield PJ, Stobart B, Vandeperre F, Valle C and Planes S (2008) Marine reserves: Size and age do matter. Ecol Lett 11:481–489

Claudet J, Osenberg CW, Domenici P, Badalamenti F, Milazzo M, Falcon JM, Berticco I, Benedetti-Cecchi L, Garcia-Charton J-A, Goni R, Borg JA, Forcada A, Lucia GA De, Perez-Ruzafa A, Afonso P, Brito A, Guala I, Direach L Le, Sancchez-Jerez P, Somerfield PJ and Planes S (2010) Marine reserves: Fish life history and ecological traits matter. Ecol Appl 20:830–839

Cole RG (1994) Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in Northeastern New Zealand. Biol Conserv 70:93–99

Cole RG, Syms C, Davey NK, Gust N, Notman P, Stewart R, Radford CA, Carbines G, Carr MH and Jeffs AG (2007) Does breathing apparatus affect fish counts and observations? A comparison at three New Zealand fished and protected areas. Mar Biol 150:1379–1395

Collins DL, Langlois TJ, Bond T, Holmes TH, Harvey ES, Fisher R and McLean DL (2016) A novel stereo-video method to investigate fish-habitat relationships. Methods Ecol Evol

Cooke SJ and Cowx IG (2006) Contrasting recreational and commercial fishing: Searching for common issues to promote unified conservation of fisheries resources and aquatic environments. Biol Conserv 128:93–108

Cote IM, Mosquera I and Reynolds JD (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. J Fish Biol 59:178–189

Denny CM, Willis TJ and Babcock RC (2004) Rapid recolonisation of snapper Pagrus auratus: Sparidae within an offshore island marine reserve after implementation of no-take status. Mar Ecol Prog Ser 272:183–190

Dorman SR, Harvey ES and Newman SJ (2012) Bait effects in sampling coral reef fish assemblages with stereo-BRUVs. PLoS One 7:1–12

Edgar GJ and Barrett NS (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. J Exp Mar Bio Ecol 242:107–144

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro M a, Bernard ATF, Berkhout J, Buxton CD, Campbell SJ, Cooper AT, Davey M, Edgar SC, Försterra G, Galván DE, Irigoyen AJ, Kushner DJ, Moura R, Parnell PE, Shears NT, Soler G, Strain EM and Thomson RJ (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–20

Feary DA, Cinner JE, Graham NAJ, and Januchowski-Hartley FA (2011) Effects of Customary Marine Closures on Fish Behaviour, Spear-Fishing Success, and Underwater Visual Surveys. Conserv Biol 25:341–349

Fitzpatrick BM (2012) Coral reef fish habitat associations and implications for research, monitoring and the design of marine protected areas

Fitzpatrick BM, Harvey ES, Langlois TJ, Babcock R and Twiggs E (2015) Effects of fishing on fish assemblages at the reefscape scale. Mar Ecol Prog Ser 524:241–253

Froese R and Pauly. D (2015) Fishbase. FishBase

Gell FR and Roberts CM (2003) Benefits beyond boundaries: The fishery effects of marine reserves. Trends Ecol Evol 18:448–455

Goetze JS, Jupiter SD, Langlois TJ, Wilson SK, Harvey ES, Bond T and Naisilisili W (2015) Diver operated video most accurately detects the impacts of fishing within periodically harvested closures. J Exp Mar Bio Ecol 462:74–82

Graham NAJ and Nash KL (2012) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326

Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ and White AT (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev 90:1215–1247

Grüss A, Kaplan DM and Hart DR (2011) Relative impacts of adult movement, larval dispersal and harvester movement on the effectiveness of reserve networks. PLoS One 6

Halpern BS (2003) The Impact of Marine Reserves: Do Reserves Work and Does Reserve Size Matter? Ecol Appl 13:S117–S137

Halpern BS and Warner RR (2002) Marine reserves have rapid and lasting effects. Ecol Lett 5:361–366

Harvey ES, Cappo M, Butler JJ, Hall N and Kendrick GA (2007) Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Mar Ecol Prog Ser 350:245–254

Harvey E and Shortis M (1996) A system for stereo-video measurement of subtidal Organisms. Mar Technol Soc J 29:10–22

Hastie T and Tibshirani R (1986) Generalized Additive Models. Stat Sci 1:297–310

Hilborn R, Stokes K, Maguire JJ, Smith T, Botsford LW, Mangel M, Orensanz J, Parma A, Rice J, Bell J, Cochrane KL, Garcia S, Hall SJ, Kirkwood GP, Sainsbury K, Stefansson G and Walters C (2004) When can marine reserves improve fisheries management? Ocean Coast Manag 47:197–205

Holmes TH, Wilson SK, Travers MJ, Langlois TJ, Evans RD, Moore GI, Douglas RA, Shedrawi G, Harvey ES and Hickey K (2013) A comparison of visual- and stereo-video based fish community assessment methods in tropical and temperate marine waters of Western Australia. Limnol Oceanogr Methods 11:337–350

How JR (2013) The biology and ecology of epinephilidae species and their implications to fisheries management.

Hurvich CM and Tsai C-L (1989) Regression and time series model selection in small samples. Biometrika 76:297–307

Januchowski-Hartley FA, Graham NAJ, Feary DA, Morove T and Cinner JE (2011) Fear of fishers: Human predation explains behavioural changes in coral reef fishes. PLoS One 6

Januchowski-Hartley FA, Nash KL and Lawton RJ (2012) Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. Mar Ecol Prog Ser 469:113–119

Jind S (2012) A comparison of two underwater visual sampling techniques used to estimate tropical reef fish communities

Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. J Exp Mar Bio Ecol 222:11–30

Langlois TJ, Anderson MJ and Babcock RC (2005) Reef-Associated Predators Influence Adjacent Soft-Sediment Communities. 86:1508–1519

Langlois TJ and Ballantine WJ (2005) Marine ecological research in New Zealand: Developing predictive models through the study of no-take marine reserves. Conserv Biol 19:1763–1770

Langlois TJ, Fitzpatrick BR, Fairclough D V., Wakefield CB, Hesp SA, McLean DL, Harvey ES and Meeuwig JJ (2012) Similarities between Line Fishing and Baited Stereo-Video Estimations of Length-Frequency: Novel Application of Kernel Density Estimates. PLoS One 7:1–9

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G and Watson DL (2010) Cost-efficient sampling of fish assemblages: Comparison of baited video stations and diver video transects. Aquat Biol 9:155–168

Langlois TJ, Harvey ES and Meeuwig JJ (2012) Strong direct and inconsistent indirect effects of fishing found using stereo-video: Testing indicators from fisheries closures. Ecol Indic 23:524–534

Langlois TJ, Newman SJ, Cappo M, Harvey ES, Rome BM, Skepper CL and Wakefield CB (2015) Length selectivity of commercial fish traps assessed from in situ comparisons with stereo-video: Is there evidence of sampling bias? Fish Res 161:145–155

Legg CJ and Nagy L (2006) Why most conservation monitoring is, but need not be, a waste of time. J Environ Manage 78:194–199

Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airam S and Warner RR (2009) Biological effects within no-take marine reserves: A global synthesis. Mar Ecol Prog Ser 384:33–46

Liao JG, Wu Y and Lin Y (2010) Improving Sheather and Jones' bandwidth selector for difficult densities in kernel density estimation. J Nonparametr Stat 22:105–114

Lin X and Zhang D (1999) Inference in generalized additive mixed models by using smoothing splines. J R Stat Soc - Ser B Stat Methodol 61:381–400

Lincoln SMP (1988) Improving multispecies rocky reefs fish censuses by counting different groups of species using different procedures. Environ Biol Fishes 26:29–37

Lowry M, Folpp H, Gregson M and Suthers I (2012) Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries. J Exp Mar Bio Ecol 416–417:243–253

Mackie M and Black R (1996) Research on two serranid species (Serranidae: Epinephelinae) in Western Australian waters. (I) The biology, ecology, and mechanisms of sex-change in the chinaman cod (Epinephelus rivulatus) at Ningaloo Reef. (II) The biology of the bar-cheeked coral trout. 57:142 pp

Mallet D and Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952-2012). Fish Res 154:44–62

McLaren BW, Langlois TJ, Harvey ES, Shortland-Jones H and Stevens R (2015) A small no-take marine sanctuary provides consistent protection for small-bodied by-catch species, but not for large-bodied, high-risk species. J Exp Mar Bio Ecol 471:153–163

McLean DL, Langlois TJ, Newman SJ, Holmes TH, Birt MJ, Bornt KR, Bond T, Collins DL, Evans SN, Travers MJ, Wakefield CB, Babcock RC and Fisher R (2016) Distribution, abundance, diversity and habitat associations of fishes across a bioregion experiencing rapid coastal development. Estuar Coast Shelf Sci 178:36–47

Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio GC and Romano F (2005) Cascading human impacts, marine protected areas; and the structure of Mediterranean reef assemblages. Ecol Monogr 75:81–102

Nash KL, Allen CR, Barichievy C, Nyström M, Sundstrom S and Graham NAJ (2014) Habitat structure and body size distributions: Cross-ecosystem comparison for taxa with determinate and indeterminate growth. Oikos 123:971–983

Newman SJ and Williams DM (2001) Spatial and temporal variation in assemblages of Lutjanidae, Lethrinidae and associated fish species among mid-continental shelf reefs in the central great barrier reef. Mar Freshw Res 52:843–851

Pande A, MacDiarmid AB, Smith PJ, Davidson RJ, Cole RG, Freeman D, Kelly S and Gardner JPA (2008) Marine reserves increase the abundance and size of blue cod and rock lobster. Mar Ecol Prog Ser 366:147–158

Pillans R, Babcock R, Patterson T, How J and Hyndes G (2011) Adequacy of zoning in the Ningaloo Marine Park Final Report. CSIRO Publ:123

Pillans RD, Bearham D, Boomer A, Downie R, Patterson TA, Thomson DP and Babcock RC (2014) Multi year observations reveal variability in residence of a tropical demersal fish, Lethrinus nebulosus: Implications for spatial management. PLoS One 9

Priede IG, Bagley PM, Smith A, Creasey S and Merrett NR (1994) Scavenging deep demersal fishes of the Porcupine Seabight, north-east Atlantic: observations by baited camera, trap and trawl. J Mar Biol Assoc United Kingdom 74:481

Quesne WJF Le and Codling EA (2009) Managing mobile species with MPAs: The effects of mobility, larval dispersal, and fishing mortality on closure size. In: ICES Journal of Marine Science. 122–131

R Core Team (2015) R: A language and environment for statistical computing.

Raftery AE (1995) Bayesian model selection in social research. Sociol Methodol 25:111–163

Rife AN, Aburto-Oropeza O, Hastings PA, Erisman B, Ballantyne F, Wielgus J, Sala E and Gerber L (2013) Long-term effectiveness of a multi-use marine protected area on reef fish assemblages and fisheries landings. J Environ Manage 117:276–283

Roberts CM, Bohnsack JA, Gell F, Hawkins JP and Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science (80-) 294:1920–1923

Rotherham D, Underwood AJ, Chapman MG and Gray CA (2007) A strategy for developing scientific sampling tools for fishery-independent surveys of estuarine fish in New South Wales, Australia. ICES J Mar Sci 64:1512–1516

Russ GR and Alcala AC (1996) Marine reserves: Rates and patterns of recovery and decline of large predatory fish. Ecol Appl 6:947–961

Russ GR and Alcala AC (2004) Marine reserves: Long-term protection is required for full recovery of predatory fish populations. Oecologia 138:622–627

Russ GR, Alcala AC, Maypa AP, Calumpong HP and White AT (2004) Marine Reserve Benefits Local Fisheries. Ecol Appl 14:597–606

Russ GR, Cheal AJ, Dolman AM, Emslie MJ, Evans RD, Miller I, Sweatman H and Williamson DH (2008) Rapid increase in fish numbers follows creation of world's largest marine reserve network. Curr Biol 18

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ and Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20:74–80

SeaGIS Pty Ltd (2014) Three-dimensional stereo measurement in visual sampling of fish population.

Sheather SJ and Jones MC (1991) A reliable data based bandwidth selection method for kernel density estimation. J R Stat Soc Ser B 53:683–690

Shedrawi G, Harvey ES, McLean DL, Prince J, Bellchambers LM and Newman SJ (2014) Evaluation of the effect of closed areas on a unique and shallow water coral reef fish assemblage reveals complex responses. Coral Reefs 33:579–591

Shortis MR and Harvey ES (1998) Design and calibration of an underwater stereo-video system for the monitoring of marine fauna populations. Int Arch Photogramm Remote Sens 32:792–799

Smallwood CB and Beckley LE (2012) Spatial distribution and zoning compliance of recreational fishing in Ningaloo Marine Park, north-western Australia. Fish Res 125–126:40–50

Smallwood CB, Beckley LE, Moore SA and Kobryn HT (2011) Assessing patterns of recreational use in large marine parks: A case study from Ningaloo Marine Park, Australia. Ocean Coast Manag 54:330–340

Tweedie M (1984) An index which distinguishes between some important exponential families. In: Statistics: Applications and new directions: Proc. Indian statistical institute golden Jubilee International conference.p 579–604

Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr Mar Biol An Annu Rev 19:513–605

Walters CJ, Hilborn R and Parrish R (2007) An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. Can J Fish Aquat Sci 64:1009–1018

Wand M (2012) KernSmooth: Functions for kernel smoothing for Wand and Jones (1995).

Watson DL (2006) Use of underwater stereo–video to measure fish assemblage structure, spatial distribution of fishes and change in assemblages with protection from fishing

Watson DL, Anderson MJ, Kendrick GA, Nardi K and Harvey ES (2009) Effects of protection from fishing on the lengths of targeted and non-targeted fish species at the Houtman Abrolhos Islands, Western Australia. Mar Ecol Prog Ser 384:241–249

Watson D and Harvey E (2007) Behaviour of temperate and sub-tropical reef fishes towards a stationary SCUBA diver. Mar Freshw Behav Physiol 40:85–103

Watson DL, Harvey ES, Anderson MJ and Kendrick GA (2005) A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. Mar Biol 148:415–425

Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ and Shedrawi G (2010) Assessing reef fish assemblage structure: How do different stereo-video techniques compare? Mar Biol 157:1237–1250

Watson DL, Harvey ES, Kendrick GA, Nardi K and Anderson MJ (2007) Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. Mar Biol 152:1197–1206

Wernberg T, Bennett S, Babcock RC, Bettignies T De, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA and Tuya F (2016) Climate-driven regime shift of a temperate marine ecosystem. Science (80-) 353:169–172

Westera M (2003) The effect of recreational fishing on targeted fishes and tropic structure, in a coral reef marine park

Westera M, Lavery P and Hyndes G (2003) Differences in recreationally targeted fishes between protected and fished areas of a coral reef marine park. J Exp Mar Bio Ecol 294:145–168

Wickham H (2016) tidyr: Easily Tidy Data with `spread()` and `gather()` Functions.

Wickham H, Francois R (2016) dplyr: A Grammar of Data Manipulation.

Willis TJ and Anderson MJ (2003) Structure of cryptic reef fish assemblages: Relationships with habitat characteristics and predator density. Mar Ecol Prog Ser 257:209–221

Willis TJ and Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. Mar Freshw Res 51:755–63

Willis TJ, Millar RB and Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper Pagrus auratus (Sparidae) in northern New Zealand marine reserves. J Appl Ecol 40:214–227

Wilson SK, Babcock RC, Fisher R, Holmes TH, Moore J a Y andThomson DP (2012) Relative and combined effects of habitat and fishing on reef fish communities across a limited fishing gradient at Ningaloo. Mar Environ Res 81:1–11

12.1.7 SUPPLEMENTARY MATERIAL

Table S12.1.1 Family and species of the targeted species recorded with stereo-BRUVs and stereo-DOVs; abundance, total number (#) of measured individuals, total number of measured individuals over minimum legal length (MLL) and percentage of deployments/transects are reported for each species, where over four individuals per method were recorded, MLL for retention by recreational fishing of each species is also reported, where MLL is NA a minimum legal length is not stated within the recreational fishing guide (2016) for this species.

	BRUV				DOV				
FAMILY/SPECIES	ABUNDANCE	TOTAL # MEASURED	TOTAL # > MLL	% OF DEPLOYMENTS	ABUNDANCE	TOTAL # MEASURED	TOTAL # > MLL	% OF TRANSECTS	MLL
Carangidae									
Carangoides fulvoguttatus	143	98	98	59.6%	2	2	2	1.0%	1
Gnathanodon speciosus	9	9	9	6.7%	1	1	1	1.0%	1
Epinephelidae									
Epinephelus fasciatus	22	15	0	20.2%	12	7	0	9.8%	NA
Epinephelus rivulatus	140	102	102	60.7%	4	4	4	3.9%	1
Plectropomus spp	4	3	2	4.5%	2	1	1	2.0%	450
Lethrinidae									
Lethrinus nebulosus	109	63	22	66.3%	429	307	17	28.4%	410
Scombridae									
Scomberomorus spp	11	4	0	4.5%	-	-	-	-	900

Table S12.1.2 Summary of all species recorded in this study, the total number (#) of individuals, species, families and targeted species and the most ubiquitous families and species (percent of deployments/transects) and the most abundant families and species (MaxN/abundance) per method (stereo-BRUV/stereo-DOV) are listed.

	STEREO-BRUV	STEREO-DOV
Total # individuals	14227	27728
Total # species	234	169
Total # families	42	32
Total # targeted species	12	8
Most ubiquitous families	Labridae (100%)	Labridae (100%)
	Mullidae (98.9%)	Pomacentridae (100%)
	Lethrinidae (97.8%)	Scaridnae (100%)
	Scarinae (97.8%)	Nemipteridae (99%)
	Chaetodontidae (96.6%)	Acanthuridae (92.2%)
Most ubiquitous species	*Thalassoma lunare* (95.5%)	*Scolopsis bilineata* (99.0%)
	Lethrinus atkinsoni (92.1%)	*Scaridnae sp10* (97.1%)
	Scaridnae sp10 (86.5%)	*Chlorurus sordidus* (91.2%)
	Scolopsis bilineata (83.1%)	*Dascyllus aruanus* (87.3%)
	Acanthurus grammoptilus (80.9%)	*Thalassoma lunare* (87.3%)
Most abundant families	Pomacentridae (3468)	Pomacentridae (17577)
	Acanthuridae (2342)	Scaridnae (3632)
	Labridae (2334)	Acanthuridae (2526)
	Scaridnae (1853)	Labridae (1338)
	Mullidae (875)	Lethrinidae (663)
Most abundant species	*Acanthurus triostegus* (1380)	*Chromis viridis* (5497)
	Chromis viridis (1371)	*Chromis atripectoralis* (3699)
	Scaridnae sp10 (989)	*Dascyllus aruanus* (3546)
	Thalassoma lunare (978)	*Scaridnae sp10* (2279)
	Lethrinus atkinsoni (501)	*Acanthurus triostegus* (1859)

12.2 Quantifying shark depredation in a recreational fishery in the Ningaloo Marine Park and Exmouth Gulf, Western Australia

Authors: Mitchell JD, McLean DL, Collin SP, Taylor S, Jackson G, Fisher R, Langlois TJ.

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ABSTRACT

Shark depredation in recreational fisheries can cause higher mortality rates in target fish species, injuries to sharks from fishing gear, and negative impacts on the recreational fishing experience. This study quantified the spatial variation and frequency of shark depredation in a boat-based recreational fishery in the Ningaloo Marine Park (NMP) and Exmouth Gulf (EG), Western Australia, by surveying 248 fishing vessels at west coast boat ramps and 155 vessels at EG coast boat ramps, from July 2015 to May 2016. Shark depredation occurred on 38.7% of fishing trips from west coast boat ramps and 41.9% of trips from EG coast boat ramps. The mean shark depredation rate per fishing trip (number of fish depredated/total number of fish hooked) was 13.7(±3.3)% (mean (± 95% confidence interval)) for demersal fishing (n=185) and 11.8(±6.8)% for trolling (n=63) for west coast boat ramps, compared to 11.5(±2.8)% (n=128) and 7.2(±8.4)% (n=27) for EG coast ramps. Depredation rates varied substantially across the study area, with higher depredation occurring in areas which received greater fishing pressure. Generalised Additive Mixed Models (GAMMs) indicated that depth, number of boats fishing within 5 km and survey period were important for determining the depredation rate for boats launching from west coast boat ramps. For the EG coast boat ramps, fishing pressure and decreasing latitude were positively correlated with number of fish depredated. This study is the first quantitative assessment of shark depredation in an Australian recreational fishery, and provides important insights that can assist recreational fishers and managers in reducing depredation.

12.2.1 INTRODUCTION

Depredation refers to the partial or complete consumption of a live hooked fish by a free-swimming predator before that fish can be retrieved to the fishing boat (Gilman et al. 2008; MacNeil et al. 2009). This occurs in commercial and recreational fisheries worldwide (Sumner et al. 2002; Nishida and Shiba 2005; MacNeil et al. 2009; Labinjoh 2014; Mitchell et al. in prep.), and is caused by a diverse range of predators, including sharks, large predatory teleosts, cetaceans, pinnipeds, seabirds and squid (Meyer et al. 1992; Donoghue et al. 2003; Gilman et al. 2008; Remeslo et al. 2015; van den Hoff et al. 2017)**.** Depredating hooked fish is likely to be an opportunistic and energy efficient feeding strategy for these animals, compared to capturing prey naturally (Madigan et al. 2015). Depredation by sharks is problematic in commercial fisheries, due to costly losses of target fish and fishing gear, as well as high bycatch and mortality of sharks (IOTC 2007; Gilman et al. 2008; MacNeil et al. 2009). As a result of these impacts, past research has quantified depredation rates in pelagic longline fisheries worldwide, with loss rates ranging from <1% to 20% (Lawson 2001; IOTC 2007; Gilman et al. 2008; MacNeil et al. 2009). Shark depredation in recreational fisheries has received far less attention, with very little published research quantifying its occurrence (Sumner et al. 2002; Williamson et al. 2006; Labinjoh 2014), despite anecdotal reports of it regularly occurring in a number of recreational fisheries worldwide, including in Australia, mainland USA, Hawaii and South Africa. Depredation in recreational fisheries is an important issue, due to its potential to cause higher mortality in target fish species, hooking injuries to sharks, loss of fishing gear and a reduction in the quality of the recreational fishing experience. Furthermore, the extra cryptic mortality caused by depredation is often not accounted for in commercial or recreational fisheries assessments, and may therefore lead to underestimation of target species mortality.

This study investigated and quantified shark depredation in a boat-based recreational rod-and-line fishery in Exmouth Gulf (EG) and the Ningaloo Marine Park (NMP), which are located in north-west Western Australia (Figure 12.2.1a), where shark depredation is anecdotally reported to regularly occur (Exmouth Game Fishing Club, pers. comm). This location is regarded to be one of the best recreational fishing areas in Australia for boat-based rod-and-line fishing, for both pelagic (e.g. Spanish mackerel *Scomberomorus commerson*) and demersal (e.g. red emperor *Lutjanus sebae*) species (Sumner et al. 2002; CALM and MPRA 2005; Williamson et al. 2006). As a result, this fishery receives a relatively high level of fishing effort; for example 55,000 boat fishing days were recorded across the north-west (Gascoyne) region of Western Australia over a recent 12 month survey period (2011-12), with an estimated 16,884(±2,270) (number of individuals (± standard error)) spangled emperor *Lethrinus nebulosus* (equal to 35.3(±4.8) tonnes) caught and retained during this time period (Ryan et al. 2013). The NMP plays an important role in biodiversity conservation in this region, with a zoning plan that includes areas open to fishing and sanctuary zones where no fishing is permitted, the latter of which comprises 34% of the marine park (CALM and MPRA 2005) (Figure 12.2.1a,b). Targeted recreational fishing for sharks is uncommon in this region (Ryan et al. 2013), and there is a commercial ban on shark fishing between Steep Point (26.15˚S, 113.16˚E) and Broome (17.96˚S, 122.22˚E) (Simpfendorfer and Donohue 1998; McAuley and Simpfendorfer 2003; McAuley et al. 2005). Also, the NMP and EG have been identified as being an important parturition and nursery area for a range of shark populations (Speed et al. 2011; Escalle et al. 2015; Oh et al. 2016; Speed et al. 2016).

To quantify depredation within a recreational fishery, the present study conducted a boat ramp survey to gather information on depredation rates and locations, in addition to a range of environmental variables and fishing methods used. It was hypothesised that depredation rates would vary spatially, and that proportionally higher depredation rates would occur in areas that receive regular and consistent fishing pressure, due to the attraction of sharks to chemical and auditory cues created by fishing activity, and the associated availability of hooked fish to feed on. Likewise, the depth of fishing was expected to be an important factor determining depredation rate, due to its influence on seabed habitat type and the distribution and abundance of sharks (Espinoza et al. 2014; Rizzari et al. 2014). This study ultimately aimed to provide baseline data on shark depredation in a recreational fishery in Western Australia, which will inform fisheries and marine park management strategies in this area, as well as broadening our understanding of shark depredation.

12.2.2 METHODS

Study location

Data collection for this study was undertaken in Western Australia, at Coral Bay (23.16˚S, 113.77˚E) and Tantabiddi (21.91˚S, 113.98˚E) boat ramps, which are referred to as west coast boat ramps from herein, and Bundegi (21.83˚S, 114.17˚E) and Exmouth marina (21.96˚S, 114.14˚E) boat ramps, which are referred to as EG coast boat ramps (Figure 12.2.1a). Boat ramps were grouped in this way due to the oceanographic, bathymetric and ecological differences between the west coast and EG coast. The former is characterised by a shallow (<10 m) lagoon close to the coast, followed by an extensive north-south oriented fringing reef which drops away steeply to deep water with increasing distance from the coast (CALM and MPRA 2005). Conversely, the former is shallow with mostly bare sand substrate throughout its area, apart from isolated reef and seagrass patches and islands (Kenyon et al. 2003).

Boat ramp survey data

Data on shark depredation were collected directly from fishers using a boat ramp survey conducted from July 2015 to May 2016. A systematic sampling strategy was used, where each boat ramp was sampled on 10 randomly selected days across three survey trips in July/August (winter) 2015, September/October (spring) 2015 and April (autumn) 2016, producing a total sample size of 40 days. The Primary Sampling Unit (PSU) was each sampling day (Murphy 2008; Jones and Pollock 2012; Levy and Lemeshow 2013). The time of year of the three sampling trips was systematically chosen to provide coverage of the peak fishing season from April – October (Sumner et al. 2002; Ryan et al. 2013). Sampling was also stratified by day type, with each boat ramp sampled in a ratio of two weekdays for each weekend day (Jones and Pollock 2012; Smallwood and Gaughan 2013). Each daily survey period was from 10 am - 6 pm, with all boats interviewed as they returned to the boat ramp after fishing.

To facilitate consistent data collection, interviews were conducted by the same researcher using a pre-set questionnaire and map on the software application ‘Collector for ArcGIS’ (Environmental Systems Research Institute (ESRI) 2015, Redlands, CA, USA). Each interview consisted of 20 short-answer questions, including boat level questions and individual fisher questions (see Appendix 1 for list of survey questions), and lasted 3 - 5 minutes. Before commencing the boat ramp survey at the west coast and EG coast boat ramps, survey questions were pilot tested at a boat ramp in Perth, Western Australia, to ensure that they were easy to interpret and provided reliable data. In the survey at the west coast and EG coast boat ramps, the species identity of depredated fish was rarely available due to sharks mostly breaking off the fishing line at depth, with no sighting of the fish or remains retrieved. Fish that were caught undamaged and retained by fishers were not identified due to time constraints. A depredation event was assumed to have occurred when fishers retrieved a partially consumed fish, or when a shark snapped off the line shortly after a fish was hooked. The response rate, i.e. the percentage of boats approached that either completed the survey or did not wish to take part, was 97.14%, with only 2.86% (12 out of 419) of boats not wishing to take part. The survey used in this study was designed to cover all daytime boat-based recreational fishing from boats launching from the four main access points (boat ramps) serving the NMP and EG. Boats ranging from 3 m to 9 m in length were able to launch from these access points and were thus covered by the survey scope. A broad fisher demographic was also represented in the survey data, including fishers of both sexes ranging from approximately 10 to 80 years old, local residents as well as visitors from Western Australia and interstate, and a wide range of experience levels, from first time fishers to professional and ex-professional fishers. Due to time and logistical constraints, some boat-based recreational fishing in the region was, however, outside the scope of the survey used in this study, including vessels launching from beaches, private access points or marinas, as well as those fishing at night or on multi-day trips (Figure 12.2.1).

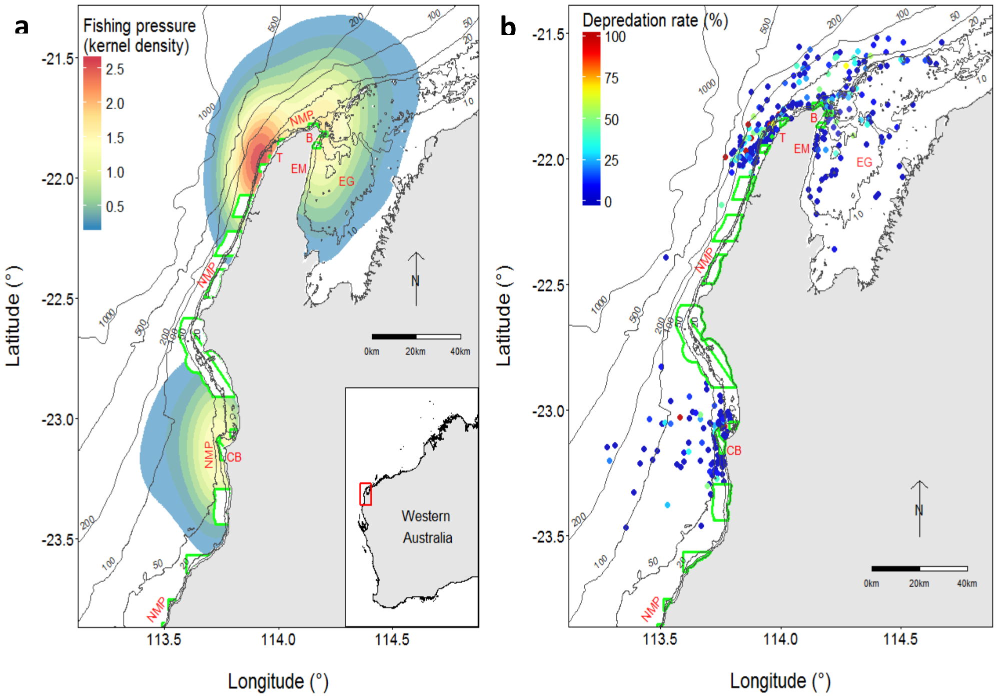

Figure 12.2.1 (a) Spatial variation in estimated fishing pressure, as calculated using kernel density estimation to analyse the density distribution of the 248 and 155 (403 in total) boat-based fishing locations (for both demersal fishing and trolling) reported by boats launching from west coast boat ramps (Coral Bay (CB) and Tantabiddi (T)) and Exmouth Gulf (EG) coast boat ramps (Bundegi (B) and Exmouth marina (EM)), respectively. Red areas represent locations of highest estimated fishing pressure and blue the lowest estimated fishing pressure. Labelled contour lines show depth in metres. Ningaloo Marine Park (NMP) sanctuary zone boundaries are delineated by solid green lines. (b) Spatial variation in the rate of shark depredation (the percentage of hooked fish consumed by sharks) for the 248 fishing trips which launched from west coast boat ramps and 155 fishing trips which launched from EG coast boat ramps. Colour scale represents the range of shark depredation rate values for all fishing trips, from dark blue for 0% of hooked fish depredated to dark red for 100% of fish depredated.

Sea surface temperature data

Satellite Sea Surface Temperature (SST) data were sourced retrospectively from the US National Oceanic and Atmospheric Administration (NOAA 2016). These data were in the form of high resolution Optimum Interpolation (OI) of SST (see Reynolds et al. (2007) for detail on OI SST), collected by Advanced Very High Resolution Radiometer (AVHRR) instruments on polar orbiting satellites (NOAA 2016). The data were daily mean SST values at a spatial resolution of 0.25˚ x 0.25˚ grid squares (NOAA 2016). SST values were extracted for the date, time and latitude/longitude position closest to each fishing location, to allow assessment of the influence of SST on shark depredation rate.

Table 12.2.1 Summary of fishing methods, fisher demographics and boat sizes that were in scope and out of scope for the boat ramp survey conducted in this study.

IN SCOPE	OUT OF SCOPE
Boat-based line fishing	Shore-based fishing and spearfishing
Boats returning to boat ramps between 10 am and 6 pm	Boats returning to boat ramps before 10 am or after 6 pm
Boats <9 m that could be launched and retrieved from a boat ramp	Boats >9 m that were unable to launch from a boat ramps
Single day fishing trips	Multi-day fishing trips
Boats returning to the boat ramp being surveyed that day	Boats returning to other boat ramps in the study area that were not being surveyed that day
Boats fishing in the study area during the July/August 2015, September/October 2015 and April 2016 survey periods	Boats fishing at other times of year outside of the three survey periods
Boats launching from Coral Bay, Tantabiddi, Bundegi and Exmouth marina boat ramps	Boats launching from private moorings in Exmouth marina, beaches or other access points near coastal campsites
Local fishers and those from outside locations	
Male and female fishers ranging from approximately 10 to 80 years old	
Fishers targeting both demersal and pelagic fish species	
A range of fisher experience levels, from novice first time fishers to professional fishers	

Shark depredation rate

Survey data collected from the west coast boat ramps (Coral Bay and Tantabiddi) and the EG coast boat ramps (Bundegi and Exmouth marina) were treated separately throughout, due to differences in the depth profile, habitat types and fishing methods used in these two areas. Additionally, to ensure all data points were independent, entries where the same boat had been interviewed multiple times were removed, so that each boat was represented by a single data point only (the first time they were interviewed). This was possible through the recording of boat registration numbers, and it was necessary due to the quality and reliability of data declining after multiple interviews, due to survey fatigue. Only data from the two main fishing methods – demersal fishing (where the boat was either anchored or drifting and bait was used) and trolling (where lures were towed close to the surface to target pelagic fish, covering distances from 1 – 20 km), were used, due to small sample sizes (<30 data points) for other methods such as squid jigging or fishing with stationary lures floating on the surface. The sample size for these two fishing methods was 185 demersal fishing trips and 63 trolling trips (248 in total) for the west coast boat ramps and 128 demersal and 27 trolling trips (155 in total) for EG coast boat ramps. The 248 boats surveyed for the west coast boat ramps represented an estimated 5.8% of the total fishing trips that occurred from these ramps over a 12-month period, from July 2015 to June 2016, based on boat ramp traffic counter figures of 4,248 visits by vehicles towing boat trailers over this period (Department of Biodiversity Conservation and Attractions, Government of Western Australia, unpubl. data). This total value of 4,248 visits represented 70% of the total number of visits for vehicles with boat trailers (6,069), because it was estimated that 30% of vessels launching from these boat ramps engaged in recreational activities other than fishing, such as diving or whale watching. These values also assume that all vehicles which crossed the traffic counter and entered the boat ramp launched their boat, which does not always occur, for example if the occupants decided to go to another boat ramp due to weather conditions. Calculation of the percentage of total boat launches represented by the survey sample was not possible for the EG coast boat ramps, because traffic counter data were not available for both of these ramps.

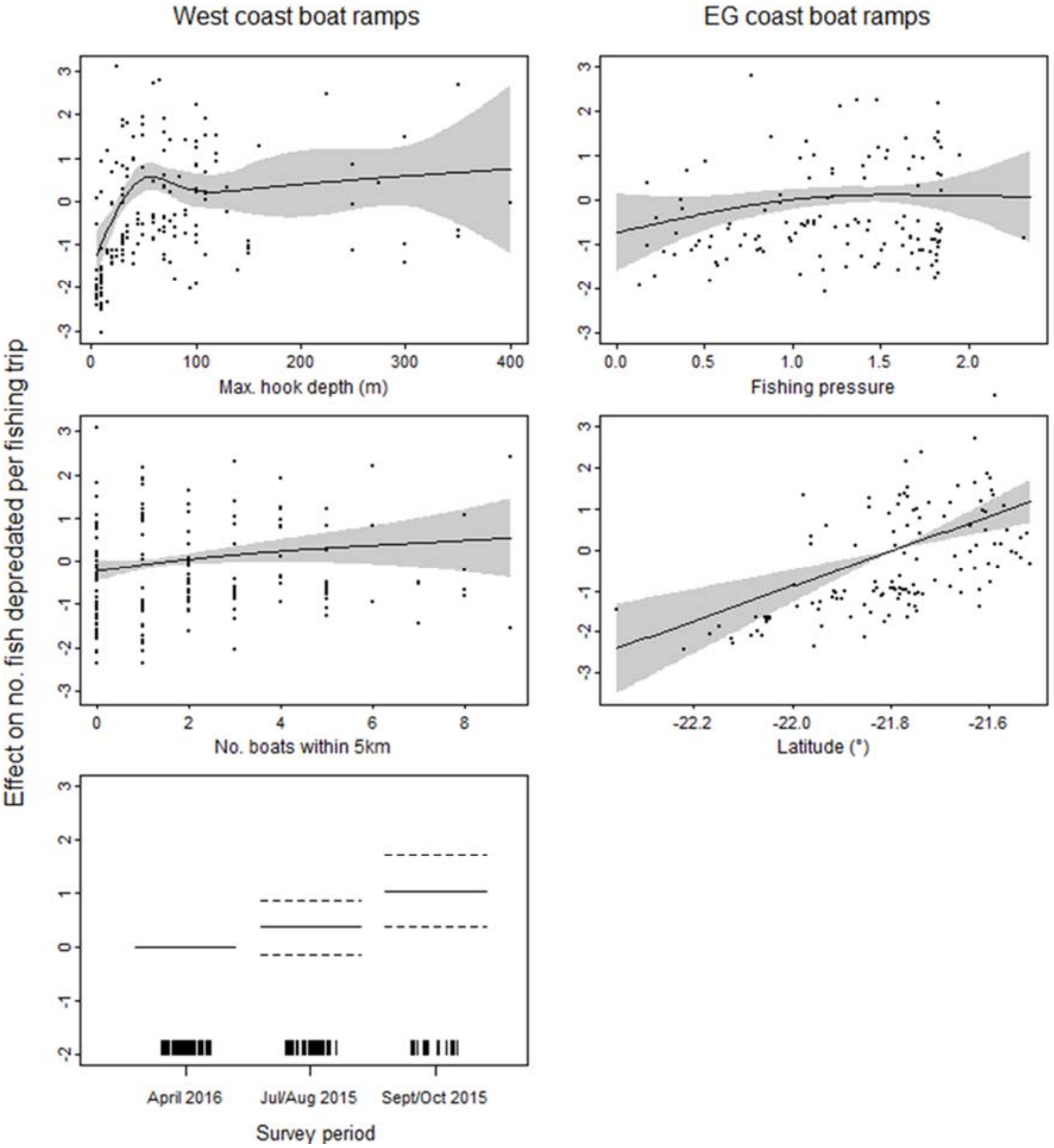

Figure 12.2.2 Effect of individual smoothed continuous predictor variables and the factor variable survey period on the number of fish depredated per fishing trip, across their range of values. Columns represent the best-fitting Tweedie Generalised Additive Mixed Models (GAMMs) for the west coast boat ramps (Coral Bay and Tantabiddi) and the Exmouth Gulf (EG) coast boat ramps (Bundegi and Exmouth marina). Solid black lines represent the fitted GAMM smooth curves and shaded regions (or dashed lines for the factor variable survey period) delineate 95% confidence intervals (fitted smooth curve +/- 2 Standard Error). Points represent model residuals.

Shark depredation rate was analysed at the level of each individual fishing trip, as opposed to at the PSU level of each sampling day, because there was expected to be a large degree of variation in fishing methods, spatial fishing locations and thus depredation rates between trips. The depredation rate for each fishing trip was calculated as a percentage value from the number of hooked fish partially or completely depredated by sharks/total number of fish hooked (which included fish caught and retained, fish caught and released and fish depredated). Shark depredation only included fish that were consumed from a fishing hook whilst being retrieved to a boat, not those which were consumed after being released, which is known as post-release predation (Raby et al. 2014). Spatial variation in depredation rate was visualised by plotting all approximate latitude/longitude fishing locations in the study area on a map, with a colour scale (dark blue = 0%, dark red = 100%) to indicate depredation rate for each trip.

Generalised Additive Mixed Model analysis

To quantify the influence of spatial, environmental and fishing method variables on the rate of shark depredation, Generalized Additive Mixed Models (GAMMs) (Lin and Zhang 1999) were used. GAMMs are an extension of Generalized Additive Models (GAMs) (Hastie and Tibshirani 1986; Wood 2006), which utilise smoothing techniques to account for noise and non-linearity in the predictor variables (Craven and Wahba 1978; Wood 2008). GAMMs also differ from GAMs in that they include both fixed and random effects, with the fixed effects assessing the impact of each predictor variable on the response at specific levels, and the random effects evaluating the impact of variations between levels for grouped data (Bolker et al. 2009; Zuur et al. 2009). Due to the small sample size for trolling and other fishing methods reported in this study, GAMMs were only run on demersal fishing data. Raw count data for the number of fish depredated per trip were used as the response variable, because this form of data was more appropriate for GAMM analysis than a calculated rate of depredation per trip. However, the raw count data had many zeros (54% of data points) and were over-dispersed, due to the high number of zeros and low values, as well as a large range (0 – 50) in the number of fish depredated per trip. Zero-inflated and over-dispersed response data are common in fisheries datasets (Maunder and Punt 2004; Venables and Dichmont 2004), and different approaches have been used to model this form of data, including delta two-part models (Lo et al. 1992), negative binomial models (Zeileis et al. 2008; MacNeil et al. 2009), zero-inflated mixture models (Minami et al. 2007; Arab et al. 2008; MacNeil et al. 2009; Zuur et al. 2009) and Tweedie models (Tweedie 1984; Candy 2004; Shono 2008; Tascheri et al. 2010; Coelho et al. 2016).

This study applied a full-subsets GAMM approach, which tests all possible combinations of the specified predictor variables to identify the best-fitting model (McLean et al. 2016; Fisher in prep.). The predictor variables tested in these GAMMs (Table 12.2.2) were checked for potential correlation, to ensure that collinearity was within acceptable levels denoted by Pearson's correlation coefficient values <0.28 (Graham 2003). The final dataset used for GAMM analysis had 170 data points for the west coast boat ramps and 123 for the EG coast boat ramps. The date of each sampling day in Julian Day format was also included as a random factor, to account for any variation at the day level. Total number of fish hooked was used as an offset in the GAMMs, because the proportion of fish lost to depredation is directly dependent on total number of fish hooked. This offset variable was highly skewed, therefore it was log(x + 1) transformed to achieve an even distribution for more robust model fitting (Zuur et al. 2009).

Table 12.2.2 Predictor variables considered for Generalised Additive Mixed Model (GAMM) analysis of shark depredation, the metric used to represent that variable and its hypothesised importance to depredation.

PREDICTOR VARIABLE	METRIC USED IN GAMM	HYPOTHESISED IMPORTANCE TO SHARK DEPREDATION
Smoothed continuous predictor variables		
Latitude	Latitude coordinates	Latitude influences shark distribution patterns and defines different fishing grounds accessible from the four different boat ramps. Latitude also acts as a proxy for spatial variability caused by other factors not included in the model, such as habitat type
Depth of fishing	Maximum hook depth (m)	Depth governs available shark habitat and influences distribution patterns, thus affecting abundance
Temperature	Sea Surface Temperature (SST; ˚C)	Temperature influences the activity patterns (including feeding behaviour) of sharks
Time of day	Median time between times lines in and time of lines out	The activity patterns of sharks, especially for feeding, varies throughout diel periods
Fishing effort for that trip	Fishing trip duration (hours from lines in to lines out)	Longer fishing times provide greater opportunity for sharks to locate fishing boats and depredate on hooked fish
Number of boats fishing within 5 km	Number of boats fishing within a 5 km radius of the boat in question on the same day, calculated using the minimum linear distance to the recorded lat/long locations of other boats fishing on that day, with the 'RANN' package (version 2.5.1) (Arya et al. 2017) in R. This metric assumed that vessels launching from other ramps on the same day would not fish in overlapping areas, due to the relatively large distances between boat ramps	The number of other boats fishing in the surrounding area will influence the likelihood of attracting sharks into that area, due to the increased magnitude of sound and odour cues from fishing boats and the availability of hooked fish
Fishing pressure	Kernel density value for each fishing trip location – based on the density distribution of all 403 fishing locations (see Figure 12.2.1a)	Higher fishing pressure in specific areas may act to provide sharks with regular and predictable opportunities to depredate upon hooked fish. This may lead to sharks remaining in these areas for longer time periods and potential changes in their behaviour, influencing the likelihood of depredation occurring in that location
Categorical factor predictor variable		
Survey period	Month/year of survey	The time of year influences seasonal movement patterns and distribution of shark species, due to changes in environmental factors and through movement linked to reproduction. Additionally, changes in weather patterns and currents occur throughout the year, influencing fishing dynamics

Each of the model distributions discussed previously (e.g. negative binomial, zero-inflated mixture models etc.), were tested using this full-subsets GAMM approach, and the Tweedie distribution was identified by goodness of fit metrics, particularly the distribution of model residuals (which were visualised in residual plots) and the percentage of deviance explained, to be the most appropriate for this dataset. Separate Tweedie GAMMs were run for the west coast boat ramps (Coral Bay and Tantabiddi) and the EG coast boat ramps (Bundegi and Exmouth marina). To identify the combination of predictor variables that produced the best-fitting model, all possible combinations were tested and ranked by Akaike Information Criterion (AIC) (Akaike 1974) values, with the most parsimonious model being that within two AIC values of the lowest AIC and having the smallest number of predictor variables (Burnham and Anderson 2002). The maximum number of predictor variables allowed in this approach was three, to prevent potential overfitting, and the AIC criteria of being within two units of the lowest AIC was used because models that have less than two units of difference show negligible change in goodness-of-fit (Raftery 1995; Burnham and Anderson 2002). Additionally, AIC weights (wAIC) (Burnham and Anderson 2002) were used to give extra strength to the model selection, applying the averaged wAIC approach set out in McLean et al. (2016) and Fisher (in prep.). The robustness and fit of the final models selected by the full-subsets approach was also checked by visualisation of residual plots, which confirmed normal distribution of residuals, independence of data points and goodness-of-fit of the fitted to the observed response values. Plots were then generated for the best-fitting models, to show the effect of each predictor variable on the response across its range of values. Predictor variable importance values, which represented the average wAIC of all models containing that variable, calculated on a scale between zero and one and multiplied by the R^2 value for the most parsimonious model (McLean et al. 2016; Fisher in prep.), were also generated, and plotted to identify the relative importance of all the predictor variables tested in both models.

All data analysis was conducted in the R language for statistical computing (R Development Core Team 2015), and GAMMs were run using the 'mgcv' package (version 1.8-17) (Wood and Scheipl 2015).

12.2.3 RESULTS

Shark depredation rate

From the 248 fishing trips (including both demersal fishing and trolling) recorded at west coast boat ramps, 2,420 fish were caught undamaged (including both those retained and those released) and 354 were reported to have been depredated by sharks, whereas in the 155 trips from EG coast boat ramps, 2,068 fish were caught undamaged and 344 were depredated. Shark depredation occurred on 38.7% of fishing trips from west coast boat ramps and on 41.9% of fishing trips from EG coast boat ramps (Table 12.2.3). By fishing method, the mean shark depredation rate was 13.7(±3.3)% (mean (± 95% confidence interval)) for demersal fishing and 11.8(±6.8)% for trolling at west coast boat ramps, compared to 11.5(±2.8)% and 7.2(±8.4)% at EG coast ramps (Table 12.2.3).

Table 12.2.3 Percentage of fishing trips affected by shark depredation and the mean shark depredation rate per fishing trip (calculated as the total number of fish depredated/total number of fish hooked (including both those retained and released) * 100) for demersal fishing and trolling trips launching from west coast (Coral Bay and Tantabiddi) and Exmouth Gulf (EG) coast (Bundegi and Exmouth marina) boat ramps. Values in parentheses represent 95% Confidence Intervals (C.I.; 1.96 * Standard Error).

METRIC	WEST COAST BOAT RAMPS	EG COAST BOAT RAMPS
Percentage of fishing trips affected by shark depredation	38.7%	41.9%
Mean shark depredation rate per fishing trip – demersal fishing	13.7(±3.3)%	11.5(±2.8)%
Mean shark depredation rate per fishing trip – trolling	11.8(±6.8)%	7.2(±8.4)%

Spatial variation in shark depredation rate

Shark depredation showed substantial spatial variation across the study area, with values for individual trips ranging between 0% and 100% (Figure 12.2.1b). The vast majority of fishing trips were, however, at the lower end of this scale, with values between 0% and 20%, as shown by the high number and density of low values in Figure 12.2.1b. Higher rates of depredation (25% - 50%) were experienced in a number of trips close to the Tantabiddi boat ramp, particularly in the 50 m - 100 m depth range, as denoted by the light blue points in Figure 12.2.1b. Additionally, this area included seven individual trips that reported >80% depredation, as shown by the red points. The area at the northern end of EG, as well as north of Bundegi boat ramp, also showed a number of fishing trips where depredation rates were 25% – 50%. However, it must be noted that the latitude/location positions represented in Figure 12.2.1b were approximate, especially in the case of trolling trips, where boats covered distances ranging from 1 – 20 km.

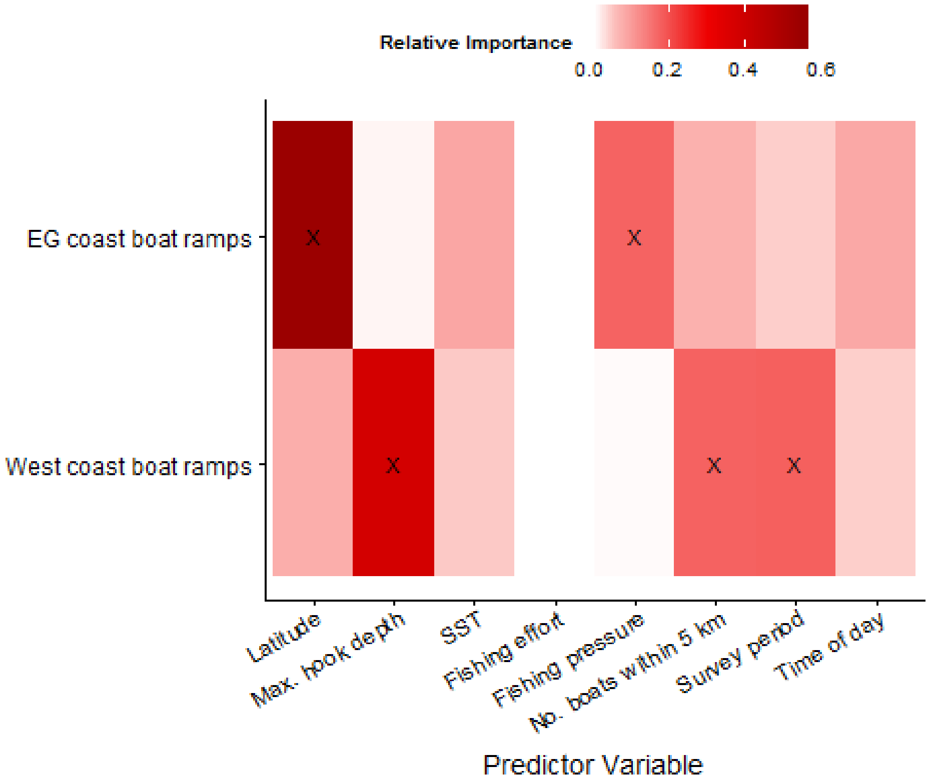

Figure 12.2.3 Relative importance of the predictor variables tested in Generalised Additive Mixed Models (GAMMs) (Table 12.2.2), for predicting the number of fish depredated by sharks per fishing trip, across the west coast boat ramps (Coral Bay and Tantabiddi) and the Exmouth Gulf (EG) coast boat ramp (Bundegi and Exmouth marina) models. Colour scale indicates the level of importance for each predictor variable, from white for very low relative importance values, to dark red for high relative importance. Predictor variables which featured in the most parsimonious model for the west coast boat ramps or the EG coast boat ramps (Table 12.2.4) are labelled with an 'X'. Predictor variable relative importance values represent the average Akaike Information Criterion weights (wAIC) of all models with that variable in, which is then calculated on a scale between zero and one and multiplied by the R^2 value for most parsimonious model.

Generalised Additive Mixed Model analysis

In the most parsimonious model for the west coast boat ramps, maximum hook depth, number of boats within 5 km and survey period explained 36.6% of the deviance in the response variable (number of fish depredated by sharks per trip) (Table 12.2.4). Maximum hook depth was an important predictor of the number of fish depredated across all of the west coast models, as indicated by a high relative importance value of 0.38 (Figure 12.2.3). This variable showed a distinctly non-linear relationship with number of fish depredated per trip, with a peak at 60 m (Figure 12.2.2). The number of boats fishing within 5 km on the same day was another important predictor across all of the west coast models, and showed a positive linear relationship of increasing rates of depredation with increasing number of boats fishing within 5 km. The factor variable survey period showed slightly higher importance than the number of boats within 5 km, with a strong positive effect on depredation from the lowest value for the April (autumn) 2016 survey trip to the highest for the Sept/Oct (spring) 2015 survey trip.

Table 12.2.4 Best-fitting Tweedie Generalised Additive Mixed Models (GAMMs) for predicting the number of fish depredated by sharks per fishing trip, for boats launching from the west coast boat ramps (Coral Bay and Tantabiddi) and the Exmouth Gulf (EG) coast boat ramps (Bundegi and Exmouth marina). AIC = Akaike Information Criterion, wAIC = Akaike Information Criterion weights, % dev. expl. = overall percentage of deviance in the response that was explained by the combination of predictor variables in the best models, edf = estimated degrees of freedom, n = number of data points for that GAMM.

SPATIAL AREA COVERED	BEST-FITTING GAMM	AIC	WAIC	% DEV. EXPL.	EDF	N
West coast boat ramps	Max. hook depth + no. boats within 5 km + survey	541.49	0.25	36.6	9	170
EG coast boat ramps	Fishing pressure + latitude	414.08	0.21	54.9	4.64	123

In the most parsimonious model for the EG coast boat ramps, fishing pressure and latitude explained 54.9% of the deviance in the response. Fishing pressure displayed a relatively high level of importance across all of the EG coast models (Figure 12.2.3), with a broadly positive relationship of increasing number of fish depredated with increasing fishing pressure (Figure 12.2.2). Latitude was a very important variable across all EG coast models, with a strong positive linear relationship between decreasing latitude and the number of fish depredated. The remaining predictor variables tested in the west coast and EG coast GAMMs had little effect on the number of fish depredated, with relative importance values <0.1 (Figure 12.2.3).

12.2.4 DISCUSSION

Shark depredation rate

A high response rate and the large variation in fishing methods, locations, boat sizes and fisher demographics captured by the boat ramp survey, enabled this study to obtain important baseline data on shark depredation rates within the NMP and EG. By quantifying the rate of shark depredation and its spatial variation, as well as identifying how spatial and environmental factors and fishing methods influenced the number of fish depredated in this fishery, this study provides an important addition to the existing global literature on shark depredation. This is highlighted by the fact that very little data exists for depredation in recreational, compared to commercial, fisheries, therefore the results in this study increase understanding of the impacts and potential underlying factors driving shark depredation.

Previous research conducted recreational fishing surveys in the north-west (Gascoyne) region of Western Australia in 1998/99, with estimates reported for the numbers of fish depredated in the NMP for certain species (Sumner et al. 2002). The reported values varied widely by species, with spangled emperor *Lethrinus nebulosus*, the most commonly caught demersal species, having an estimated catch of 22,575 individuals retained, 25,056 individuals released and 2,482 depredated by sharks (Sumner et al. 2002), which represents a 5.2% depredation rate (number of fish depredated/total number of fish hooked). In another area of north-west Western Australia known as the Pilbara region, a similar survey from 1999-2000 recorded estimated depredation rates of 5% for coral trout *Plectropomus spp.* and 1.3% for blackspot tuskfish *Choerodon schoenleinii* (Williamson et al. 2006). However, the estimated depredation rates for the majority of other species were much lower, at <1% for the Gascoyne and <2% for the Pilbara (Sumner et al. 2002; Williamson et al. 2006). The results of both of these previous surveys should, however, be viewed with caution, because the number of fish depredated was only estimated, by multiplying the per hour depredation rate by the estimated total number of fishing hours. Additionally, the species identification for fish consumed by sharks was likely to have been unreliable, because depredation often happened at depth and no remains of the fish were retrieved.

Beyond Western Australia, the vast majority of data on shark depredation comes from large-scale commercial pelagic longline fisheries, with studies reporting depredation rates of 3.9% in the US Northwest Atlantic pelagic longline fishery, between 1992 and 2006 (MacNeil et al. 2009), and <5% for the longline fisheries of seven countries operating in the Indian Ocean (IOTC 2007). However, rates as high as 20% have been recorded in the Australian east coast tuna and billfish longline fishery (Gilman et al. 2008). A small-scale study in a recreational charter fishery operating on the Protea Banks in KwaZulu-Natal, South Africa, recorded an overall mean depredation rate of 8.4% (43 fish depredated out of 512 hooked), with 75% of trips experiencing at least one depredation event (Labinjoh 2014). By fishing method, the depredation rate was 18.6% for pelagic fishing and 1.9% for demersal fishing (Labinjoh 2014). Although the overall rate of depredation in this charter fishery was similar to this study, there was a markedly higher prevalence of depredation (75% versus 38.7% for the west coast boat ramps and 41.9% for the EG coast boat ramps (Table 12.2.3)). This may be caused by this fishery using larger boats (>6 m) and carrying more fishers (up to 11) (Labinjoh 2014), compared to this study, with the greater fishing effort more likely to attract sharks. The higher depredation rate for pelagic versus demersal fishing in this fishery, compared to the opposite result in this study, is unexpected, because sharks would be able to follow and depredate upon fish hooked by boats targeting demersal fish more easily, due to them being stationary or slowly drifting, compared to boats moving through an area at 10 km h^{-1} whilst trolling. This disparity in results may also have occurred because different teleost species were targeted in these fisheries, and different shark species (with dissimilar feeding ecology and behaviour) were responsible for depredation. Likewise, the dynamics of the two fisheries, including their fisher demographics, methods and equipment used, may have contributed to these varied results. The small temporal scope (three month period) and low sample size of this study in South Africa, with just 16 trips sampled (compared to 403 in this study), must be considered when interpreting the reported values for shark depredation rate, as there will be a larger degree of variability and uncertainty in the results. Lastly, across these previous studies and this study, shark depredation rates may also have been overestimated, due to depredation by large predatory teleosts, e.g. cod/grouper *Epinephelus spp.* and barracuda *Sphyraena spp.*, being wrongly attributed to sharks. Indeed, research on red snapper *Lutjanus campechanus* catch rates in the Gulf of Mexico reported only 42% of depredation events to be caused by sharks, as observed by video cameras mounted on fishing lines, with great barracuda *Sphyraena barracuda*, greater amberjack *Seriola dumerili* and Warsaw grouper *Hyporthodus nigritus* responsible for the other 58% (Streich 2016).

When considering the results of this study, it is important to note that the sample size represented only a small portion (5.8% of trips from west coast boat ramps) of the total fishing effort that occurred in this fishery over the annual period from July 2015 to June 2016. The results obtained should therefore not be used as an indicator of the entire fishery, due to this small sample size, the lack of temporal coverage and replication over multiple years, and the fact that other forms of fishing were outside the scope of the survey (Table 12.2.1). Despite this, and overall, the results obtained in this study still offer a baseline assessment of shark depredation rates in this region of Western Australia, and build on previous research in recreational fisheries, providing important information to guide fisheries and marine park management in this region.

Spatial variation and GAMM analysis

Shark depredation rates and fishing pressure showed a substantial degree of spatial variation in the results of this study (Figure 12.2.1a,b), although when interpreting these results, it is important to consider the relatively small sample size of the survey data, as well as the limited temporal coverage of the surveys. Additionally, the scope of the survey must be noted (Table 12.2.1), because large areas where there appears to be no fishing pressure in Figure 12.2.1a, such as the area approximately half-way between Tantabiddi and Coral Bay boat ramps (close to 22.5˚S), does receive fishing pressure from vessels launching from beaches and access points near coastal campsites in this area (Smallwood and Beckley 2012), but this was not recorded due to being outside the scope of this survey. Whilst these limitations prevent extrapolation of the results to cover the whole fishery in this region, this study nonetheless provides important baseline information. In particular, the presence of fishing pressure and no. boats within 5 km as key predictor variables in the EG coast and west coast GAMMs respectively (Table 12.2.4, Figure 12.2.2, Figure 12.2.3), indicates an important influence of fishing activity on depredation. Likewise, the overlap of multiple trips which experienced higher depredation rates (>25% fish depredated), with the area of higher fishing pressure close to Tantabiddi boat ramp, further highlights the potential relationship between fishing pressure and depredation. It is possible that sharks may be attracted to areas that receive high and consistent levels of fishing pressure, by responding to sensory cues created by fishing activity, notably boat engine noise, fish oil and blood and hydrodynamic and electrical disturbances created by struggling hooked fish, which are detected at different ranges (Kalmijn 1972; Corwin 1989; Haine et al. 2001; Collin and Marshall 2003; Dallas et al. 2010; Collin 2012). The overlap of these cues with the availability of hooked fish to depredate upon, which is an energy efficient feeding strategy compared to capturing free-swimming prey, may have created a behavioural association for sharks. Past research has recorded evidence of conditioning in sharks in a laboratory setting (Clark 1959; Guttridge and Brown 2014), and this potential process was also suggested to occur in the NMP, where sharks showed increasingly faster arrival times to a baited camera deployed over consecutive days in a fishing area (Schifiliti 2014).

In the Breede Estuary in South Africa, active acoustic telemetry recorded a bull shark *Carcharhinus leucas* remaining close to fishing boats for extended periods, as well as clear movements towards boats in response to engine noise (McCord and Lamberth 2009), further supporting the possibility that sharks associate these sensory cues with food. Madigan et al. (2015) proposed that the availability of recreationally hooked pelagic fish to depredate upon may even be influencing the site fidelity and migratory movements of oceanic whitetip sharks *Carcharhinus longimanus*, which return to a localised area in The Bahamas each year. Likewise, changes in movement, feeding patterns and behaviour in a range of shark species has been observed, as a result of provisioning conducted by ecotourism activities (Johnson and Kock 2006; Fitzpatrick et al. 2011; Maljkovic and Cote 2011; Bruce and Bradford 2013; Brunnschweiler and Barnett 2013; Brena et al. 2015). However, other studies have recorded negligible effects (Laroche et al. 2007; Hammerschlag et al. 2012), and there is a possibility that depredation is just an opportunistic behaviour that occurs without any behavioural association. Further work is therefore needed to identify and rigorously test the behavioural processes underpinning shark depredation. Nonetheless, the identification of discrete areas of higher depredation and the influence of fishing pressure, is a particularly significant finding of this study, because this information can be used directly by fishers and fisheries managers to reduce depredation by avoiding such areas.

In this study, the number of fish depredated by sharks varied with depth, a relationship also recorded by MacNeil et al. (2009), who reported lower depredation rates on deeper longline sets. The relationship between depth and depredation reported in this study, particularly the peak in depredation at 60 m, may have occurred due to the distribution and abundance of sharks. For example, past research has reported reef sharks spending a greater proportion of time, and being present in higher densities, in deeper outer-reef slope zones, compared to shallower reef flat, back reef and lagoon areas, due to habitat type and the presence of stronger currents (Wetherbee et al. 1997; Field et al. 2011; Rizzari et al. 2014). However, further research is needed to definitively identify the shark species responsible for depredation in this fishery, which would add important context to the spatial variation in depredation rate recorded in this study.

The importance of latitude and its positive linear relationship with depredation in the EG coast model (Figure 12.2.2, Figure 12.2.3), may have been linked to change in habitat type from the central EG to the northern section. This is because there is a transition from shallow (<20 m) bare sand substrate with isolated patch reefs and seagrass beds in the central and southern region of the EG (higher latitude), to larger and deeper (>20 m) sections of coral substrate and islands in the northern region (lower latitude) (Kenyon et al. 2003). This greater proportion of reef habitat at the northern end of the EG may have supported a greater abundance and diversity of sharks, thus leading to higher depredation rates. Indeed, previous research has identified that habitat influences the distribution and diversity of reef sharks, with closer proximity to reef habitat, greater coral cover and higher structural complexity all leading to higher species richness (Chin et al. 2012; Espinoza et al. 2014). Latitude was also recorded to have a significant effect on depredation rate in the Portuguese Indian Ocean longline fishery (Muñoz-Lechuga et al. 2016), although this was at a much larger scale and may have reflected the impact of environmental variables such as sea temperature, rather than habitat. Whilst latitude may act as a proxy for certain spatially heterogeneous variables, future work should focus on directly incorporating small scale habitat variation and data on shark distribution and abundance into analyses.

Survey period showed an important influence on depredation in the west coast GAMM, with the highest depredation occurring in Sept/Oct (spring) 2015. Similarly, time of year was an important covariate influencing depredation in the US Atlantic longline fishery, with a higher likelihood of depredation occurring in summer (MacNeil et al. 2009). The result recorded in this study may have reflected the seasonal movement patterns, and therefore localised abundance of shark species responsible for depredation, which can be driven by environmental factors and reproductive cycles. For example, dusky sharks *Carcharhinus obscurus* and sandbar sharks *Carcharhinus plumbeus* move southwards from the northern regions of Western Australia in the autumn months to give birth (Simpfendorfer et al. 1996; McAuley and Simpfendorfer 2003; McAuley et al. 2005), although it is unknown whether these species cause depredation. The results reported for the survey period variable may have also been caused by changes in fisher behaviour, because wind and tide patterns may determine the accessibility of certain fishing locations at different times of year, influencing fisher site choice (Tink 2015), and thus depredation rates. However, the limited temporal scope and replication of this study, with sampling conducted at discrete periods throughout a single year rather than continuous coverage over multiple years, restricts the confidence with which these inferences can be made.

Fishing effort per trip, time of day and SST had little effect on the number of fish depredated per fishing trip, as indicated by their low relative importance values (Figure 12.2.3). Higher fishing effort in the form of a longer trip might be expected to increase the chance of depredation occurring, due to the greater likelihood of attracting sharks, although this result was not reflected in the GAMMs. This may have been due to the spatial distribution and abundance of sharks, because areas with a higher abundance of sharks would likely experience depredation early in the trip, whereas in areas where few sharks were present, no depredation would occur regardless of the trip duration. Also, depredation can only occur if hooked fish are available, therefore the number of fish hooked is a more important determinant of depredation than the trip duration. Time of day/night can influence shark activity patterns (Nixon and Gruber 1988; Garla et al. 2006), although this variable had little effect on the number of fish depredated in the GAMMs in this study, perhaps because the majority of fishing occurred at similar times, with none happening at night. Lastly, SST might also be expected to influence depredation, because it is known to affect the activity patterns of sharks (Sims et al. 2006; DiGirolamo et al. 2012). However, this variable also had little effect on depredation in the GAMMs. This result could have occurred because multiple shark species were responsible for depredation, thus the thermal ranges and activity patterns of these species would vary, and be influenced by seasonal changes in sea temperature. Overall, the GAMM results from this study provided insights into the underlying factors influencing shark depredation in this recreational fishery, and identified a number of important avenues for future research.

Ecological, socio-economic and fisheries management implications

The results reported in this study highlight the common occurrence of shark depredation in this recreational fishery, and therefore its significance as a fisheries and marine park management issue. Over long timescales, shark depredation in this fishery may potentially have a negative impact on target fish populations, due to the cumulative total mortality of fish comprising the cryptic mortality caused by depredation, in addition to the mortality derived from fishers retaining fish. This is particularly the case where fishers aim to catch their permitted daily bag limit of five demersal fish per person in this region (Department of Fisheries Government of Western Australia 2016), because in the process they may lose, on average, an extra 13.7% of hooked fish to shark depredation for west coast boat ramps or 11.5% for EG coast boat ramps. For example, a boat with five fishers aiming to catch their boat limit of 25 fish, may lose an additional three fish to shark depredation on each trip. Therefore, over the thousands of fishing trips that occur in the NMP and EG each year, this extra mortality may be substantial. Sharks can also be impacted through the retention of fishing gear in their jaws and digestive systems, which may occur after they depredate upon a hooked fish and break off the line. Within the study area, sharks were regularly observed with fishing hooks in their jaw (J. Mitchell unpubl. data), which can cause abscesses and tissue necrosis in the jaw (Bansemer and Bennett 2010). However, in some cases, retained hooks may fall out naturally or be dislodged when the shark feeds, reducing the likelihood of long-term injury. If fishing hooks are retained in the digestive system, more serious injuries such as perforations of the gastric wall and liver can occur, along with associated bacterial infections (Borucinska et al. 2002). These injuries can thus cause reduced fitness due to restricted feeding capacity and disease, possibly leading to eventual death (Borucinska et al. 2002, Bansemer and Bennett 2010, Whitney et al. 2012). Additionally, the recreational fishing experience may be negatively impacted by depredation, due to the loss of prized fish and fishing gear. Indeed, this study recorded estimated costs for gear lost on fishing trips where depredation events occurred, which ranged from AUD$10 to AUD$200, with a mean value of AUD$38. As a result, the regular occurrence of depredation in this fishery may lead to increased human-wildlife conflict over time, as has been reported in US recreational fisheries, where other predators, such as goliath grouper *Epinephelus itajara* (Shideler et al. 2015), California sea lions *Zalophus californianus* (Cook et al. 2015) and common bottlenose dolphins *Tursiops truncatus* (Powell and Wells 2011), depredate hooked fish. In light of this, it is important that further research on shark depredation is undertaken in this fishery, to increase our knowledge of the factors influencing it and to identify measures for reducing its occurrence.

Future directions

In addition to the incorporation of behavioural, habitat and shark species data in future modelling and analytical approaches, there is a need to expand the temporal and spatial scope of data collection, to provide long-term data on trends in depredation across Western Australia. Quantifying the proportion of released fish that are consumed by sharks is another important avenue for future research, as this may further increase mortality of target fish species. The deployment of video cameras underneath fishing boats and deeper in the water column may enable effective collection of this data. Moreover, cameras could be used to identify shark species responsible for depredation, whilst also assessing the proportion of depredation events caused by large predatory teleosts rather than sharks. Finally, future work should aim to assess the efficacy of a wide range of measures for reducing depredation. For example, modifications to fishing methods may lead to lower depredation rates, i.e. avoiding the use of burley and bait where possible and instead using lures. Likewise, utilising electric fishing reels to allow faster retrieval of hooked fish, especially when demersal fishing at depths >50 m, and only fishing with a single hook on each line, to prevent multiple fish being caught simultaneously, would further reduce the chances of depredation occurring. The results of this study suggest that altering spatial fishing patterns may reduce depredation, particularly by avoiding areas where higher depredation were recorded, i.e. west of Tantabiddi boat ramp and at the northern end of EG. Likewise, regularly moving to other fishing locations will further minimise the predictability of fishing effort, allowing sharks less time to locate and move towards fishing boats. When possible, fishing with the boat engine turned off may also reduce the chance of attracting sharks, due to the potential behavioural associations of sharks discussed previously. Lastly, whilst a range of shark deterrents have been tested for the purpose of improving human safety and reducing shark bycatch, further development and testing of deterrents specifically for use against shark depredation should be prioritised.

Conclusion

This study provided the first quantitative assessment of shark depredation in a recreational fishery in Australia, and will act as a vital baseline for future studies in this regionally important fishery. Analysis of the influence of different fishing methods and the effects of spatial and environmental factors on depredation, will inform fisheries and marine park management in this globally significant area, particularly by providing information that can help fishers to reduce shark depredation rates. On a broader level, this study also offers an important perspective for comparison with depredation in larger-scale commercial longline fisheries, which are impacted by shark depredation worldwide.

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12.2.6 REFERENCES

Akaike H (1974) A new look at statistical m identification. IEEE T Automat Contr 19:716–723

Arab A, Wildhaber ML, Wikle CK, Gentry CN (2008) Zero-inflated modeling of fish catch per unit area resulting from multiple gears: application to channel catfish and shovelnose sturgeon in the Missouri River. N Am J Fish Manage 28:1044-1058

Arya S, Mount D, Kemp S, Jefferis G (2017) RANN: fast nearest neighbour search (wraps ANN library) using L2 metric. https://cran.r-project.org/web/packages/RANN/index.html (accessed 10 Sept 2016)

Bansemer CS, Bennett MB (2010) Retained fishing gear and associated injuries in the east Australian grey nurse sharks (*Carcharias taurus*): implications for population recovery. Mar Freshwater Res 61:97-103

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127-135

Borucinska J, Kohler N, Natanson L, Skomal G (2002) Pathology associated with retained fishing hooks in blue sharks, *Prionace glauca* (L.), with implications for their conservation. J Fish Dis 25:515-521

Brena PF, Mourier J, Planes S, Clua E (2015) Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales. Mar Ecol-Prog Ser 538:273-283

Bruce BD,Bradford RW (2013) The effects of shark cage-diving operations on the behaviour and movements of white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia. Mar Biol 160:889-907

Brunnschweiler JM, Barnett A (2013) Opportunistic visitors: long-term behavioural response of bull sharks to food provisioning in Fiji. PLoS One 8:DOI: 10.1371/journal.pone.0058522

Burnham K, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

CALM, MPRA (2005) Management plan for the Ningaloo Marine Park and Muiron Islands marine management area: 2005-2015, Deparment of Conservation and Land Management (CALM) and Marine Parks and Reserves Authority (MPRA), Perth

Candy S (2004) Modelling catch and effort data using generalised linear models, the Tweedie distribution, random vessel effects and random stratum-by-year effects. CCAMLR Sci 11:59-80

Chin A, Tobin A, Simpfendorfer C, Heupel M (2012) Reef sharks and inshore habitats: patterns of occurrence and implications for vulnerability. Mar Ecol-Prog Ser 460:115-125

Clark E (1959) Instrumental conditioning of lemon sharks. Science 130:217-218

Coelho R, Santos MN, Lino PG (2016) Standardized CPUE of blue shark in the Portuguese pelagic longline fleet operating in the North Atlantic. ICCAT Collect Vol Sci Pap 72:1044-1066

Collin SP, Marshall NJ (2003) Sensory Processing in Aquatic Environments. Springer-Verlag, New York

Collin SP (2012) The neuroecology of cartilaginous fishes: sensory strategies for survival. Brain Behav Evolut 80:80-96

Cook TC, James K, Bearzi M (2015) Angler perceptions of California sea lion (*Zalophus californianus*) depredation and marine policy in Southern California. Mar Policy 51:573-583

Corwin JT (1989) Functional anatomy of the auditory system in sharks and rays. J Exp Zool 252:62-74

Craven P, Wahba G (1978) Smoothing noisy data with spline functions. Numer Math 31:377-403

Dallas L, Shultz A, Moody A, Sloman K, Danylchuk A (2010) Chemical excretions of angled bonefish *Albula vulpes* and their potential use as predation cues by juvenile lemon sharks *Negaprion brevirostris*. J Fish Biol 77:947-962

Department of Fisheries Government of Western Australia (2016) Recreational fishing guide 2016, Government of Western Australia, Department of Fisheries, Perth

DiGirolamo A, Gruber S, Pomory C, Bennett W (2012) Diel temperature patterns of juvenile lemon sharks *Negaprion brevirostris*, in a shallow-water nursery. J Fish Biol 80:1436-1448

Donoghue M, Reeves RR, Stone GS (2003) Report of the workshop on interactions between cetaceans and longline fisheries, Apia, Samoa, November 2002. Report No. 03-1, New England Aquarium Press, Boston

Escalle L, Speed C, Meekan M, White W, Babcock R, Pillans R, Huveneers C (2015) Restricted movements and mangrove dependency of the nervous shark *Carcharhinus cautus* in nearshore coastal waters. J Fish Biol 87:323-341

Espinoza M, Cappo M, Heupel MR, Tobin AJ, Simpfendorfer CA (2014) Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. PLoS One 9:DOI: 10.1371/journal.pone.0106885

Field I, Meekan M, Speed C, White W, Bradshaw C (2011) Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. Coral Reefs 30:61-71

Fisher R (in prep.) Development of a novel full-subsets approach for Generalised Additive Mixed Modelling.

Fitzpatrick R, Abrantes KG, Seymour J, Barnett A (2011) Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behaviour? Coral Reefs 30:569-577

Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. Mar Biol 149:189

Gilman E, Clarke S, Brothers N, Alfaro-Shigueto J, Mandelman J, Mangel J, Petersen S, Piovano S, Thomson N, Dalzell P, Donoso M, Goren M, Werner T (2008) Shark interactions in pelagic longline fisheries. Mar Policy 32:1-18

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809-2815

Guttridge TL, Brown C (2014) Learning and memory in the Port Jackson shark, *Heterodontus portusjacksoni*. Anim Cogn 17:415-425

Haine OS, Ridd PV, Rowe RJ (2001) Range of electrosensory detection of prey by *Carcharhinus melanopterus* and *Himantura granulata.* Mar Freshwater Res 52:291-296

Hammerschlag N, Gallagher AJ, Wester J, Luo J, Ault JS (2012) Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. Funct Ecol 26:567-576

Hastie T, Tibshirani R (1986) Generalized Additive Models. Stat Sci:297-310

IOTC (2007) Workshop on the depredation in the tuna longline fisheries in the Indian Ocean, Indian Ocean Tuna Commission, Victoria

Johnson R, Kock A (2006) South Africa's white shark cage-diving industry - is their cause for concern? In: Nel DC, Peschak TP (eds) Finding a balance: white shark conservation and recreational safety in the inshore waters of Cape Town, South Africa. World Wildlife Fund, Cape Town, p 3

Jones CM, Pollock KH (2012) Recreational angler survey methods: estimation of effort, harvest, and released catch. In: Zale AV, Parrish DL, Sutton TM (eds) Fisheries techniques manual (third edition). American Fisheries Society, Bethseda, p 883-919

Kalmijn AJ (1972) Bioelectric fields in seawater and the function of the ampullae of Lorenzini in elasmobranch fishes. Report No. 72-83, Scripps Institution of Oceanography, San Diego

Kenyon R, Haywood M, Loneragan N, Manson F, Toscas P (2003) Benthic habitats in Exmouth Gulf. In: Loneragan N, Kenyon R, Crocos P, Ward R, Lehnert S, Haywood M, Arnold S, Barnard R, Burford M, Caputi N, Kangas M, Manson F, McCulloch R, Penn J, Sellars M, Grewe P, Ye Y, Harch B, Bravington M, Toscas P and Meadows J (eds) Developing techniques for enhancing prawn fisheries, with a focus on brown tiger prawns (*Penaeus esculentus*) in Exmouth Gulf Final Report to FRDC for project FRDC 1999/222. CSIRO, Cleveland

Labinjoh L (2014) Rates of shark depredation of line-caught fish on the Protea Banks, KwaZulu-Natal. MSc dissertation, University of Cape Town, Cape Town

Laroche RK, Kock AA, Dill LM, Oosthuizen WH (2007) Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. Mar Ecol-Prog Ser 338:199-209

Lawson T (2001) Predation of tuna by whales and sharks in the western and central Pacific Ocean 14th meeting of the standing committee on tuna and billfish. Secretariat of the Pacific Community, Noumea

Levy PS, Lemeshow S (2013) Sampling of populations: methods and applications. John Wiley and Sons Ltd., New York

Lin X, Zhang D (1999) Inference in generalized additive mixed models by using smoothing splines. J Roy Stat Soc B 61:381-400

Lo NC-H, Jacobson LD, Squire JL (1992) Indices of relative abundance from fish spotter data based on delta-lognormal models. Can J Fish Aquat Sci 49:2515-2526

MacNeil MA, Carlson JK, Beerkircher LR (2009) Shark depredation rates in pelagic longline fisheries: a case study from the Northwest Atlantic. ICES J Mar Sci 66:708-719

Madigan DJ, Brooks EJ, Bond ME, Gelsleichter J, Howey LA, Abercrombie DL, Brooks A,Chapman DD (2015) Diet shift and site-fidelity of oceanic whitetip sharks *Carcharhinus longimanus* along the Great Bahama Bank. Mar Ecol-Prog Ser 529:185-197

Maljkovic A,Cote IM (2011) Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. Biol Conserv 144:859-865

Maunder MN, Punt AE (2004) Standardizing catch and effort data: a review of recent approaches. Fish Res 70:141-159

McAuley RB, Simpfendorfer C (2003) Catch composition of the Western Australian temperate demersal gillnet and demersal longline fisheries, 1994 to 1999, Government of Western Australia, Department of Fisheries, Perth

McAuley RB, Lenanton R, Chidlow J, Allison R, Heist E (2005) Biology and stock assessment of the thickskin (sandbar) shark, *Carcharhinus plumbeus*, in Western Australia and further refinement of the dusky shark, *Carcharhinus obscurus,* stock assessment, Government of Western Australia, Department of Fisheries, Perth

McCord ME, Lamberth SJ (2009) Catching and tracking the world's largest Zambezi (bull) shark *Carcharhinus leucas* in the Breede Estuary, South Africa: the first 43 hours. Afr J Mar Sci 31:107-111

McLean DL, Langlois TJ, Newman SJ, Holmes TH, Birt MJ, Bornt KR, Bond T, Collins DL, Evans SN, Travers MJ (2016) Distribution, abundance, diversity and habitat associations of fishes across a bioregion experiencing rapid coastal development. Estuar Coast Shelf Sci 178:36-47

Meyer MA, Kotze PGH, Brill GW (1992) Consumption of catch and interference with linefishing by South-African (cape) fur seals *Arctocephalus-pusillus-pusillus*. S Afr J Marine Sci 12:835-842

Minami M, Lennert-Cody CE, Gao W, Roman-Verdesoto M (2007) Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. Fish Res 84:210-221

Mitchell JD, Langlois TJ, McLean DL, Collin SP (in prep.) Shark depredation in commercial and recreational fisheries: a review of existing literature and research gaps.

Muñoz-Lechuga R, Rosa D, Coelho R (2016) Depredation in the Portuguese pelagic longline fleet in the Indian Ocean, Indian Ocean Tuna Commission, Victoria

Murphy P (2008) An overview of Primary Sampling Units (PSUs) in multi-stage samples for demographic surveys, American Statistical Association, Government Statistics Section, Washington DC

Nishida T, Shiba Y (2005) Report of the predation survey by the Japanese commercial tuna longline fisheries (September 2000 - December 2004), National Research Institute of Far Seas Fisheries, Shizuoka

Nixon AJ, Gruber SH (1988) Diel metabolic and activity patterns of the lemon shark (*Negaprion brevirostris*). J Exp Zool Part A 248:1-6

NOAA (2016) High resolution optimum interpolation sea surface temperature data. http://www.esrl.noaa.gov/psd/ (accessed 12 Sept 2016)

Oh BZ, Sequeira AM, Meekan MG, Ruppert JL, Meeuwig JJ (2016) Predicting occurrence of juvenile shark habitat to improve conservation planning. Conserv Biol 31:635-645

Powell JR, Wells RS (2011) Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Mar Mammal Sci 27:111-129

R Development Core Team (2015) R studio: integrated development environment for R (version 3.2.2). www.rstudio.com (accessed 19 Feb 2016)

Raby GD, Packer JR, Danylchuk AJ, Cooke SJ (2014) The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. Fish Fish 15:489-505

Raftery AE (1995) Bayesian model selection in social research (with discussion). Sociol Methodol 25:111-195

Remeslo AV, Yakushev MR, Laptikhovsky V (2015) Alien vs. predator: interactions between the colossal squid (*Mesonychoteuthis hamiltoni*) and the Antarctic toothfish (*Dissostichus mawsoni*). J Nat Hist 49:2483-2491

Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily high-resolution-blended analyses for sea surface temperature. J Climate 20:5473-5496

Rizzari JR, Frisch AJ, Magnenat KA (2014) Diversity, abundance, and distribution of reef sharks on outer-shelf reefs of the Great Barrier Reef, Australia. Mar Biol 161:2847-2855

Ryan KL, Wise BS, Hall NG, Pollock KH, Sulin EH, Gaughan DJ (2013) An integrated system to survey boat-based recreational fishing in Western Australia 2011/12, Government of Western Australia, Department of Fisheries, Perth

Schifiliti M (2014) Are depredation rates by reef sharks influenced by fisher behaviour? MSc dissertation, University of Western Australia, Perth

Shideler GS, Carter DW, Liese C, Serafy JE (2015) Lifting the goliath grouper harvest ban: angler perspectives and willingness to pay. Fish Res 161:156-165

Shono H (2008) Application of the Tweedie distribution to zero-catch data in CPUE analysis. Fish Res 93:154-162

Simpfendorfer C, Lenanton RCJ, Unsworth P (1996) Stock assessment of large coastal and demersal sharks Government of Western Australia, Department of Fisheries, Perth

Simpfendorfer C, Donohue K (1998) Keeping the fish in 'fish and chips': research and management of the Western Australian shark fishery. Mar Freshwater Res 49:593-600

Sims DW, Wearmouth VJ, Southall EJ, Hill JM, Moore P, Rawlinson K, Hutchinson N, Budd GC, Righton D, Metcalfe JD (2006) Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. J Anim Ecol 75:176-190

Smallwood CB, Beckley LE (2012) Spatial distribution and zoning compliance of recreational fishing in Ningaloo Marine Park, north-western Australia. Fish Res 125:40-50

Smallwood CB, Gaughan DJ (2013) Aerial surveys of shore-based recreational fishing in Carnarvon and Shark Bay: June to August 2012, Government of Western Australia, Department of Fisheries Perth

Speed CW, Meekan MG, Field IC, McMahon CR, Stevens JD, McGregor F, Huveneers C, Berger Y, Bradshaw CJA (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. Mar Ecol-Prog Ser 429:261-275

Speed CW, Meekan MG, Field IC, McMahon CR, Harcourt RG, Stevens JD, Babcock RC, Pillans RD, Bradshaw CJA (2016) Reef shark movements relative to a coastal marine protected area. Reg Stud Mar Sci 3:58-66

Streich MK (2016) Ecology of red snapper in the western Gulf of Mexico: comparisons among artificial and natural habitats. PhD dissertation, Texas A&M University, Corpus Christi

Sumner NR, Williamson PC, Malseed BE (2002) A 12-month survey of recreational fishing in the Gascoyne bioregion of Western Australia during 1998-99, Government of Western Australia, Department of Fisheries, Perth

Tascheri R, Saavedra-Nievas J, Roa-Ureta R (2010) Statistical models to standardize catch rates in the multi-species trawl fishery for Patagonian grenadier (*Macruronus magellanicus*) off Southern Chile. Fish Res 105:200-214

Tink CJ (2015) Use of surveys and agent-based modelling to assess the management implications of the behaviours of specialised recreational boat fishers. PhD dissertation, Murdoch University, Perth

Tweedie M (1984) An index which distinguishes between some important exponential families, Proc Indian Statistical Institute golden jubilee international conference. Indian Statistical Institute, Calcutta

van den Hoff J, Kilpatrick R, Welsford D (2017) Southern elephant seals (*Mirounga leonina* Linn.) depredate toothfish longlines in the midnight zone. PLoS One 12:DOI: 10.1371/journal.pone.0172396

Venables WN, Dichmont CM (2004) GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fish Res 70:319-337

Wetherbee BM, Crow GL, Lowe CG (1997) Distribution, reproduction and diet of the gray reef shark Carcharhinus amblyrhynchos in Hawaii. Mar Ecol-Prog Ser:181-189

Whitney NM, Pyle RL, Holland KN, Barcz JT (2012) Movements, reproductive seasonality, and fisheries interactions in the whitetip reef shark (*Triaenodon obesus*) from community-contributed photographs. Environ Biol Fish 93:121-136

Williamson PC, Sumner NR, Malseed BE (2006) A 12-month survey of recreational fishing in the Pilbara region of Western Australia during 1999-2000, Government of Western Australia, Department of Fisheries, Perth

Wood S (2006) Generalized additive models: an introduction with R. CRC Press, Boca Raton

Wood S (2008) Fast stable direct fitting and smoothness selection for generalized additive models. J Roy Stat Soc B 70:495-518

Wood S, Scheipl F (2015) Package 'gamm4' (version 0.2-3). Generalized Additive Mixed Models using mgcv and lme4. https://cran.r-project.org/web/packages/gamm4/gamm4.pdf (accessed 12 April 2016)

Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. J Stat Softw 27:1-25

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

12.2.7 APPENDIX 1

List of boat ramp survey questions:

Boat questions – answers cover all the fishers on the boat:
- What time did lines enter the water?
- What time did lines leave the water?
- What fishing method was used?
- What type of bait/lure was used?
- Was berleying used?
- What was the maximum depth of hooks?
- What was the minimum depth of hooks?
- Approximate fishing location (recorded as a point location on the 'Collector for ArcGIS map)?
- How many fish did you catch, including both those kept and those returned?
- Did you experience shark depredation?
- If yes, how many fish were partly or completely depredated by sharks?
- Were these fish consumed completely or was part of the fish (e.g. the head) retrieved?
- Boat name/number?
- Boat length?
- Time of interview?

Individual fisher questions – answers apply to just the fisher being interviewed:
- Have you been interviewed about shark bite-offs before?
- How many times have you fished from this boat ramp before?
- How many days have you fished from a boat in the last year?
- How many years have you been fishing for?

Part V Report appendices

13. Report appendices

13.1 Report appendix 1. Data

Large amounts of data have been collected as part of the PMCP project. Storage and open access of these data are part of the project's remit. Many different types of data are being collected and produced by the project, making their management complex.

13.1.1 METADATA RECORDS AND DATA STORAGE

The data collated, collected and generated by the project are documented through metadata records. A metadata system is used to record specific attributes of a dataset including fields such as dataset title, abstract, geographic location, time period, subject category(s), search words, data quality, location, access constraints, links to other documentation, contact details, etc.

Table A13.1.1 Titles of metadata records residing in MarLIN2.

TITLE
Biodiversity Characterisation of Pilbara Marine Regions (Epibenthic Sled, Trawl, Towed Video and Sediment)
Coral Reef Broadscale Invertebrate Survey - 2013 – 2015
Coral Reef Health Broadscale Reef Fish Survey - Reef Fish Short Transect Survey (Biomass Estimate) 2013-2016
Coral Reef Health Broadscale Reef Fish Survey - Reef Fish Short Transect Survey (Fish Counts) 2013-2016
Coral Reef Health Broadscale Reef Fish Survey - Reef Fish Short Transect Survey 2013-2015
Coral Reef Health Broadscale Reef Fish Survey - Reef Target Fish Long Survey (Biomass Estimate) 2013-2016
Coral Reef Health Broadscale Reef Fish Survey - Reef Target Fish Long Survey (Fish Counts) 2013-2016
Coral Reef Health Broadscale Reef Fish Survey - Reef Target Fish Survey 2013-2015
Coral Reef Health Broadscale Survey - Reef Benthic Survey: Benthic Cover(%) From Photo Transects 2013-2016
Coral Reef Health Broadscale Survey - Reef Benthic Survey 2013 - 2015
Coral Reef Health Sediment Survey 2013 - 2015
Coral Reef Health - Coral calcification and paleoclimatology
Landsat Imagery of the Pilbara Marine Regions (Landsat8) - 2013
Macroalgae and seagrass biomass and diversity across the Pilbara Region in November 2013 and May 2014
Pilbara Marine Conservation Partnership (PMCP) - Environmental Drivers: Coastal Reef Monitoring (Ningaloo) 2014-2015
Pilbara Marine Conservation Partnership (PMCP) - Environmental Drivers: Coastal Reef Monitoring (Onslow Coast) 2016

CSIRO has developed "marlin"–a metadata system based on the open source GeoNetwork software (www.geonetwork-opensource.org), utilising common standards including the Marine Community profile. This allows metadata to be transferred across different metadata systems facilitating discovery and reuse. This system currently contains 37 metadata records (Table A13.1.1) relating to this project (http://www.marlin.csiro.au). All these metadata records can be listed by using the advanced search filter “pmcp “.

Because the metadata software is based on open standards, all metadata records are made available to the international research community, and can be directly harvested by other portals that support open standards. This allows the metadata records related to the PMCP data to be freely searchable worldwide. Each metadata record contains information on where the data are stored and who to contact to obtain them.

PMCP data are stored in the Pawsey Super Computing Centre (www.pawsey.org.au), an unincorporated joint venture between CSIRO, Curtin University, Edith Cowan University, Murdoch University and The University of Western Australia. The PMCP project has a 50Tb storage quota, and is storing 42 Tb of data on this system, the majority of which is video data.

Data are also made available by researchers to Data Access Portals and other facilities for data download and exploration. This information is added to the metadata records as researchers make data accessible through these facilities, and can then be accessed directly.

13.1.2 DATA MANAGEMENT

Most biological data collected by the PMCP project are managed via Oracle databases. In particular, three databases: 1) a vessel database to manage the data collected during the biodiversity survey (Section 2.1) carried out in June 2013, 2) a laboratory database to manage and handle all biological data resulting from the sorting of the biodiversity survey samples (Section 2.1) and3) a database to manage Underwater Visual Census (UVC) transect data collected by the Coral Reef Health/Fish & Sharks projects (Part 3 and 4).

Vessel database

The vessel database allowed real time data entry and storage of photographs at sea. This was crucial for the ongoing organisation of sampling and for the analysis of preliminary data upon return. Table A13.1.2–Table A13.1.6 are examples of the summary tables available through the vessel database.

Table A13.1.2 Count of sites sampled during the PMCP biodiversity survey.

	VIDEO/TAPPITY	SLED AND SEDIMENT	TRAWL
Site Count	123	111	43

Table A13.1.3 Count of sites where each sort group was collected by sled and trawl during the PMCP biodiversity survey.

VESSEL_SORT_GROUP	SLED	TRAWL
Fishes	88	40
Fishes: Syngnathids	9	2
Ascidians: colonial	72	14
Ascidians: solitary	43	4
Brachiopoda	1	0
Bryozoa	86	17
Crustaceans	101	19
Echinoderms: Asteroids	86	12
Echinoderms: Crinoids	47	10
Echinoderms: Crinoids (Frozen)	37	10
Echinoderms: Echinoids	81	9
Echinoderms: Holothuroids	59	8
Echinoderms: Holothuroids: Synaptids	12	1
Echinoderms: Ophiuroids	73	8
Soft corals	86	21
Hard corals	56	11
Hydroids	66	5
Molluscs: Cephalopods	23	28
Molluscs: non-shelled	19	1
Molluscs: with shells	95	14
Sponges (ethanol)	93	30
Large animal, not retained	3	9
Miscellaneous	12	9
Mixed plants	15	2
Seagrass	2	3
Algae	72	22
Trash (rocks etc.)	108	25

Table A13.1.4 Count of sites each sediment type was recorded at least once by video during the PMCP biodiversity survey.

SCODE	SUBSTRATE	VIDEO	MINIMUM % SUBSTRATE	MAXIMUM % SUBSTRATE
S0	No Sediment name	9	0.33	16.9
S1	Soft Mud	4	0.53	98.34
S2	Silt (Sandy Mud)	15	0.37	100
S3	Sand	81	0.82	100
S4	Coarse Sand	63	0.7	100
S5	Sand Waves/Dunes	23	4.08	100
S6	Rubble (5-50 mm)	21	0.63	86.67
S7	Stones (50-250 mm)	6	0.16	3.76
S8	Rocks (>250 mm)	14	0.54	48.43
S9	Bedrock/Reef	31	0.96	100

Table A13.1.5 Count of sites each type of biohabitat recorded at least once using video during the PMCP biodiversity survey.

BCODE	BENTHIC BIOHABITAT	VIDEO
B0	No Biohabitat	121
B1	Alcyonarians Dense	2
B2	Alcyonarians Medium	1
B3	Alcyonarians Sparse	6
B4	Whip Garden Dense	2
B5	Whip Garden Medium	15
B6	Whip Garden Sparse	39
B7	Gorgonian Garden Dense	3
B8	Gorgonian Garden Medium	12
B9	Gorgonian Garden Sparse	38
B10	Sponge Garden Dense	3
B11	Sponge Garden Medium	18
B12	Sponge Garden Sparse	60
B13	Hard Coral Garden Dense	2
B14	Hard Coral Garden Medium	1
B15	Hard Coral Garden Sparse	5
B16	Live Coral Reef	6
B17	Bioturbated	36
B18	Flora	3
B19	Seagrass	9
B20	Algae	27
B21	Halimeda	5
B23	Bivalve Shell Beds	1
B24	Tube Polychaete Beds	2

Table A13.1.6 Count of sites each type of animal recorded at least once using video during the PMCP biodiversity survey.

ACODE	ANIMAL	VIDEO
A1	Solitary Coral	34
A2	Bryozoan	11
A3	Hydroid	32
A4	Crinoid	78
A5	Urchin	16
A6	Starfish	28
A7	Crab	4
A8	Holothurian	7
A9	Gastropod	1
A10	Ascidian	7
A11	Anemone	10
A12	Sea Pen	68
A13	Non Commercial Fish	67
A14	Commercial Fish	6
(null)	No animals recorded	123

Laboratory database

The Laboratory Database and data entry interface was designed in consultation with project staff, allowing entry of: Identification, count, weight and images of Operational Taxonomic Units (OTUs) from SLED and TRAWL samples.

These data are loaded or entered using a web based data entry interface (Oracle Application Express) into a relational Oracle database and images are stored in an Oracle directory. Figure A13.1.1 Relationship diagram for the data from the sorting of the biodiversity survey. is a relationship diagram for the laboratory database to manage data emerging from the sorting of the biodiversity survey and Table A13.1.7 provides a description of the tables included in it.

Table A13.1.7 Description of the tables included in the laboratory database to manage data emerging from the sorting of the biodiversity survey (Section 2.1)

TABLE_NAME	COMMENTS
LAB_CHEMICALS	a list of chemicals that may be used as fixative or preservative for voucher specimens.
LAB_ID_QA_CODES	list of confidence in taxonomic identification to be used for particular identifier of a particular Operation Taxonomic Unit (OTU), required by Western Australian Museum (WAM)
LAB_KNOWN_TAXA	a list of marine taxa that are already known to occur in the Pilbara region, that can be selected from during the data entry process to add to the table lab_otu
LAB_LAB	identification weight and count of operational taxonomic units(OTU) from the samples collected aboard the survey
LAB_LAB_IMAGES	images of specimens after identification in the laboratory
LAB_OTU	operational taxonomic units identified in the laboratory by taxonomists
LAB_OTU_IMAGES	images of Voucher specimens after identification in the laboratory
LAB_TAXONOMISTS	List of people who have identified specimens by taxonomic group and a rank of confidence in taxonomic expertise for that group
LAB_VOUCHER	count and preservation details of operational taxonomic units (OTUs) identified in the laboratory by taxonomists and kept as voucher specimens
LOCATION_INFO_WAM_IMPORT	information about sampling sites derived from GIS by Ian Mcleod for inclusion in export for WAM (Western Australian Museum) voucher database
PHOTO	image data table, containing photos and metadata
TAPPITY_KEYS	keyboard shortcuts used to describe video footage in real time for June 2013 Gorgon Trip extracted from file keys.xml
VESSEL_SAMPLE	details of sample to be sent to laboratory for identification

Table A13.1.8 is a summary of the data available through the Laboratory Database.

Table A13.1.8 Count of OTUs (taxa names) identified by taxonomists for sled and trawl collected during the PMCP biodiversity survey.

VESSEL_SORT_GROUP	TOTAL	TRAWL	SLED	SLED & TRAWL	SLED NOT IN TRAWL	TRAWL NOT IN SLED
Fishes	195	128	93	26	67	102
Fishes: Syngnathids	6	2	6	2	4	0
Crustaceans	201	25	194	18	176	7
Echinoderms: Asteroids	32	9	32	9	23	0
Echinoderms: Crinoids	49	22	44	17	27	5
Echinoderms: Echinoids	30	6	30	6	24	0
Echinoderms: Holothuroids	26	9	26	9	17	0
Echinoderms: Holothuroids: Synaptids	2	1	2	1	1	0
Echinoderms: Ophiuroids	33	10	33	10	23	0
Soft Corals	112	29	106	23	83	6
Hard corals	47	15	42	10	32	5
Molluscs: Cephalopods	11	6	8	3	5	3
Molluscs: non-shelled	12	1	12	1	11	0
Molluscs: with shells	12	1	12	1	11	0
Sponges	303	96	284	77	207	19
Seagrass	4	1	3	0	3	1
Algae	70	19	66	15	51	4

Underwater Visual Census Database

The Underwater Visual Census database and data entry interface was designed in consultation with Project staff, allowing entry or loading of Data collected during sampling of transects for underwater visual census.

Figure A 13.1.2 is a relationship diagram for the UVC database to manage data emerging from the UVC transect sampling and Table A13.1.9 provides a description of the tables included in it. A summary of the data currently available in the Underwater Visual Census database can be seen in Table A13.1.10.

Table A13.1.9 Description of the tables included in the database to manage data emerging from the UVC transect sampling (Part 3).

TABLE_NAME	COMMENTS
ALGAE_CODES	list of algae used for per_algae_cover
ATTRIBUTES	list of possible attributes that can be used in the site_attributes table
CORAL_GROWTH_CODES	list of codes used for coral growth forms
DIVERS	list of dive personnel for UVC operations
FACIES	lookup table for facies values for use as values in site_attributes table where attribute_name = facies
FISHUVC	count of fish and other taxa of interest by size and gender from uvc operation
OPERATION_TYPE	list of operation types - used in uvc_operations
PER_ALGAE_COVER	percent algae growth on transect by form - adds up to 100 for each operation
PER_CORAL_GRTH_FORM	percent coral growth on transect by form - adds up to 100 for each operation
PER_SEAGRASS_COVER	percent seagrass growth on transect - adds up to 100 for each operation where seagrass is present
PROJECT_REGIONS	Details of region used in project description – name, Country, sate/province
PROJECT_REGION_SITES	List of sites with the region located at Site_id attached to region identifier
REEF	list of reefs sampled by UVC operations associated with site attributes where attribute_name = REEF_ID
SEAGRASS_CODES	list of seagrass used for per_seagrass_cover
SITES	site attributes
SITE_ATTRIBUTES	site attributes and values
STATUS	lookup table for status values - for use as list in site_attributes table where attribute_name = status
STRATA	lookup table for strata values - for use as list in site_attributes table where attribute_name = strata
UVC_HABITAT	Diver and benthic habitat description as recorded for each UVC operation
UVC_OPERATION	operations performed as part of UVC survey
UVC_PERSON	list of project staff on vessel
UVC_PROJECT	Table of projects that UVC data contained in this database has been collected from
UVC_SITE_UWA_LOOKUP	lookup table for corrected site_id. List of sites and positions sent to UWA December 2013 - error noticed and this table created April 2014 Mick Haywood and Margaret Miller
UVC_TRIP	trip details
WAMSI_N_FISH_SPECIES	to be used for fish length/wt relationships
ZONE_MANAGEMENT	This table is to record zone management and management changes, Mick Haywood to complete details - currently has no constraints 22 January 2014

Table A13.1.10 Summary of the data currently available in the Underwater Visual Census Database grouped by sample type. Count of sites by sample type.

TRIP #	START DATE	END DATE	SITE COUNT	LONG TRANSECT	SHORT TRANSECT	PHOTO	MACRO-INVERTE-BRATES	RUGO-SITY	SEDI-MENT
1	05/11/2013	17/11/2013	48	47	1	42	37	40	42
2	02/03/2014	09/03/2014	171	154	44	42	0	142	0
3	05/05/2014	15/05/2014	43	39	4	43	38	38	38
4	20/05/2014	21/05/2014	11	0	0	11	0	0	0
5	01/10/2014	09/10/2014	6	0	0	6	0	0	0
6	23/10/2014	07/11/2014	44	0	44	0	0	44	0
7	10/03/2015	24/03/2015	46	31	45	32	0	45	0
8	21/04/2015	1/05/2015	19	0	14	18	0	14	0
9	4/10/2015	12/10/2015	9	0	8	8	0	5	0
10	13/10/2015	18/10/2015	8	0	0	8	0	0	0
11	4/11/2015	20/11/2015	31	0	31	30	0	32	0
12	6/03/2016	12/05/2016	35	0	34	35	28	34	0
13	11/05/2016	12/05/2016	2	0	2	0	0	2	0
14	8/07/2016	22/07/2016	22	0	18	22	0	18	0
15	27/10/2016	31/10/2016	7	0	7	0	0	7	0
16	26/11/2016	30/11/2016	13	0	0	0	0	0	0
17	4/02/2017	7/02/2017	8	0	8	0	0	8	0

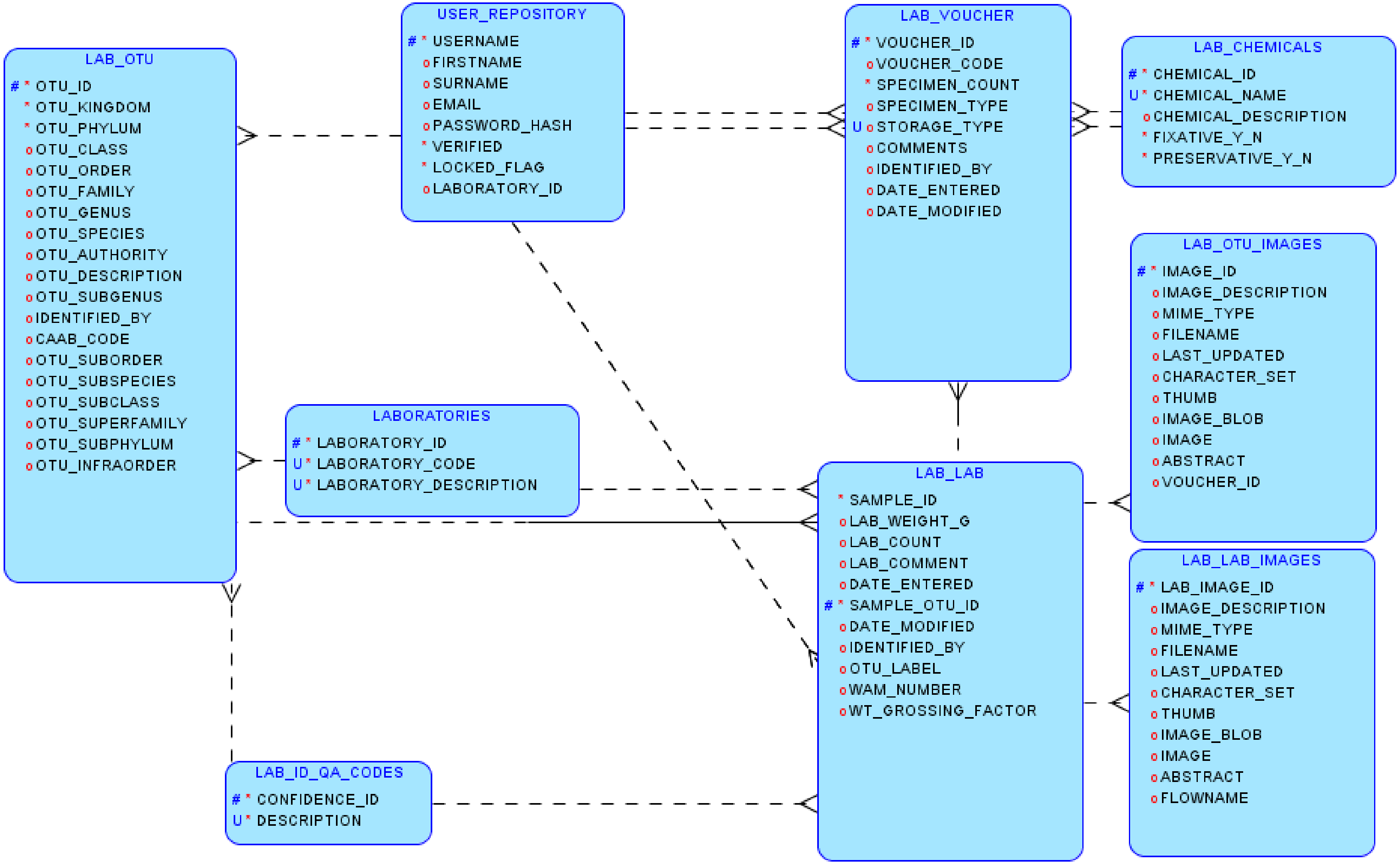

Figure A13.1.1 Relationship diagram for the data from the sorting of the biodiversity survey.

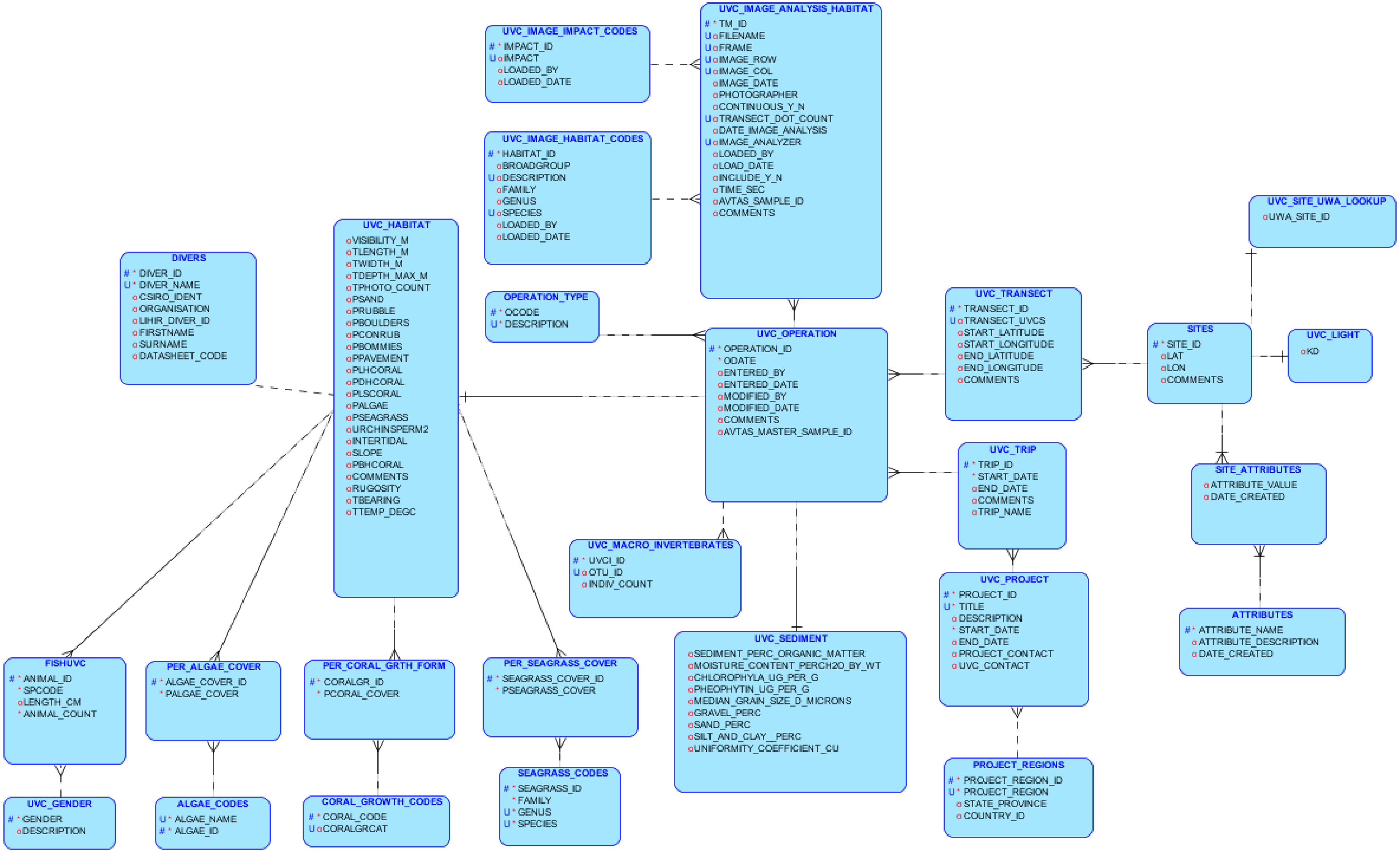

Figure A 13.1.2Relationship diagram for the database for data from the UVC transect sampling.

13.2 Report appendix 2. Supplementary published papers

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Environmental and individual effects on the behaviour and spawning movements of *Lethrinus nebulosus* on a coral reef

R. C. Babcock[A,B], *R. D. Pillans*[A] *and W. A. Rochester*[A]

[A]CSIRO Marine and Atmospheric Research, 41 Boggo Road, Dutton, Qld 4102, Australia.
[B]Corresponding author. Email: russ.babcock@csiro.au

Abstract. Spatial management of fish populations can potentially be optimised by incorporating responses to environmental variables, such as diel, tidal, lunar and seasonal factors, but individual variability in habitat use and behaviour may complicate such efforts. Acoustic tagging and tracking of 84 *Lethrinus nebulosus* in the Ningaloo Marine Park indicated that sizes of individual habitat utilisation kernels were similar across diel and tidal cycles, but varied greatly among individuals. Clearly differentiated diel and tidal habitat use patterns were evident in significant proportions of individuals, particularly in relation to tidal phase. For the majority of residents, home-range sizes were reasonably stable over periods of 2–4 years, but in some cases core areas did shift over time. At seasonal time scales, peaks of seasonal activity and home range area were recorded during spawning season (October–December). Long-distance return migrations to spawning locations were observed that were among the longest observed for any reef fish (over 130 km). Suspected spawning-related movements were recorded almost exclusively in fish >500-mm fork length, and were semilunar, following quarter moons in October–December. Significant individual-level variability in movement and habitat use patterns, evident across multiple temporal scales, has important implications for the management of *L. nebulosus* populations.

Additional keywords: diel, fish, fish personality, fisheries management, individual variation, lunar, marine protected area, passive acoustic monitoring, tidal.

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Introduction

Although an important goal of ecology is to achieve a general understanding of the behaviour and environmental requirements of any species, it is also essential to understand the dynamic aspects and variability of behavioural responses to the environment, as well as variability among individuals. Temporal and spatial behavioural variations in response to the environment are often highly important in terms of providing the context for broader generalisations about habitat use and connectivity (Verweij and Nagelkerken 2007) and provide significant information in relation to ontogenetic shifts and important life history events, such as reproduction (Lecchini and Galzin 2005). Fish are crucially important components of marine and aquatic ecosystems both in terms of ecological processes and because of their usefulness to humans. As such, they have received significant attention in terms of fundamental research to understand their behaviour and how it varies in response to a suite of environmental and developmental drivers (e.g. Pitcher 1986). The need to incorporate our growing knowledge of behavioural responses to environmental variations in fish has also received growing recognition in terms of its application to management (Claudet *et al.* 2010). More idiosyncratic variations among individuals are being described with increasing frequency (e.g. Cote *et al.* 2013; Matich and Heithaus 2015) but are still poorly understood.

The day–night cycle undoubtedly exerts a strong effect on the behaviour of fish and most other animals, and the tracking of tagged fish has shown how species use different habitats (e.g. for trevally, Afonso *et al.* 2009; and sea bream, Di Lorenzo *et al.* 2016) and different depths (e.g. *Lethrinus miniatus*, Currey *et al.* 2015; and *Sebastes melanops*, Green and Starr 2011) at different times of day. Similarly, acoustic monitoring has shown that fish use different areas at different tidal phases, for example trevally (Afonso *et al.* 2009) and jobfish (Meyer *et al.* 2007*a*), and that tidal and diel factors can interact to affect behaviour (Taylor *et al.* 2013; Belo *et al.* 2016). Lunar and tidal, as well as seasonal cycles are also drivers of variation in habitat use, often in conjunction with reproductive events. Tracking technology has revealed the lunar timing and locations of spawning events (e.g. for *Plectropomus leopardus*, Zeller 1998; and *Caranx ignobilis*, Meyer *et al.* 2007*b*), as well as details of movement pathways (e.g. *Lethrinus harak*; Taylor and Mills 2013). As a result the seasonal changes in habitat use associated with reproductive seasonality (Meyer *et al.* 2007*b*, Afonso *et al.* 2009) are now known in much greater detail.

Individual variations in behaviour can vary systematically with size, age, sex and reproductive status, such as has been reported for *Sparisoma cretense* (Afonso *et al.* 2008) and *L. harak* (Taylor and Mills 2013). Contrasting diel behavioural patterns have also been described for individuals that inhabit different habitats. For example *Siganus lineatus* from shoreline habitats foraged during the day and sheltered at night, whereas the opposite pattern was found for individuals from nearby coral reef habitats (Fox and Bellwood, 2011). It has been widely shown that behavioural attributes such as home-range size and residency can vary among individuals, and that otherwise seemingly identical fish may choose to exhibit quite different behaviours in terms of their home-range size, residency and type of habitat used (e.g. *Chrysophrys auratus*, Egli and Babcock 2004; *Lethrinus nebulosus*, Pillans *et al.* 2014; *Naso unicornis* and *Naso lituratus*, Marshell *et al.* 2011; and *Kyphosus bigibbus*, Pillans *et al.* 2017). Such variability among individuals can be greater than that seen in response to environmental factors (e.g. Marshell *et al.* 2011). Because of this, variations among individuals may have important ecological and evolutionary consequences (Bolnick *et al.* 2003), as well as practical implications for the experimental design and sample size in tracking studies (Pillans *et al.* 2014).

Detailed behavioural information from tracking studies of marine fish and sharks is increasingly being used to recommend management measures. For example, knowledge of the timing, spatial scale and location of spawning aggregation sites has been used to formulate suggested management options for both pelagic and resident reef species (e.g. Meyer *et al.* 2007*b*; Taylor and Mills 2013). In some cases, such as for the coral trout (*P. leopardus*), tracking data from spawning aggregations have contributed to the justification for actual management decisions in relation to the location of boundaries of certain no-take areas on the Great Barrier Reef, as well as the timing of seasonal fishing closures (Zeller 1998). Data such as home-range size estimates have been used to recommend minimal areas for spatial management measures, such as no-take areas and marine reserves (e.g. for *Aprion virescens*, Meyer *et al.* 2007*a*; and *Lethrinus* spp., Taylor and Mills 2013). Unfortunately, movement data are more commonly used post hoc to justify the extent of existing no-take areas as being either adequate or too small, based on a comparison of the relative size of home ranges and the size of reserves where studies are usually located (e.g. *Lethrinus* spp.; Taylor and Mills 2013).

Evaluations of the effectiveness of marine reserves seldom take into account individual-level variability in home range and residency, whether in relation to ontogenetic factors or idiosyncratic variation in behavioural patterns; however, such variability has important implications in terms of either planning or assessing the effectiveness of spatial protection measures. For example, home-range size estimates based on resident fish (usually these are the only ones present for long enough to allow such estimates to be made) underestimate the proportion of fish that will move across reserve boundaries (Babcock *et al.* 2012; Pillans *et al.* 2014). Different levels of fishing pressure may also change the spatial distribution of resident and non-resident fish across reserve boundaries, further complicating assessments and predictions of reserve effectiveness (Parsons *et al.* 2010, 2011).

Fish of the family Lethrinidae are important omnivores and generalist predators on tropical and subtropical reefs of the Indo-Pacific and, as such, are of interest from both ecological and management perspectives. Lethrinids are well represented in acoustic tracking studies (see Table S1 available as Supplementary material to this paper) and a wide range of behaviour patterns has been documented with this group, including diel, tidal, lunar and size-specific and reproductive variations. The spatial extents of home ranges and levels of residency vary widely within the group, both between and within species, and individual idiosyncratic variation in behaviour is reported in several species (Chateau and Wantiez 2008; Taylor and Mills 2013; Currey *et al.* 2014; Honda *et al.* 2016), including *L. nebulosus* (Pillans *et al.* 2014).

The present study was conducted in the Ningaloo Marine Park, where multiple-use park zoning has established a network of no-take areas as well as recreational and special purpose zones where recreational fishing is allowed. Previously, we described the home range and residency of *L. nebulosus* at Ningaloo in terms of individual size and marine park zoning status, showing that home ranges (95% kernel utilisation distribution (KUD) 8.5 ± 0.5 km^2 for residents) are significantly smaller than the mean size of no-take zones at Ningaloo (30 km^2; Pillans *et al.* 2014). However, the levels of long-term residency (>1 year) are sufficiently low (residency index (I_R) = 0.66) to suggest that no-take zones may offer only short-term protection to this species (Pillans *et al.* 2014). Despite 34% of the Ningaloo Marine Park being protected by no-take zoning, and the exclusion of commercial fishing within the rest of the park, there is evidence of population decline in *L. nebulosus,* as well as a reduction in the modal age and percentage of older fish (Marriott *et al.* 2011) along the Ningaloo coastline. Consequently, further analysis of the movement data from *L. nebulosus* populations at Ningaloo was warranted given the large dataset and apparent importance of external factors in fish behaviour.

In the present study we assessed: (1) the behaviour of *L. nebulosus*, one of the larger lethrinids and a species common throughout the Indo-Pacific; (2) whether home-range size or habitat use varied systematically at the population level in relation to environmental and ecological factors, such as diel and tidal cycles, and lunar and seasonal effects, as well as reproduction, across a range of habitats; and (3) whether multiple modes of individual behavioural variability in response to environmental factors obscured any general trends.

Materials and methods

Study site

The Ningaloo Reef Marine Park (NRMP) encompasses Australia's largest fringing reef (Conservation and Land Management and Marine Parks and Reserves Authority 2005), covering a total area of 4566 km^2. The NRMP runs along 300 km of Western Australia's coastline, from Bundegi in the northern Exmouth Gulf (21°52.93′S, 114°08.95′E) to Red Bluff in the south (24°01.87′S, 113°26.25′E; Fig. 1). In 2006, the NRMP was substantially extended and 34% of total park area incorporated into limited or no-take sanctuary zones under the revised Management Plan 2005–15 (Conservation and Land Management and Marine Parks and Reserves Authority 2005). Areas where no fishing is allowed are referred to as sanctuary zones. The NRMP is zoned for multiple uses and although no commercial fishing is allowed, recreational fishing is permitted with

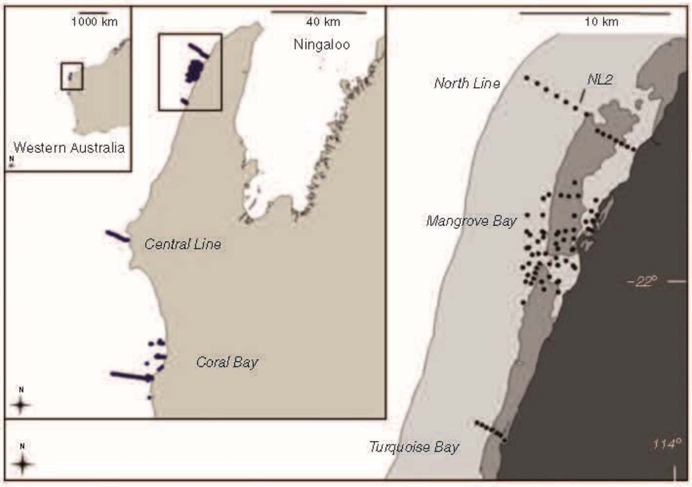

Fig. 1. Study area showing the location of the Mangrove Bay array and receiver lines at Ningaloo Reef, Western Australia.

recreational fishing catch in recreation zones controlled by possession and size limits. Fishing is also permitted in special purpose shoreline angling zones within some otherwise 'no-take' areas. Although areas of protection were chosen based on the best available knowledge and with a view to including the full spectrum of representative marine habitats, many of these decisions were made without in-depth knowledge of the biological communities that reside there and before detailed data existed on the movement patterns of Ningaloo's major fish species.

Acoustic monitoring array, fish capture and tagging

An array of acoustic receivers was located within and adjacent to the Mangrove Bay sanctuary zone (695 ha) and extended from <1-m water depth near the shoreline to the reef slope in ~50-m water depth (Fig. 1). Receivers were spaced 200–800 m apart and detection ranges generally did not overlap. The array encompassed habitats including mangrove-lined shores, limestone pavement, coral reefs interspersed with expanses of sand and areas of flat, hard substratum dominated by macroalgae (predominantly *Sargassum* spp. and other fucalean algae) within the lagoon. A continuous fringing reef created a barrier to movement out of the lagoon at low tide and during times of high swell, but a reef pass provided direct access to deeper reef slope waters. Several large *Porites*-dominated patch reefs were present in the reef pass. The reef slope consisted of spur and groove habitat, as well as areas of limestone reef interspersed with sand patches. Beyond 35-m depth, the substratum is predominantly sandy sediment with occasional flat limestone reef.

An acoustic monitoring array (VEMCO) was used to monitor the movement of individual fish. The Mangrove Bay array consisted of 50 acoustic receiver stations from December 2007 to May 2008 and 60 acoustic receiver stations from May 2008 to May 2010. From December 2007 to May 2008, all receivers were the VR2W model (VEMCO); an additional eight VR2 (VEMCO) and two VR2W receivers were added in May 2008 and lines of receiver stations were added at Turquoise Bay (10 km to the south of Mangrove Bay) and in the lagoon at Tantabiddi (10 km to the north) in 2013 to give a total of 84 receiver stations. In addition to the array, there are three cross-shelf lines of receivers, including the North Line adjacent to Mangrove Bay, extending from the reef slope (~12 m) to the 200-m isobath located along the Ningaloo Reef (Fig. 1) as part of the Ningaloo Reef Ecosystem Tracking Array operated by the Australian Integrated Marine Observing System (IMOS) Animal Tracking Facility.

Fish were captured with rod and line between November 2007 and November 2009. In all, 84 *L. nebulosus*, ranging in size from 26- to 67-cm fork length (FL), were tagged with acoustic tags at locations within the Mangrove Bay acoustic receiver array (Pillans *et al.* 2014). Individual *L. nebulosus* were tagged internally with size-appropriate VEMCO coded transmitters (tags). Range tests were conducted with the V9, V13 and V16 tags with power outputs encompassing the range used on *L. nebulosus*. Power output had little effect on detection range during testing and Pillans *et al.* (2014) demonstrated that tag type and power output had negligible effects on movement parameters of *L. nebulosus*.

Nine fish were not detected at all following release and the fate of these fish is uncertain. They are not thought to have died, but were not included in subsequent analysis. The sex of tagged fish was not usually determined because this species has a non-functional protogynous hermaphroditic life history strategy (Marriott *et al.* 2010) that prevents size-based sex determination. However, the sex of some individuals was determined during the spawning season by direct examination of the gonads at the time of tagging. The size range of fish tagged encompassed all sex and maturity stages. Fish were tagged at 34 locations on 17 occasions between 30 November 2007 and 6 November 2009, either in the lagoon or along the reef slope. Fish tagged in the lagoon were tagged in one of the following habitats: reef flat, lagoon patch reefs, Mangrove Bay and shoreline pavement. Receivers were downloaded every 3–4 months throughout the study, and the batteries were changed at least every 6 months. Capture and tagging of fish was conducted under a CSIRO Brisbane Animal Ethics Permit (Permit A2/07). Further details of tagging protocols and range testing are provided in Pillans *et al.* (2014).

Detection and spatial analysis

The KUD was calculated for resident (>30 days on at least one receiver) fish using kernel techniques (Van Winkle 1975; Worton 1989). Utilisation distribution depicts the probability of an animal occurring at a location within its home range as a function of receiver detection relocation points (White and Garrott 1990) based on a probability density function that quantifies an individual's relative use of space (Kernohan *et al.* 2001). KUD has been widely used to investigate animal movement from acoustic telemetry of a range of species ranging from marine turtles (Makowski *et al.* 2006; MacDonald *et al.* 2012) and dugongs (Zeh *et al.* 2015) to fish (Pillans *et al.* 2014). The bandwidth (or smoothing parameter; *h*) can greatly influence the shape and size of the kernel (Wand and Jones 1995; Gitzen *et al.* 2006; Pillans *et al.* 2014). Because there is no single *a priori* method for determining the most appropriate bandwidth, we tested the two most commonly used methods: (1) the reference smoothing parameter function (h_{ref}; Worton 1989); and (2) the least-squares cross-validation function (h_{lscv}; Silverman 1986). We found that h_{ref} provided the most realistic representation of space use, with h_{lscv} tending to produce unrealistic multiple kernels that were fragmented and clustered around receivers, excluding important areas occupied by *L. nebulosus*.

Behaviour at the individual level was characterised by the 50% (core area) and 95% (home range) KUDs, which were calculated for all months combined, as well as for each month–year combination that the fish was detected. The 50 and 95% KUDs represent the area on which the probability of relocating the animal is equal to 0.5 or 0.95 respectively. The 50 and 95% KUDs were calculated using the adehabitatHR package (Calenge 2011) in R (R Foundation for Statistical Computing, Vienna, Austria). Passive acoustic detections resulted in thousands to hundreds of thousands of detections of individuals on each receiver with identical *x* and *y* coordinates. To alleviate this issue, we randomly assigned acoustic detections within a 200-m radius of each receiver. This radius was chosen based on range test data from range testing within the array (for details, see Pillans *et al.* 2014) and produced KUDs of very similar size and shape to a smoothing parameter of $h = 200$ (Pillans *et al.* 2017; c.f. smoothing parameter of 1000 used by Pillans *et al.* (2014), which produced slightly larger KUD estimates).

Behaviour at the individual level was characterised by the 50 and 95% KUDs, which were calculated for all months combined, as well as for each month–year combination that the individual was detected. Where individuals were resident for more than 1 year, 50 and 95% KUDs averaged for each year were also estimated. To determine diel and tidal influences on movement and habitat use, 50 and 95% KUDs of individuals and all fish combined were calculated during the period 1 h each side of high and low tide for each month–year combination and for the entire monitoring period. Similarly, 50 and 95% KUDs were plotted for day and night using local time of sunrise and sunset. The utilisation distribution overlap index (UDOI) of Fieberg and Kochanny (2005) was used to measure the degree of overlap among individual fish, the degree of overlap between day and night and high and low tide, as well as for separate years. For two home ranges where each individual's habitat use is uniform and there is perfect overlap in 95% KUD, UDOI = 1; where there is no overlap, UDOI = 0. However, UDOI can be >1 if each utilisation distribution is non-uniformly distributed but there is nevertheless a high degree of overlap (Fieberg and Kochanny 2005). For 50% KUD we have conducted comparisons that indicate UDOI values of 0.347 for fully overlapping KUDs (i.e. simulated using the same detection data; R. C. Babcock and R. D. Pillans, unpubl. data). In the present study we used KUD location and size as our metric of habitat use rather than number of detections. The area of habitat used is a less ambiguous indicator of spatial activity than detection rate because it is not clear what aspect of behaviour is being reflected in the detection rate data.

Lunar pattern of detections

We hypothesised that seasonal detections at certain offshore receiver stations on the North Line (Fig. 1) showed a particular lunar variation. Detections of each individual were collated as presences or absences at North Line on each day from the beginning of October to the end of December. The lunar periodicity of detections was analysed by assigning a lunar day to each detection, and applying circular statistics appropriate to cyclic data. Each day of the 29.53-day lunar cycle was given an angular value (29.53/360) corresponding to the mid-point angle of each daily segment (Zar 1984). The mean angle and angular dispersion of the data could then be calculated. The significance of any lunar signal in the data was tested using Rayleigh's statistic *R* (Zar 1984).

Results

General trends in detection and kernel distribution

Results presented herein focus on specific details of home range and movement not previously investigated by Pillans *et al.* (2014). Here we report further details relating to the same individuals and examine diurnal, tidal, seasonal and interannual variability in habitat use and home-range location, as well as potential spawning-related movements.

Tagged *L. nebulosus* that were recorded at least once following release were detected up to 73 980 times on as many as 27 receivers over a maximum period of 1822 days. Throughout the detection period, over 70% of tagged fish were detected on less than 10 receivers. Thirty-nine *L. nebulosus* were detected enough times over periods of more than 30 days to calculate kernel distribution (Pillans *et al.* 2014). Kernel area for the 36 non-resident fish was not calculated, but several of these individuals ($n = 10$) were detected on distant receiver lines, or seasonally for short periods when they returned to the array area.

Diel analysis

The average extent of core habitat used (50% KUD) did not differ significantly between day and night, and 95% KUD values were highly similar between day and night-time periods (Table 1; paired *t*-test, $P = 0.43$, d.f. = 85). The range in size of individual core habitat areas varied eightfold between 40 and 325% of daytime core area values, which was far less than the variation in size among individuals, which ranged from 0.2 to 13 km^2 (a 65-fold difference). The modal 50% UDOI values were ~0.35, indicating there was a high level of overlap in core day and night habitat use in most cases (Fig. 2*a*), but over 30% of individuals showed contrasting behaviours, with day–night UDOI values lower than 0.1. This contrast indicates that the distribution of behaviours was distinctly bimodal and a sizeable minority of the population did show diel shifts in habitat use. For 95% KUDs, activity centres appeared to mostly overlap within the broader range of activity shown by individuals. However, 95% UDOI distribution showed modal values of 1.5 (Fig. 2*b*), indicating that within these broader areas the use of space varies on a diel basis. There were nevertheless a few individuals for which even 95% UDOI overlap was extremely low between day and night.

In order to assess whether variations in diel habitat use were related to particular types of habitat, we examined this variation in those nine fish with very little overlap in their core activity area (50% KUD). There was a high level of individual variation in diel habitat use, with no clear patterns discernible. Most of these fish ($n = 6$) showed movements either into mangrove-lined habitats closer to shore or onto the reef flat at night (e.g. Fig. 3*c*, *f*), whereas others showed the opposite pattern, ranging more widely during the day (Fig. 3*e*). Variations in day and night-time space use in the other individuals were not always related to habitat, and even fish located in the same part of the array could show contrasting levels of diel variation, as can be seen when comparing Fish 8030 (Fig. 3*a*) with Fish 8028 (Fig. 3*b*).

Tidal analysis

The size of habitat area used by *L. nebulosus* did not differ significantly with different tidal states, in terms of either 50 or 95% KUD (Table 1; paired *t*-test, $P = 0.35$, d.f. = 73). The range in size of individual core habitat areas varied 3.5-fold between 56 and 196% of high tide core area values, which was far less than the variation in size among individuals, which ranged from 0.2 to 13.7 km^2, a 72-fold difference. In terms of tidal variation and overlap in habitat use in the 50% UDOI, values for tagged individuals were distinctly bimodal, indicating there was substantial variation in the use of space within the population in terms of their core low tide and high tide home-range locations (Fig. 4). A minority (~13%) of individuals used markedly different areas at low tide and high tide, with the majority having a large degree of overlap between core areas at high

Table 1. Diel and tidal variation in space use by *Lethrinus nebulosus*

Data show mean (±s.d.) differences in average 50 and 95% kernel utilisation distribution (KUD) values for tagged fish between 2007 and 2009: 41 fish, 74 annual pairs of observations. *P*-values are two-tailed

	Time of day			Tidal state		
	Day	Night	$P(t \leq t)$	High	Low	$P(t \leq t)$
50% KUD (km^2)	0.76 ± 1.47	0.76 ± 1.70	0.83	0.99 ± 2.24	1.04 ± 2.49	0.35
95% KUD (km^2)	3.64 ± 5.80	3.30 ± 6.31	0.058	4.33 ± 8.94	4.53 ± 10.24	0.35

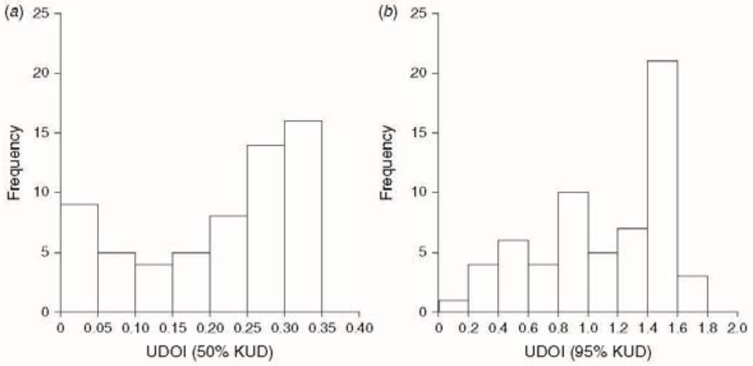

Fig. 2. Diel variation in overlap of the (*a*) 50% kernel utilisation distribution (KUD) and (*b*) 95% KUD utilisation distribution overlap index (UDOI) for *Lethrinus nebulosus*.

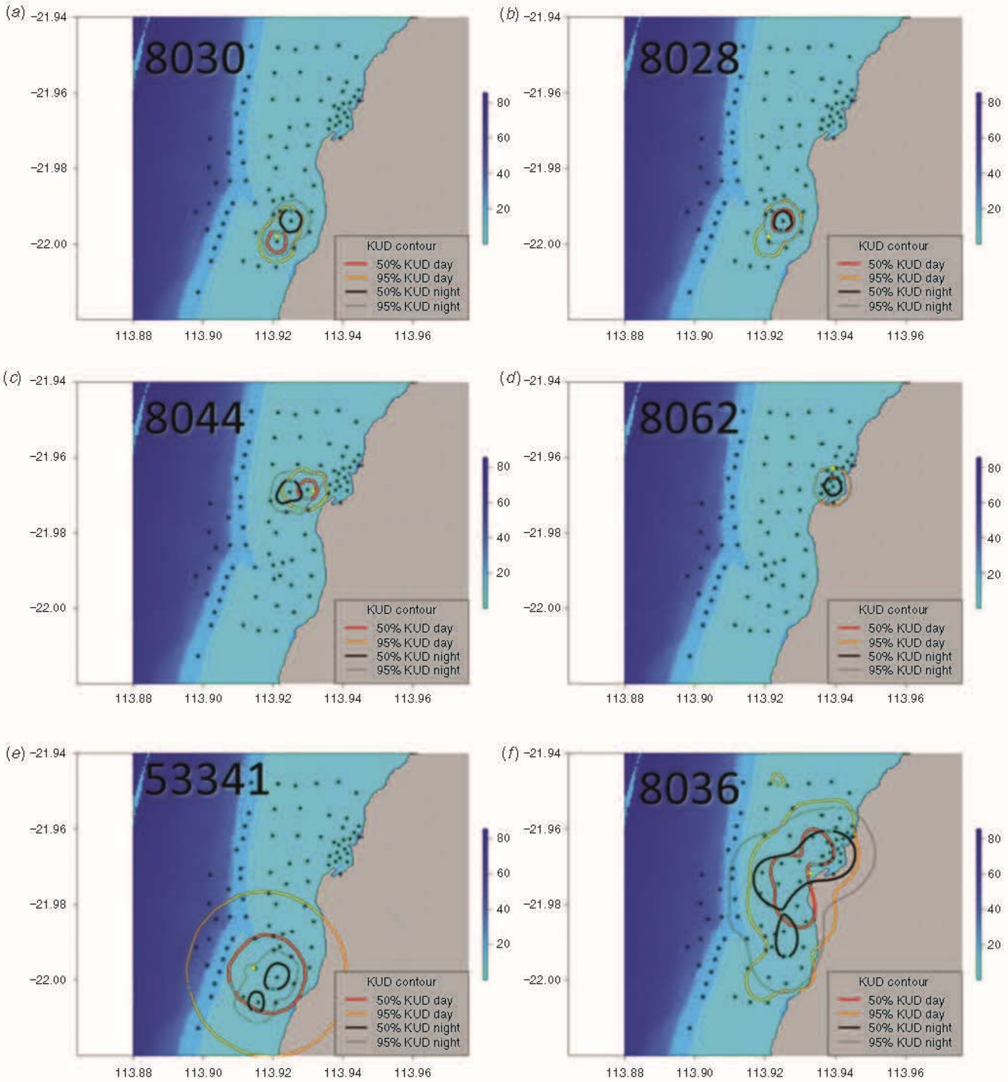

Fig. 3. Diel variation in space use by *Lethrinus nebulosus* of six representative individual fish showing 50 and 95% kernel utilisation distribution (KUD) contour lines during the day and at night. Colour scale indicates depth (m).

and low tide (Fig. 4). This trend was similar for the 95% UDOI (Fig. 4*b*), with a modal value of 1.5, indicating that in the majority of individuals there was a large degree of overlap in 95% KUD. The majority of individuals that had distinct low and high tide core and total areas were resident in the shallow nearshore water of Mangrove Bay, although they were also recorded for individuals in the outer lagoon.

In order to assess whether tidal variations in habitat use were related to particular types of habitat, we examined this variation among individuals in terms of what types of habitat were more likely to be frequented at high and low tide. Overall, although core area location did vary with tide, individual variation in habitat use was high and no clear single trend emerged (e.g. consistently moving into deeper water at low tide, or

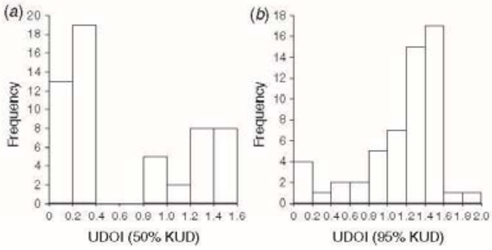

Fig. 4. Tidal variation in overlap of the (*a*) 50% kernel utilisation distribution (KUD) and (*b*) 95% KUD utilisation distribution overlap index (UDOI) for *Lethrinus nebulosus*.

consistent movement into particular habitats). Although in some cases fish appeared to move into areas closer to shore or into areas of reef flat at high tide (Fig. 5*a*, *b*), there were also fish in the same habitats that showed little or no variation in space use in relation to tide (Fig. 5*d*, *e*). Still other fish showed different levels of high and low tide space-use which did not appear closely related to access to habitat (Fig. 5*c*, *f*). Individual 8171 (Fig. 5*b*) once again provided a good example of high levels of general overlap in 95% KUD in space use while at the same time revealing clear differences in 50% KUD locations at high and low tide.

In order to further examine the role of individual-level variability in driving the potential behavioural responses to environmental variation, diel and tidal UDOI scores were compared for individuals. There was a weak but significant correlation between diel and tidal UDOI values of individual fish and for the 50% KUD ($R^2 = 0.087$, $P = 0.03$), but not for the 95% KUD overlap ($R^2 = 0.04$, $P = 0.15$). The relationship between the day–night and low tide–high tide UDOI scores suggests that there may be an interaction between tide and time of day in terms of the utilisation of certain habitats. However, only three fish (8026, 8074 and 8171), were in the groups with lowest 50% KUD overlap for both day–night and low–high comparisons. The core activity areas of these individuals were centred on three different habitats, namely shallow mangrove fringed shoreline, lagoon bommies and macroalgal-covered pavements, and there was no consistent pattern in terms of the types of habitat that may lead to interacting diel and tidal-driven habitat usage. There were also weak but significant correlations between 95% KUD size and both tidal ($R^2 = 0.18$, $P = 0.007$) and diel ($R^2 = 0.22$, $P = 0.002$) UDOI comparisons.

Interannual variation

For eight of the tagged fish it was possible to examine changes in home-range location and activity distribution across multiple years. There were large individual variations in home-range size and interannual stability of individual habitat areas. For example, the size of the KUD was similar for the majority of individuals among years, and average 50% KUD varied in size by only 10% (Fig. 6*a*–*f*). In contrast, for two fish (8047 and 8074) the area of the 50% KUD shrank or grew respectively by a factor of two or more between successive years (Fig. 6*g*, *h*). Consequently, although variability in 50% KUD extent was substantial (s.d. ±60%), this figure is misleading and does not reflect the behaviour of any single individual, underscoring the importance of understanding individual variability and the distribution of behaviours within the population. Of the eight individuals whose interannual activity is depicted (Fig. 6), four showed an increase in 50% KUD area, whereas the other four showed a decrease in overall area. Relative changes in the area of the 95% KUD were, on average, smaller and slightly less variable (mean (±s.d.) 4 ± 49%).

There were contrasting modes in the interannual stability of location of core activity centres. Although in many cases the core activity changed little from year to year, the relocation of activity centres was also reasonably common, as indicated by the mode of low (<0.05) UDOI values (Fig. 7). These relocations were usually to areas adjacent to previous activity (Fig. 6*a*, *g*), as reflected by UDOI values for 95% KUD (Fig. 7).

Seasonal variation and spawning movements

There were two distinct patterns in the seasonal variability of fish behaviour observed among resident and non-resident fish. For resident fish there were distinct increases in the 50% KUD area in October–December that reappeared consistently across the 30-month period from December 2007 to the end of May 2010 (Fig. 8). Over the rest of the year the monthly average area of habitat used remained reasonably constant (at ~0.5 km^2 50% KUD) for most of the period monitored. This period represents the tag life of individuals tagged in November 2007, as well as smaller numbers of fish tagged during subsequent years. Of the 39 resident individuals present consistently enough to be used in this analysis, nine showed seasonal movements to the reef slope (one of these was a reef slope resident that reappeared seasonally). This group of individuals included several fish caught and tagged during the spawning season at reef slope sites (e.g. Fish 8047; Fig. 6*h*). The average 50% KUD area increased more than sixfold to peak at 4.1 and 3.3 km^2 in December 2008 and October 2009 respectively (Fig. 8). Identical trends were present in the 95% KUD data (data not shown).

Peaks in KUD area of resident fish coincided with an increase in the number of fish detected at reef slope locations. For example, the additional activity centre for Fish 8047 on the reef slope in 2009 (Fig. 6*h*) was due to a period of activity in this habitat during the period October–December, after which it returned to the lagoon (Fig. 9). Similar activity involving movements to the reef slope was again observed in 2008, although it was less prolonged. Four other fish (8108, 8111, 8126 and 8171) exhibited similar behaviour, being resident in the lagoon and making brief appearances on the reef slope between October and December.

For non-resident fish, 17 of the 36 were tagged on the reef slope during the period October–December, and the majority of these provided sparse detections around the time of tagging but were not subsequently detected for extended periods of time, up to 2 years in some cases (Fig. 9). Ten of these tagged individuals (59%) exhibited distinct seasonality, and were only detected again on the Mangrove Bay reef slope and during the period October–December, often in several years (Fig. 9). For example, Fish 8095 (running ripe male) was tagged in December 2009 and

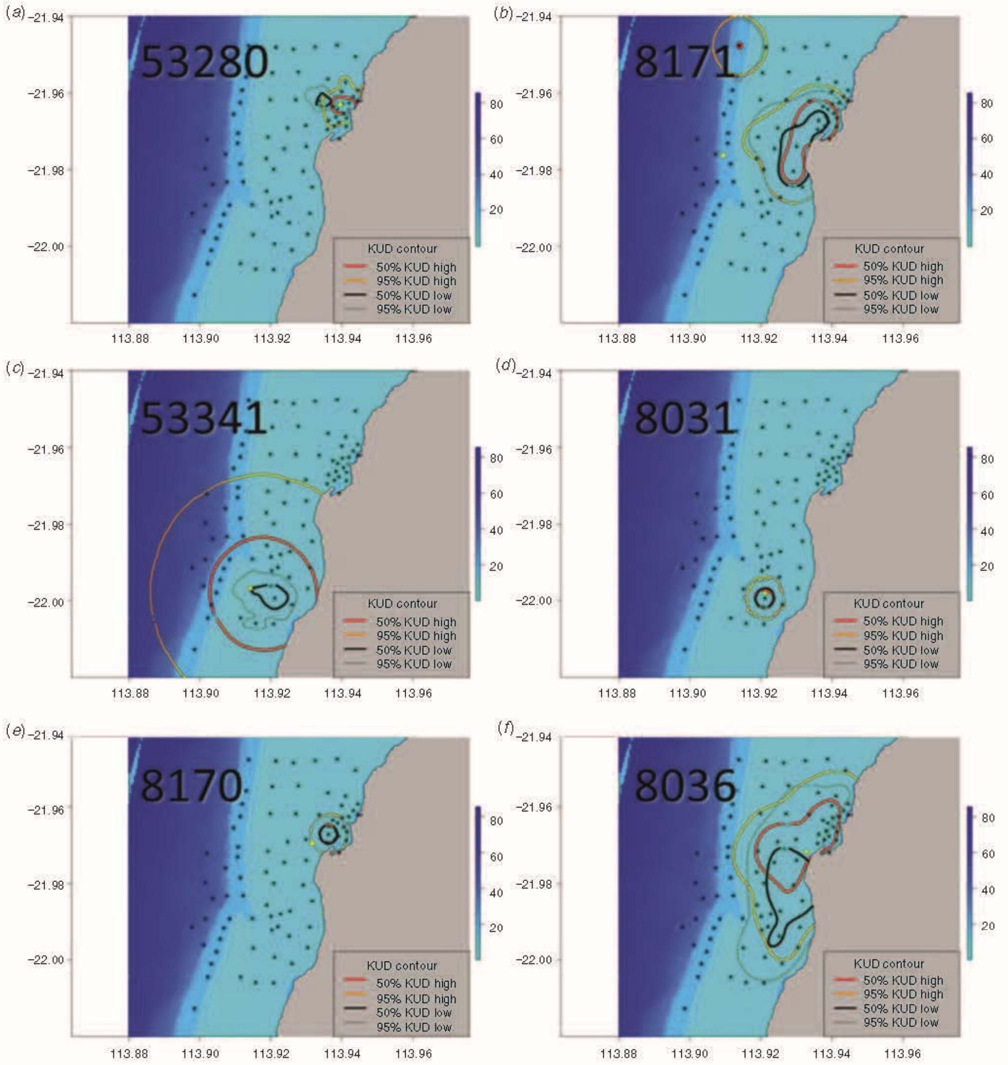

Fig. 5. Tidal variation in space use by *Lethrinus nebulosus* of six representative individual fish showing 50 and 95% kernel utilisation distribution (KUD) contour lines during high and low tide. Colour scale indicates depth (m).

was only detected again in 2010 on the reef slope in October–December. Fish 8168 was tagged in December 2007 and reappeared subsequently in 4 years on the reef slope off Mangrove Bay (2008, 2009, 2011 and 2012) before the tag reached the end of its life. In summary, both resident and non-resident fish showed seasonal patterns in home-range size and utilisation of reef slope habitats.

Migrations

Of the 10 non-resident individuals that showed distinct seasonal returns to the reef slope, a substantial proportion (30%) showed evidence of long-distance migrations. A subset of the returning non-resident fish ($n = 3$) was detected at distant locations more than 100 km to the south during their periods of absence from the

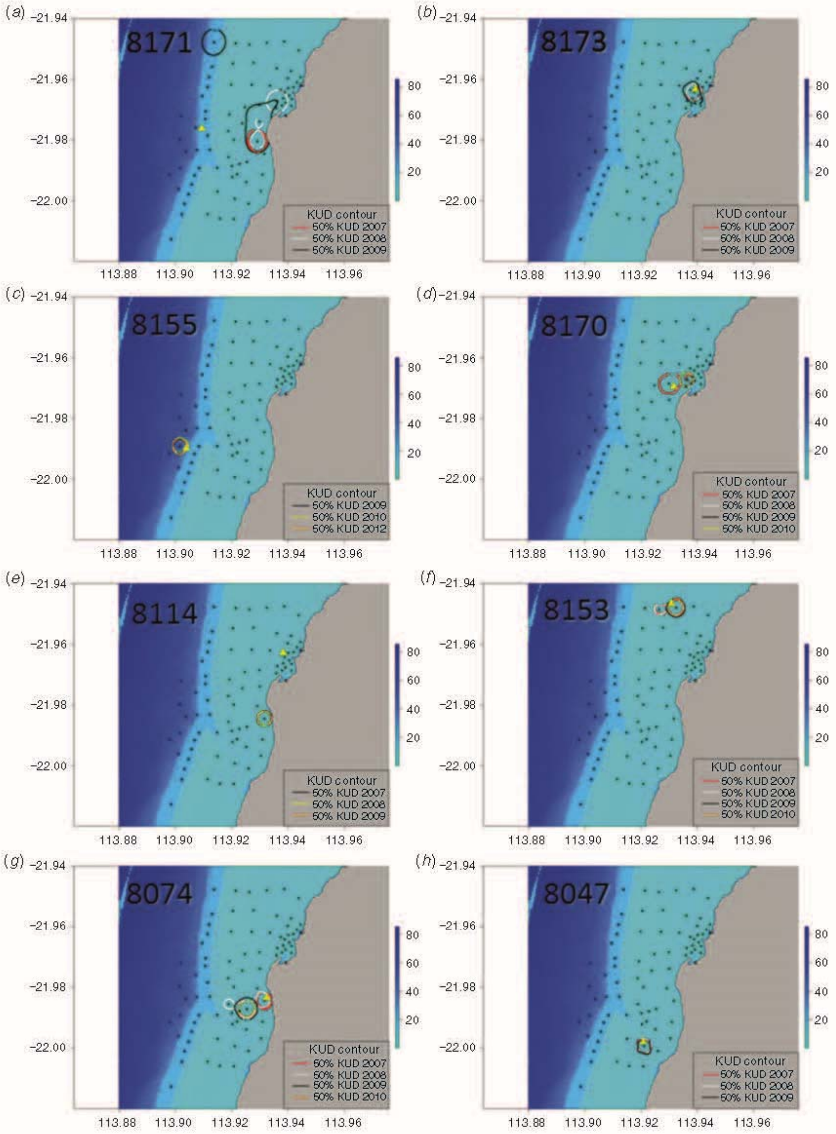

Fig. 6. Interannual variation in space use by *Lethrinus nebulosus* of eight representative individuals showing 50 and 95% kernel utilisation distribution (KUD) contour lines for each year during which the fish was resident. Colour scale indicates depth (m).

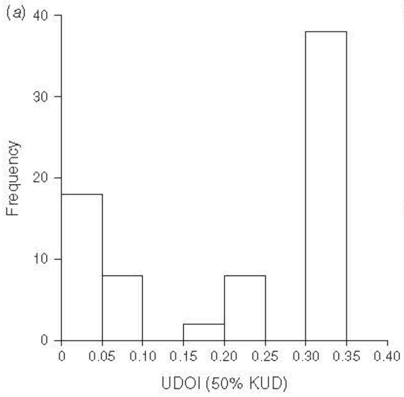

Fig. 7. Interannual variation in overlap of the (*a*) 50% kernel utilisation distribution (KUD) and (*b*) 95% KUD utilisation distribution overlap index (UDOI) for *Lethrinus nebulosus*.

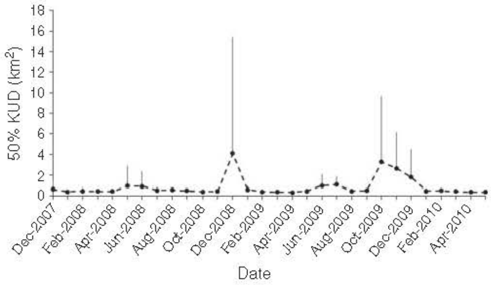

Fig. 8. Seasonal variation in the mean (±s.d.) area of the core habitat (50% kernel utilisation distribution, KUD) used by resident *Lethrinus nebulosus*.

Mangrove Bay array (Table S2). Fish 8139, 8162 and 8168 each returned multiple times to the Mangrove Bay reef slope during the period October–December and were also detected at stations at Coral Bay and on the Central Line of the Ningaloo Ecosystem Tracking Array on dates before and after their appearances at Mangrove Bay. As an example of this migratory behaviour, Fish 8139 was detected at Coral Bay, over 130 km to the south, 2 years after it was tagged. Fifteen days later, it was detected on the Mangrove Bay reef slope, where it remained for several weeks in October–December 2011. During this time it made brief forays further to the north and was detected at the North Line, before leaving the Mangrove Bay array. Twelve days later it was again detected briefly on the Coral Bay array and was not detected there again until October the next year, after which it once again travelled to Mangrove Bay. During both legs of this trip, it was recorded passing the line of receivers at Turquoise Bay, 10 km to the south of Mangrove Bay. On that occasion, the trip north took just over 48 h at an estimated speed of 2.6 km h^{-1}. One resident individual, Fish 53341, tagged in January 2009, exhibited a contrasting pattern, being present for most of the year in Mangrove Bay but travelling south to the Coral Bay array in late September–early October 2009 and in November 2010. The mean (±s.d.) travelling speed observed among these four individuals during long-distance movements in the October–December period was 1.8 ± 0.8 km h^{-1} (Table S2).

Spawning analysis

Both resident and non-resident fish exhibited even more specific seasonal behaviour likely related to spawning. Within the October–December period, brief forays to the North Line locations were a feature of the behaviour of several fish, including both resident individuals, such as Fish 8108, 8111, 8171 and 8126, and non-resident returning individuals, such as Fish 8078, 8164, 8165, 8168 and 8139 (Fig. 10; Table S3). That is, four of the nine resident fish were detected moving to the reef front in spring, and five of the 10 non-resident fish returning to Mangrove Bay appeared at the North Line during specific brief periods of time during spring. Whether fish were resident in the Mangrove Bay region or not, they were apparently almost equally likely to return to the North Line area during the October–December season.

Fish tagged in different years and with widely different behaviours were detected within hours of each other at North Line locations during these short periods (Table S3). In addition, these individuals were all detected at just one receiver station (NL2) located ~1.2 km from the reef crest at a depth of 37 m. Of the seven stations on the North Line, only one other receiver, namely NL5 (84-m depth), provided detections from Fish 8111 on 27 October 2009 between 1322 and 1934 hours universal coordinated time (UTC). The mean time of detection for fish at NL2 was 0544 hours UTC, or 2144 hours local time (3–3.5 h hours after sunset). The appearance of fish at NL2 followed a semilunar pattern, with peaks in the numbers of fish detected in the area between the first quarter moon and full moon, as well as between the third quarter moon and the new moon (Fig. 10). The mean days of detection, Lunar Days 9 and 23, were significantly

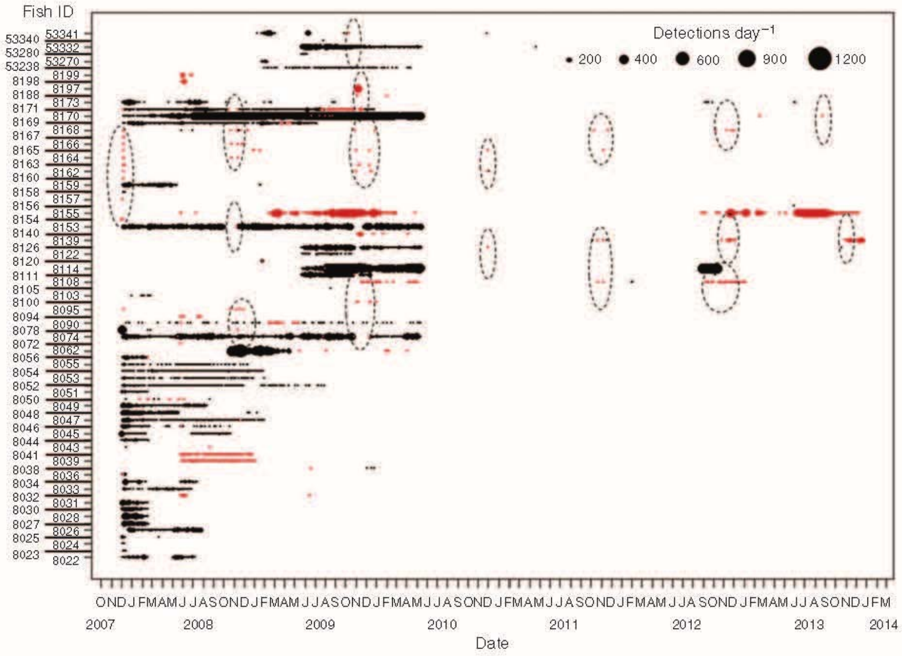

Fig. 9. Detection span of individual tagged *Lethrinus nebulosus* at Mangrove Bay. Black shading indicates lagoon detections; red shading indicates reef slope detections. Dashed circles indicate detections during the presumed October December spawning period in reef slope areas.

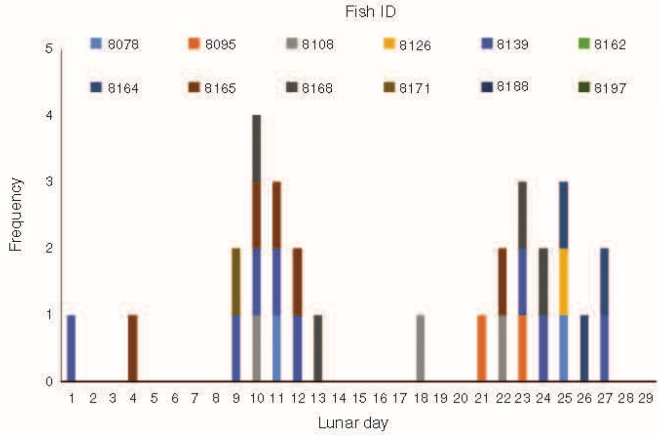

Fig. 10. Periodicity in the frequency of individual fish detected at Station NL2 during the October December period 2007 13.

non-random ($R = 12.99$, $P < 0.005$) with an angular dispersion of $s = 2$ days. All but one of the fish (8047) observed exhibiting these behaviours were over 500 mm FL, with a mean (±s.d.) size of 545 ± 50 mm FL (Table S3).

Discussion

The present study used long-term monitoring of *L. nebulosus* movements obtained from a large acoustic tracking array to characterise environmentally related variability in movement and habitat use over temporal scales ranging from diel and tidal cycles to lunar, seasonal and interannual scales. The data have also revealed high levels of variation in patterns among individuals, between physical environmental factors and behaviour, with multiple modalities evident with the population. These variations extend beyond those described previously for *L. nebulosus* (Pillans *et al.* 2014) and other species (Egli and Babcock 2004). Consequently, although some generalisations may be made in relation to the behaviour of this species, they must now include a dimension of individuality in order to characterise the dynamics of *L. nebulosus* populations.

Diel and tidal variability

Diurnal patterns of behaviour and habitat use have previously been reported for *Lethrinus miniata* on the Great Barrier Reef (Currey *et al.* 2014, 2015), *L. harak* and *Lethrinus obsoletus* in Guam (Taylor and Mills 2013) and for *L. nebulosus* in coral reef lagoon habitats in New Caledonia (Chateau and Wantiez 2008), where fish were described as moving outside the acoustic array to forage at night. The Mangrove Bay array is much more extensive than the array in New Caledonia, and the number of fish tagged was also much larger, allowing us to more clearly assess the general patterns of diurnal movement and habitat use. At Ningaloo, the majority of resident fish used the same habitat during the day as at night, with a high degree of overlap at the 95% KUD level, and even at the 50% KUD level. There were a significant proportion of individuals (30%) that used quite different areas during the day to those used at night. Similar individual diel variation (22%) in areas used was also reported for *L. harak* and *L. obsoletus* in Guam (Taylor and Mills 2013).

In terms of areal extent of habitat used, there was no difference between day and night, and, in fact, the area used during the day was slightly higher for the 95% KUD of tagged animals, suggesting that this species is at least as active during the day as it is at night. This is more consistent with the behaviour reported for *L. harak* and *L. obsoletus* (Taylor and Mills 2013), although the sample sizes at Guam were reasonably small and higher daytime activity was inferred from higher rates of detection. This interpretation may need to be viewed with caution because the detection rate of *L. miniatus* has been found to be greater during the day (Currey *et al.* 2014), but space use is reported as being larger during crepuscular periods and at night (Currey *et al.* 2015). Of those fish that did exhibit clear differences in the areas they used during the day and at night, the majority moved in to habitats closer to shore or on the reef flat. These habitats would be shallower, although the absolute difference in depth would be small given the shallow nature of the Ningaloo lagoon in this area (maximum 5–6 m).

Although there was no overall difference in area of habitat used at high versus low tide either for 50 or 95% KUD, there were differences in the areas used by individual fish at high and low tide, as demonstrated by the clear bimodality of the UDOI histograms. This was most likely due primarily to the different peak habitat use areas within kernels, as evidenced by the UDOI values greater than 1.0 for the 50% KUD data, and by values greater than 1.5 for the 95% KUD values. Where 50% KUD high and low tide kernels showed little overlap (UDOI <0.2), there was often a shift into shallow nearshore mangrove-lined habitats at high tide, but contrasting shifts, such as movement into deeper water, were also observed. At reef slope sites the shifts observed were generally parallel with the reef front. In this regard, the shifts in habitat use appeared to some extent to be an interaction between tidal and habitat availability factors, as noted for *L. harak* and *L. obsoletus* (Taylor and Mills 2013).

There was a weak correlation between variation in day–night and low tide–high tide habitat use at the 50% KUD, level but there was a lack of correlation at the 95% KUD level and no consistent trends were observed in terms of the types of habitats that may be accessed by using combined tidal and diel factors. The fact that UDOIs for both diel and tidal comparisons were weakly correlated with KUD size suggests that any apparent relationship is perhaps unlikely to be biologically meaningful and may be an artefact of the area examined because multiple foci of activity are increasingly likely as larger numbers of receivers are encompassed within the range of an individual. Any role of fish personality (e.g. Roy *et al.* 2013) that may manifest as an increased tendency to vary habitat use in relation to multiple environmental factors appeared to be weak, at least in relation to day and tide.

Seasonal and interannual variability

Because the data from *L. nebulosus* span several years, it has been possible to examine interannual variability in the location of the activity centres of long-term resident fish. Relocation of core activity centres (50% KUD) was observed in over one-third of cases, but the majority of fish showed high fidelity to a single location. This pattern of fidelity was even stronger for the 95% KUD data, indicating that shifts in core area location occurred within the overall range of a resident individual's core activity. There was little or no indication of a successive movement of activity centre across years; rather, the activity centre would tend to remain constant for ≥2 years and then shift to a new, apparently stable configuration. It must be noted that these data relate only to a subset of resident fish, and that there is a large proportion of the population that is non-resident, or resident for varying periods before apparently large-scale relocations (e.g. outside the Mangrove Bay array; Pillans *et al.* 2014).

There were clear seasonal peaks in the average size of activity centres observed in *L. nebulosus* during the months of October through December, corresponding with the peak reproductive season of this species in the Ningaloo Region (Marriott *et al.* 2010). Our observations of running ripe individuals at this time of year further corroborate this work (Table S3). Spawning aggregations are a feature of several lethrinid species, including *L. nebulosus* (Nemeth 2009). The distances that may be travelled in order to reach these aggregation sites are poorly known, but *L. harak* is estimated to travel less than 2.5 km from the lagoon to spawning sites on the adjacent outer reef (Taylor and Mills 2013). Spawning movements have been previously inferred to occur in resident *L. nebulosus* at Ningaloo (Pillans *et al.* 2014) and we have documented here several similar movements that take place over distances between 2 and 8 km (direct line distance). Such inferred spawning movements would result in larger activity centres for resident fish during months of spawning activity.

Much longer movements were observed in non-resident fish, which were detected at sites 130 km or more to the south of Mangrove Bay. If these are indeed spawning migrations, as we suggest, this places them among the longest spawning migrations of any reef fish, being exceeded only by *Epinephelus striatus* in the Caribbean (Nemeth 2009), which have been shown to move up to 240 km. Several fish repeatedly undertook these sustained and directed movements to the same locations at either Mangrove Bay or at the North Line. During these trips they maintained speeds averaging 1.7 km h^{-1} and often exceeding 2 km h^{-1} for periods of more than 48 h. Although a reasonably small subset of non-resident fish was actually detected undertaking such movements, similar behaviour may be inferred in other non-residents we observed, which, in many cases, were tagged at the same time and place as the migrating fish and reappear in the same locations on an annual basis. Given the reasonably sparse distribution of receivers along Ningaloo, it may be expected that not all these tagged individuals were detected at locations outside of Mangrove Bay. Most of the observed migrations took place from south to north, with animals returning south after the spawning season, although there was one long-distance movement in the opposite direction at this time of year. Northerly movements would represent a counter-current spawning migration because the Leeuwin Current generally flows strongly from north to south along the Ningaloo Coast. A similar counter-current migration is suggested to occur in the Red Hind (*Epinephelus guttatus*) in the tropical west Atlantic (Nemeth *et al.* 2008) and in *L. miniatus* on the Great Barrier Reef, although in this species it is thought to occur more on an ontogenetic basis, with fish progressively moving north against the East Australian Current (Williams *et al.* 2010).

There is also an ontogenetic component to the behaviour observed in migrating individuals and all but one of the 13 fish observed to move offshore at spawning time was over 50 cm FL (Table S3), suggesting that there may be a size or age threshold below which full spawning behaviour does not occur. The average size at maturity for *L. nebulosus* at Ningaloo has been estimated for males to be 278-mm total length (TL) and for females 392 mm TL (which is equivalent to 367 mm FL). The minimum legal size at capture for *L. nebulosus* is 410 mm TL (366 mm FL), which, although above the reproductive thresholds derived by Marriott *et al.* (2010) using histological methods, is well below the average size of animals found to participate in reef slope spawning movements. This is a substantial size difference that would take several years of growth to achieve (Marriott *et al.* 2011). In functional terms, 545 ± 50 mm FL may represent an effective size-at-first-reproduction, if reproductive success is related to participation in offshore spawning events. The fisheries management implications of this possibility are significant because maternal size, age or both disproportionately affect not only total egg production, but also egg quality and larval survivorship (e.g. Berkeley *et al.* 2004; Birkeland and Dayton 2005; Carter *et al.* 2015).

Spawning, lunar periodicity and aggregation site

Seasonal appearances of *L. nebulosus* on the reef slope were characterised by detections of individuals over periods of weeks or months along the reef slope receiver sites at Mangrove Bay, and the majority of detections occurred on these sites, of which there were more than 30. Among these sites, the North Line locations, NL2 in particular, stood out as a location that a significant number of fish visited, sometimes having travelled more than 100 km, but only for short periods of time, and during particular times of day and lunar phases. This site was also singled out in the case of several fish as the only reef slope site on which they were detected. Tagged fish were detected on only one other station, NL5, which was visited very briefly and by fewer fish. We suggest that NL2 is at or near a spawning aggregation site and that there is a semilunar periodicity in spawning movements to this site that peak approximately 2 days after the first-quarter and third-quarter moon. Given the tidal regimes at Ningaloo, this coincides with the period of smallest neap tides such that spawning would occur during a falling tide. The semilunar periodicity in reproduction is consistent with observations of *L. nebulosus* in the Arabian Gulf, where reduced gonad maturity has been reported around new and full moons (Grandcourt *et al.* 2010).

The depth of the NL2 site is ~37 m, which places it at the foot of the reef slope. Spawning aggregation sites have been reported on shelving substratum but at slightly shallower depths (15–18 m) for *L. nebulosus* in the Red Sea (Salem 1999). The site is also adjacent to one of the largest reef passes in the entire Ningaloo Reef system, again similar to spawning aggregation sites of *Lethrinus erythropterus* in the Solomon Islands, which are also located adjacent to reef passes (Hamilton 2005), but in much shallower water where spawning occurs around the time of new moon. In contrast, *L. harak* at Guam spawns after the full moon, although the precise locations of spawning sites are not known (Taylor and Mills 2013). Aggregation sites adjacent to passes are typical for a range of transient aggregating species such as *L. nebulosus* (Colin 2012).

Management implications of behavioural variability

The low levels of residency of *L. nebulosus* at spatial scales relevant to the size of no-take zones at Ningaloo have previously been highlighted as a factor that would negatively affect their relative numbers and biomass within sanctuary areas (Pillans *et al.* 2014). The long-distance migrations of *L. nebulosus* revealed by acoustic tracking indicate that even very large increases in the size of no-take sanctuary zones may not achieve large increases in the effect size of such protected areas for this species. Even where the core home ranges of resident fish are reasonably small, the response of protected populations to protection is predicted to be limited in situations where a proportion of the population migrates out of the protected area (Babcock *et al.* 2012). Changes to zoning provisions within the park may nevertheless still have the potential to be more efficient. For example, the effectiveness of no-take areas is likely to be related not only to their area, but also to the length of their boundaries (Kellner *et al.* 2007; Pérez-Ruzafa *et al.* 2008). Several sanctuary zones in the Ningaloo Marine Park include shoreline fishing zones along all or part of their coastal boundary (Conservation and Land Management and Marine Parks and Reserves Authority 2005), which exposes fish populations within them to a higher level of fishing pressure and may be responsible for a slow rate of recovery in *L. nebulosus* at Ningaloo (Thébaud *et al.* 2014). This is particularly the case for any fish that may exhibit behaviours such as moving into shoreline areas at high tide or at night. The present study has shown such behaviour in a substantial proportion of the tagged *L. nebulosus*, although not in the majority.

Recreational fisheries at Ningaloo do not target spawning aggregations of *L. nebulosus* and although such aggregations have yet to be directly observed, their existence does seem likely given the seasonal timing, location and tightly defined temporal and spatial characteristics of a subset of tag detections. Coral reef spawning aggregation fisheries elsewhere have proven to be highly vulnerable to overfishing exploitation and may be manageable only by establishing closed seasons and spatial closures around spawning aggregation sites (Russell *et al.* 2012). Such actions are available for application at Ningaloo, although this would be more of a preventative measure given that spawning aggregations are not currently fished. Additional measures to increase the minimum legal length of *L. nebulosus* to at least 545 mm FL, which appears to be the size of functional first reproduction, would probably be of more immediate benefit because it would increase the probability that individuals would successfully reproduce (e.g. Froese *et al.* 2008), although size-selective fishing may have other, undesirable effects on fished populations, such as removing fast-growing individuals from the population (e.g. Biro and Post 2008; Zhou *et al.* 2010).

Conclusions

Using data from 39 long-term resident spangled emperor within an array of receivers covering ~28 km^2 of shoreline, lagoon and reef slope habitats within the Ningaloo Marine Park, we have demonstrated a high degree of individual variability in home range use at diurnal and tidal scales. The sizes of the 50 and 95% KUDs were not consistently affected by tide or time of day, and variation in home-range location was itself highly variable. Some individuals moved into shallower water at night or at high tide, but overall there was no clear pattern in habitat choice, even where significant variability was present. Similarly, for long-term residents there was little evidence of shifts in the core area outside that encompassed by the home range, although, as demonstrated by Pillans *et al.* (2014), a large proportion of tagged fish moved outside the detection range of the array and presumably reflect different behavioural types (residents *v.* nomads). Seasonal movements were primarily in adult fish over 545 mm TL and were attributed to annual spawning between October and December. Several fish were shown to move from established home ranges in the lagoon to the reef slope during this period, whereas other individuals were recorded moving up to 130 km to and from spawning areas over multiple years. The extensive spawning movements along the Ningaloo coast combined with the use of shoreline habitats during the night and at high tide suggest that even adults resident within sanctuary zones are not fully protected. Furthermore, those individuals that appear to partake in annual offshore spawning movements were significantly larger than minimum legal size (366 mm TL), which has important implications for the sustainability of the fishery if sexually mature fish do not participate in spawning aggregations.

Supplementary material

Summary table of lethrinid tracking studies (Table S1), detection details of migrating individuals (Table S2) and biometric details of presumed spawning individuals (Table S3). The Supplementary material is available from the journal online.

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References

Afonso, P., Fontes, J., Holland, K. N., and Santos, R. S. (2008). Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. *Marine Ecology Progress Series* **359**, 215–227. doi:10.3354/MEPS07272

Afonso, P., Fontes, J., Holland, K. N., and Santos, R. S. (2009). Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design. *Marine Ecology Progress Series* **381**, 273–286. doi:10.3354/MEPS07946

Babcock, R. C., Egli, D. P., and Attwood, C. G. (2012). Individual-based model of reef fish populations in temperate marine reserves based on acoustic telemetry and census data. *Environmental Conservation* **39**, 282–294. doi:10.1017/S0376892912000148

Belo, A. F., Pereira, T. J., Quintella, B. R., Castro, N., Costa, J. L., and de Almeida, P. R. (2016). Movements of *Diplodus sargus* (Sparidae) within a Portuguese coastal Marine Protected Area: are they really protected? *Marine Environmental Research* **114**, 80–94. doi:10.1016/J.MARENVRES.2016.01.004

Berkeley, S. A., Chapman, C., and Sogard, S. M. (2004). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**, 1258–1264. doi:10.1890/03-0706

Birkeland, C., and Dayton, P. K. (2005). The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution* **20**, 356–358. doi:10.1016/J.TREE.2005.03.015

Biro, P. A., and Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 2919–2922. doi:10.1073/PNAS.0708159105

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**, 1–28. doi:10.1086/343878

Calenge, C. (2011). 'Home Range Estimation in R: the adehabitatHR Package.' (Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France.)

Carter, A. B., Carton, A. G., McCormick, M. I., Tobin, A. J., and Williams, A. J. (2015). Maternal size, not age, influences egg quality of a wild, protogynous coral reef fish *Plectropomus leopardus*. *Marine Ecology Progress Series* **529**, 249–263. doi:10.3354/MEPS11277

Chateau, O., and Wantiez, L. (2008). Human impacts on residency behaviour of spangled emperor, *Lethrinus nebulosus*, in a marine protected area, as determined by acoustic telemetry. *Journal of the Marine Biological Association of the United Kingdom* **88**, 825–829. doi:10.1017/S0025315408001434

Claudet, J., Osenberg, C. W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J. M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J. A., Goñi, R., Borg, J. A., Forcada, A., De Lucia, G. A., Pérez-Ruzafa, A., Afonozo, P., Brito, A., Guala, I., Le Diréach, L., Sanchez-Jerez, P., Somerfield, P. J., and Planes, S. (2010). Marine reserves: fish life history and ecological traits matter. *Ecological Applications* **20**, 830–839. doi:10.1890/08-2131.1

Colin, P. L. (2012). Timing and location of aggregation and spawning in reef fishes. In 'Reef fish Spawning Aggregations: Biology, Research and Management'. (Eds S. Sadovy de Mitcheson and P. L. Colin.) pp. 117–158. (Springer: Dordrecht, Netherlands)

Conservation and Land Management and Marine Parks and Reserves Authority (2005). Management plan for the Ningaloo Marine Park and Muiron Islands Marine Management Area: 2005–2015. Management Plan Number 52, Western Australia Department of Conservation and Land Management, Perth, WA, Australia.

Cote, J., Fogarty, S., Tymen, B., Sih, A., and Brodin, T. (2013). Personality-dependent dispersal cancelled under predation risk. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **280**, 20132349. doi:10.1098/RSPB.2013.2349

Currey, L. M., Heupel, M. R., Simpfendorfer, C. A., and Williams, A. J. (2014). Sedentary or mobile? Variability in space and depth use of an exploited coral reef fish. *Marine Biology* **161**, 2155–2166. doi:10.1007/S00227-014-2497-4

Currey, L. M., Heupel, M. R., Simpfendorfer, C. A., and Williams, A. J. (2015). Assessing fine-scale diel movement patterns of an exploited coral reef fish. *Animal Biotelemetry* **3**, 41. doi:10.1186/S40317-015-0072-5

Di Lorenzo, M., Fernandez, T. V., Badalamenti, F., Guidetti, P., Starr, R. M., Giacalone, V. M., Di Franco, A., and D'Anna, G. (2016). Diel activity and variability in habitat use of white sea bream in a temperate marine protected area. *Marine Environmental Research* **116**, 1–9. doi:10.1016/J.MARENVRES.2016.02.007

Egli, D. P., and Babcock, R. C. (2004). Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus auratus*) in a temperate no-take marine reserve. *ICES Journal of Marine Science* **61**, 1137–1143. doi:10.1016/J.ICESJMS.2004.07.004

Fieberg, J., and Kochanny, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *The Journal of Wildlife Management* **69**, 1346–1359. doi:10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Fox, R. J., and Bellwood, D. R. (2011). Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. *Functional Ecology* **25**, 1096–1105. doi:10.1111/J.1365-2435.2011.01874.X

Froese, R., Stern-Pirlot, A., Winker, H., and Gascuel, D. (2008). Size matters: how single-species management can contribute to ecosystem-based fisheries management. *Fisheries Research* **92**, 231–241. doi:10.1016/J.FISHRES.2008.01.005

Gitzen, R. A., Millspaugh, J. J., and Kernohan, B. J. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *The Journal of Wildlife Management* **70**, 1334–1344. doi:10.2193/0022-541X(2006)70[1334:BSFFAO]2.0.CO;2

Grandcourt, E. M., Al Abdessalaam, T. Z., Francis, F., and Al Shamsi, A. T. (2010). Reproductive biology and implications for management of the spangled emperor *Lethrinus nebulosus* in the southern Arabian Gulf. *Journal of Fish Biology* **77**, 2229–2247. doi:10.1111/J.1095-8649.2010.02799.X

Green, K. M., and Starr, R. M. (2011). Movement of small adult black rockfish: implications for the design of MPAs. *Marine Ecology Progress Series* **14**, 219–230. doi:10.3354/MEPS09263

Hamilton, R. J. (2005). Indigenous ecological knowledge (IEK) of the aggregating and nocturnal spawning behaviour of the longfin emperor, *Lethrinus erythropterus*. In 'SPC Traditional Marine Resource Management and Knowledge Information Bulletin 18'. pp. 9–17. (South Pacific Commission: Nouméa, New Caledonia.)

Honda, K., Uy, W. H., Baslot, D. I., Duvin, A., Pantallano, S., Nakamura, Y., and Nakaoka, M. (2016). Diel habitat-use patterns of commercially important fishes in a marine protected area in the Philippines. *Aquatic Biology* **24**, 163–174. doi:10.3354/AB00646

Kellner, J. B., Tetreault, I., Gaines, S. D., and Nisbet, R. M. (2007). Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications* **17**, 1039–1054. doi:10.1890/05-1845

Kernohan, B. J., Gitzen, R. A., and Millspaugh, J. J. (2001). Analysis of animal space use and movements. In 'Radio Tracking and Animal Populations'. (Eds J. J. Millspaugh and J. M. Marzluff.) pp. 126–166. (Academic Press: San Diego, CA, USA.)

Lecchini, D., and Galzin, R. (2005). Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Marine Biology* **147**, 47–58. doi:10.1007/S00227-004-1543-Z

MacDonald, B. D., Lewison, R. L., Madrak, S. V., Seminoff, J. A., and Eguchi, T. (2012). Home ranges of East Pacific green turtles *Chelonia mydas* in a highly urbanized temperate foraging ground. *Marine Ecology Progress Series* **461**, 211–221. doi:10.3354/MEPS09820

Makowski, C. A., Seminoff, J. A., Salmon, M. A., and English, G. (2006). Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Marine Biology* **148**, 1167–1179. doi:10.1007/S00227-005-0150-Y

Marriott, R. J., Jarvis, N. D. C., Adams, D. J., Gallash, A. E., Norriss, J., and Newman, S. J. (2010). Maturation and sexual ontogeny in the spangled emperor, *Lethrinus nebulosus*. *Journal of Fish Biology* **76**, 1396–1414. doi:10.1111/J.1095-8649.2010.02571.X

Marriott, R. J., Adams, D. J., Jarvis, N. D. C., Moran, M. J., Newman, S. J., and Craine, M. (2011). Age-based demographic assessment of fished stocks of *Lethrinus nebulosus* in the Gascoyne Bioregion of Western Australia. *Fisheries Management and Ecology* **18**, 89–103. doi:10.1111/J.1365-2400.2010.00754.X

Marshell, A., Mills, J. S., Rhodes, K. L., and McIlwain, J. (2011). Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. *Coral Reefs* **30**, 631–642. doi:10.1007/S00338-011-0770-2

Matich, P., and Heithaus, M. R. (2015). Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). *Oecologia* **178**, 347–359. doi:10.1007/S00442-015-3253-2

Meyer, C. G., Papastamatiou, Y. P., and Holland, K. N. (2007*a*). Seasonal, diel and tidal movements of green jobfish (*Aprion viriscens*) at remote Hawaiian atolls: implications for marine protected area design. *Marine Biology* **151**, 2133–2143. doi:10.1007/S00227-007-0647-7

Meyer, C. G., Holland, K. N., and Papastamatiou, Y. P. (2007*b*). Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine protected areas. *Marine Ecology Progress Series* **333**, 13–25. doi:10.3354/MEPS333013

Nemeth, R. S. (2009). Dynamics of reef fish and decapod crustacean spawning aggregations: underlying mechanisms, habitat linkages, and trophic interactions. In 'Ecological Connectivity among Tropical

Coastal Ecosystems'. (Ed. I. Nagelkerken.) pp. 73–134. (Springer: Dordrecht, Netherlands.)

Nemeth, R. S., Kadison, E., Blondeau, J. E., Idrisi, N., Watlington, R., Brown, K., Smith, T., and Carr, O. (2008). Regional coupling of red hind spawning aggregations to oceanographic processes in the eastern Caribbean. In 'Caribbean Connectivity: Implications for Marine Protected Area Management'. (Eds R. Grober-Dunsmore and B. D. Keller.) Marine Sanctuary Conservation Series ONMS-08-07, pp. 170–183. (National Oceanic and Atmospheric Administration: Silver Spring, MD, USA.)

Parsons, D. M., Morrison, M. A., and Slater, M. J. (2010). Responses to marine reserves: decreased dispersion of the sparid *Pagrus auratus* (snapper). *Biological Conservation* **143**, 2039–2048. doi:10.1016/J.BIOCON.2010.05.009

Parsons, D. M., Morrison, M. A., McKenzie, J. R., Hartill, B. W., Bian, R., and Francis, R. I. C. C. (2011). A fisheries perspective of behavioural variability: differences in movement behaviour and extraction rate of an exploited sparid, snapper (*Pagrus auratus*). *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 632–642. doi:10.1139/F2011-005

Pérez-Ruzafa, A., Martín, E., Marcos, C., Zamarro, J. M., Stobart, B., Harmelin-Vivien, M., Polti, S., Planes, S., García-Charton, J. A., and González-Wangüemert, M. (2008). Modelling spatial and temporal scales for spill-over and biomass exportation from MPAs and their potential for fisheries enhancement. *Journal for Nature Conservation* **16**, 234–255. doi:10.1016/J.JNC.2008.09.003

Pillans, R. D., Bearham, D., Boomer, A., Downie, R. A., Patterson, T. A., Thomson, D. P., and Babcock, R. C. (2014). Multi-year observations reveal variability in residence of a tropical demersal fish, *Lethrinus nebulosus*: implications for spatial management. *PLoS One* **9**(9), e105507. doi:10.1371/JOURNAL.PONE.0105507

Pillans, R. D., Babcock, R. C., Thomson, D. P., Haywood, M. D. E., Downie, R. A., Vanderklift, M. A., and Rochester, W. (2017). Habitat influences on home range and schooling behaviour in an herbivorous fish (*Kyphosus bigibbus*) revealed by acoustic tracking. *Marine and Freshwater Research*. [Published online 1 Febraury 2017]. doi:10.1071/MF16199

Pitcher, T. J. (1986). 'The Behaviour of Teleost Fishes.' (Springer: New York, USA.)

Roy, M. L., Roy, A. G., Grant, J. W., and Bergeron, N. E. (2013). Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature, and habitat use. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 1082–1091. doi:10.1139/CJFAS-2012-0274

Russell, M. W., Luckhurst, B. E., and Lindeman, K. C. (2012). Management of spawning aggregations. In 'Reef Fish Spawning Aggregations: Biology, Research and Management'. (Eds S. Sadovy de Mitcheson and P. L. Colin.) pp. 371–404 (Springer: New York, NY, USA.)

Salem, M. (1999). Management of fishing in the Ras Mohammed National Park with special reference to the fishery for *Lethrinus nebulosus* (Forsskal, 1775). Ph.D. Thesis, University of York, York, UK.

Silverman, B. W. (1986). 'Density Estimation for Statistics and Data Analysis.' (Chapman and Hall: London, UK.)

Taylor, B. M., and Mills, J. S. (2013). Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. *Coral Reefs* **32**, 1077–1087. doi:10.1007/S00338-013-1065-6

Taylor, M. D., McPhan, L., van der Meulen, D. E., Gray, C. A., and Payne, N. L. (2013). Interactive drivers of activity in a free-ranging estuarine predator. *PLoS One* **8**, e80962. doi:10.1371/JOURNAL.PONE.0080962

Thébaud, O., Ellis, N., Little, L. R., Doyen, L., and Marriott, R. J. (2014). Viability trade-offs in the evaluation of strategies to manage recreational fishing in a marine park. *Ecological Indicators* **46**, 59–69. doi:10.1016/J.ECOLIND.2014.05.013

Van Winkle, W. (1975). Comparison of several probabilistic home-range models. *The Journal of Wildlife Management* **39**, 118–123. doi:10.2307/3800474

Verweij, M. C., and Nagelkerken, I. (2007). Short and long-term movement and site fidelity of juvenile Haemulidae in back-reef habitats of a Caribbean embayment. *Hydrobiologia* **592**, 257–270. doi:10.1007/S10750-007-0772-9

Wand, M. P., and Jones, M. C. (1995). 'Kernel smoothing. Monographs on Statistics and Applied Probability, Vol. 60.' (Chapman and Hall/CRC Press: New York, NY, USA.)

White, G. C., and Garrott, G. A. (1990). 'Analysis of Wildlife Radio-tracking Data.' (Academic Press: San Diego, CA, USA.)

Williams, A. J., Little, L. R., Punt, A. E., Mapstone, B. D., Davies, C. R., and Heupel, M. R. (2010). Exploring movement patterns of an exploited coral reef fish when tagging data are limited. *Marine Ecology Progress Series* **405**, 87–99. doi:10.3354/MEPS08527

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168. doi:10.2307/1938423

Zar, J. H. (1984). 'Biostatistical Analysis.' (Prentice-Hall International: Englewood Cliffs, NJ, USA.)

Zeh, D. R., Heupel, M. R., Limpus, C. J., Hamann, M., Fuentes, M. M. P. B., Babcock, R. C., Pillans, R. D., Townsend, K. A., and Marsh, H. (2015). Is acoustic tracking appropriate for air-breathing marine animals? Dugongs as a case study. *Journal of Experimental Marine Biology and Ecology* **464**, 1–10. doi:10.1016/J.JEMBE.2014.11.013

Zeller, D. C. (1998). Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. *Marine Ecology Progress Series* **162**, 253–263. doi:10.3354/MEPS162253

Zhou, S., Smith, A. D., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S., Bulman, C., Bayliss, P., and Sainsbury, K. (2010). Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 9485–9489. doi:10.1073/PNAS.0912771107

Marine and Freshwater Research, 2017, **68**, 1422–1437
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Supplementary material

Environmental and individual effects on the behaviour and spawning movements of *Lethrinus nebulosus* on a coral reef

R. C. Babcock[A,B], *R. D. Pillans*[A] *and W. A. Rochester*[A]

[A]CSIRO Marine and Atmospheric Research, 41 Boggo Road, Dutton, Qld 4102, Australia.

[B]Corresponding author. Email: russ.babcock@csiro.au

Supplementary material

Table S1. Lethrinid acoustic tracking studies

Behavioural variations with populations in relation to environmental and ecological factor

Species (*Lethrinus*)	Home range 95% (km^2)	Residency (I_R)	Diurnal variation	Tidal variation	Ontogenetic variation	Individual variation	Spawning movements	Habitat	Authors
L. nebulosus (*n* = 6)	-	0.02–0.67%	Yes, more active during day	–	Possible – small fish disappeared	Yes	Possibly	No, but wind and human influences.	Chateau and Wantiez 2008
L. nebulosus (*n* = 84)	8.5	0.66	–	–	Yes residency, No home range	Yes	Yes	Mixed	Pillans *et al.* 2014
L. harak (*n* = 12)	0.02.6 ± 0.02.9	0.51	Yes, more active in day, different day and night locations	Yes, neap –low tide shift	Yes increased with size	Yes, some moved diurnally some didn't	Yes, full–last quarter, daily	Shallow back-reef	Taylor and Mills 2013
L. obsoletus (*n* = 6)	0.008 ± 0.01	0.97	Yes, more active in day,	None detected	None detected	Yes, diurnal pattern in some	None detected	Shallow back-reef	Taylor and Mills 2013
L. miniata (*n* = 60)	1.93 ± 0.27	<50%; *n* = 26; >5 days	Some, individual variability with depth	Monthly pattern, some fish	No	Yes, vertical movements in some	Not examined	Reef slope	Currey *et al.* 2014
L. harak (*n* = 6)	-	1	–	–	–	–	–	Mixed habitat	Honda *et al.* 2016
L. atkinsoni (*n* = 5)	-	0.95	–	–	–	–	–	Coral reef	Honda *et al.* 2016
L. obsoletus (*n* = 2)	-	0.71	–	–	–	–	–	Coral reef	Honda *et al.* 2016

Table S2. Selected detection details for *L. nebulosus* detected migrating from distant locations to spawning areas in the Mangrove Bay region

Tag ID	Start latitude	Date	Time	Finish latitude	Date	Time	Distance (km)	Days	Total hours	Rate (km h^{-1})
8139	–23.07	7-Oct-2011	08:46	–21.8957	22-Oct-2011	09:41	144	15	360.9167	0.398984
8139	–21.8957	7-Nov-2011	12:30	–23.07	19-Nov-2011	17:54	144	12	293.5667	0.490519
8139	–22.0863	2-Dec-2012	16:30	–22.99	5-Dec-2012	16:11	125	2	48.68333	2.567614
8139	–22.0011	2-Dec-2012	12:17	–22.0863	2-Dec-2012	16:25	9.5	0	4.133333	2.298387
8139	–22.0045	25-Dec-2013	09:34	–22.0879	25-Dec-2013	16:21	9.5	0	6.783333	1.400491
8162	–22.9996	31-Oct-2009	17:50	–21.9979	2-Dec-2009	19:19	121	2	49.65	2.437059
8162	–21.9839	14-Dec-2009	10:14	–22.9996	17-Dec-2009	12:13	125	3	73.98333	1.68957
8162	–22.6027	1-Dec-2010	15.44	–23.07	3-Dec-2010	23:38	57	2	55.9	1.019678
8168	–22.6027	9-Oct-2012	02:37	–22.0045	10-Oct-2011	09:14	71	1	30.56667	2.322792
8168	–22.9914	11-Nov-2012	15:46	–22.0863	11-Nov-2012	19:45	11	0	3.983333	2.761506
8168	–22.0128	2-Dec-2012	14:01	–22.6027	3-Dec-2012	20:30	71	1	30.48333	2.329142

Table S3. Biometric information and behavioural descriptions of individual *L. nebulosus* detected undertaking suspected spawning related activity at Ningaloo

Tag ID	Date tagged	Location tagged	Fork length (FL cm)	Behavioural details
8047	3-Dec-07	Lagoon	41	Resident lagoon. Exclusively in lagoon for more than two years, detected offshore in November 2008
8078	1-Dec-07	Lagoon	56	Non-resident, reappeared 11-Nov-2008 at NL2 only
8095	6-Dec-07	Reef slope	59	Non-resident, running ripe male. Detected again one year after tagging October–December 2008
8108	4-Nov-09	Reef slope	54.5	Resident slope. Detected at NL2 at quarter moons, present within minutes of Fish 8139 on 7-Nov-2011 and on the same day as Fish 8165.
8111	23-May-09	Lagoon	55	Resident lagoon exclusively. Detected at NL5 on 27-Oct-2009. Absent until 2011 when it returned to lagoon until late 2012.
8126	23-May-09	Lagoon	53	Resident lagoon. Detected at NL2 1-Dec-2010. Returned to lagoon April 2011
8139	9-Nov-09	Reef slope	53.5	Non-resident. Female. Reappeared 2011, 2012, 2013, including several years at NL2. Detected returning to Coral Bay before or after appearances at Mangrove/NL2. Present at NL2 at same time as 8108 and 8165 in 2011.
8162	6-Dec-07	Reef slope	67	Non-resident. Reappeared on reef slope 2 and 3 years later, appears at Coral Bay and Norwegian Bay in December 2009 and 2010.
8163	6-Dec-07	Reef slope	57	Non-Resident. Reappears on reef slope in 2009
8164	6-Dec-07	Reef slope	51	Non-resident. Male, running ripe when tagged. Reappeared in 2008 detected only at NL2, 26–28-Oct-2008
8165	6-Dec-07	Reef slope	54	Non-resident. Reappeared on reef slope in 2008, 2009, 2010 and 2011. Present at NL2 on 7-Nov-2011 within hours of 8139 and 8108.
8166	6-Dec-07	Reef slope	56	Non-resident. Reappeared October–December 2008 on reef slope.
8168	6-Dec-07	Reef slope	57	Non-resident. Reappears on reef slope in 2008, 2009, 2011, 2012. Also detected on Central Line as well as at North Line in 2012 (within hours of 8139).
8171	6-Dec-07	Reef slope	56	Resident in lagoon. Seasonally moves to reef slope in 2008, 2009. Detected at NL2 (=5?) on 16-Oct-2008.
8153	30-Nov-07	Lagoon	53	Resident in Lagoon. Consistently detected in lagoon except for several weeks in October–November of 2008 and 2009. Detected outside South Passage on return to Mangrove Bay in November 2008.

References

Chateau, O., and Wantiez, L. (2008). Human impacts on residency behaviour of spangled emperor, *Lethrinus nebulosus*, in a marine protected area, as determined by acoustic telemetry. *Journal of the Marine Biological Association of the United Kingdom* **88**, 825–829. doi:10.1017/S0025315408001434

Currey, L. M., Heupel, M. R., Simpfendorfer, C. A., and Williams, A. J. (2014). Sedentary or mobile? Variability in space and depth use of an exploited coral reef fish. *Marine Biology* **161**, 2155–2166. doi:10.1007/s00227-014-2497-4

Honda, K., Uy, W. H., Baslot, D. I., Duvin, A., Pantallano, S., Nakamura, Y., and Nakaoka, M. (2016). Diel habitat-use patterns of commercially important fishes in a marine protected area in the Philippines. *Aquatic Biology* **24**, 163–174. doi:10.3354/ab00646

Pillans, R. D., Bearham, D., Boomer, A., Downie, R. A., Patterson, T. A., Thomson, D. P., and Babcock, R. C. (2014). Multi-year observations reveal variability in residence of a tropical demersal fish, *Lethrinus nebulosus*: implications for spatial management. *PLoS One* **9**(9), e105507. doi:10.1371/journal.pone.0105507

Taylor, B. M., and Mills, J. S. (2013). Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. *Coral Reefs* **32**, 1077–1087. doi:10.1007/s00338-013-1065-6

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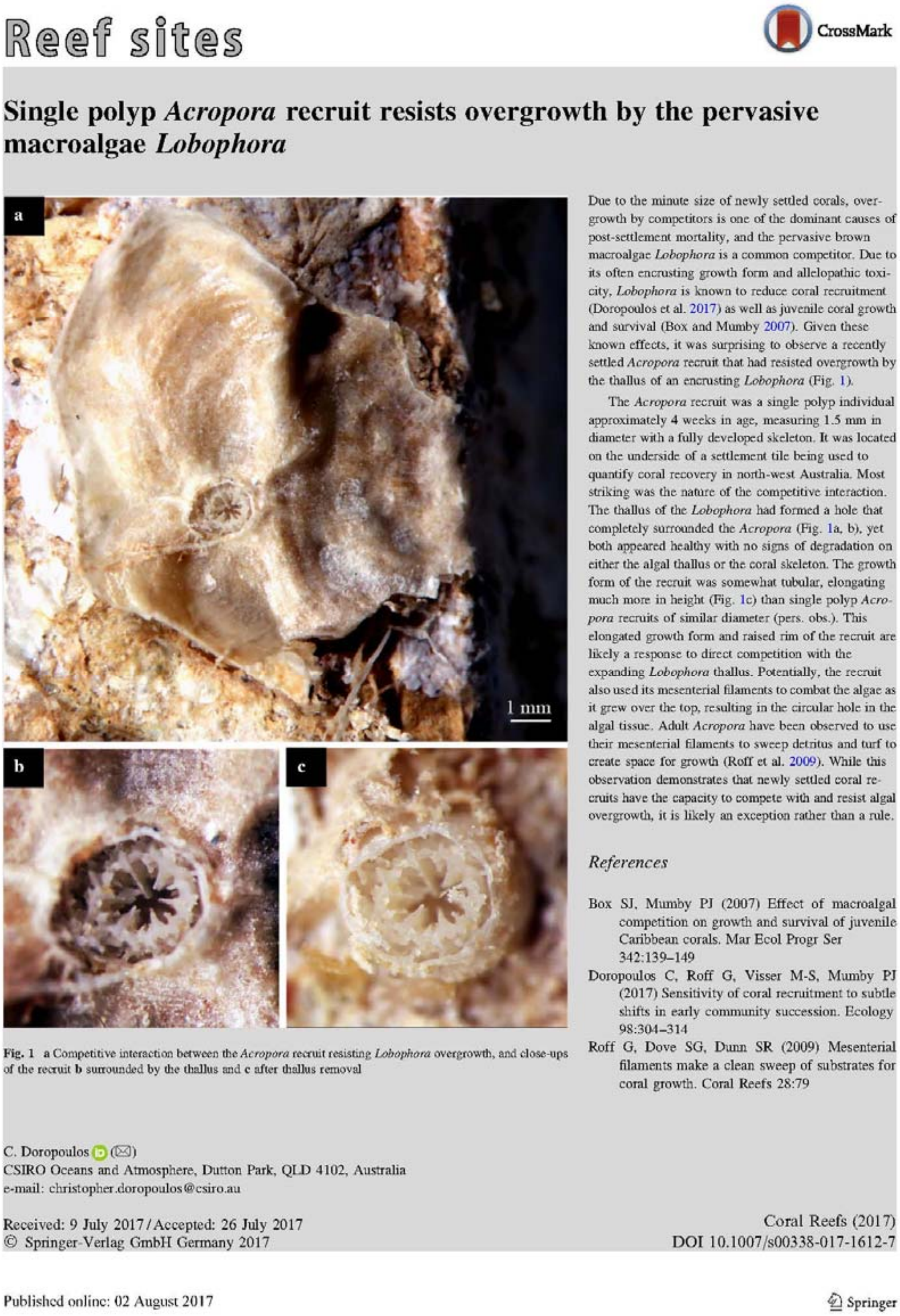

Reef sites

Single polyp *Acropora* recruit resists overgrowth by the pervasive macroalgae *Lobophora*

Fig. 1 a Competitive interaction between the *Acropora* recruit resisting *Lobophora* overgrowth, and close-ups of the recruit **b** surrounded by the thallus and **c** after thallus removal

Due to the minute size of newly settled corals, overgrowth by competitors is one of the dominant causes of post-settlement mortality, and the pervasive brown macroalgae *Lobophora* is a common competitor. Due to its often encrusting growth form and allelopathic toxicity, *Lobophora* is known to reduce coral recruitment (Doropoulos et al. 2017) as well as juvenile coral growth and survival (Box and Mumby 2007). Given these known effects, it was surprising to observe a recently settled *Acropora* recruit that had resisted overgrowth by the thallus of an encrusting *Lobophora* (Fig. 1).

The *Acropora* recruit was a single polyp individual approximately 4 weeks in age, measuring 1.5 mm in diameter with a fully developed skeleton. It was located on the underside of a settlement tile being used to quantify coral recovery in north-west Australia. Most striking was the nature of the competitive interaction. The thallus of the *Lobophora* had formed a hole that completely surrounded the *Acropora* (Fig. 1a, b), yet both appeared healthy with no signs of degradation on either the algal thallus or the coral skeleton. The growth form of the recruit was somewhat tubular, elongating much more in height (Fig. 1c) than single polyp *Acropora* recruits of similar diameter (pers. obs.). This elongated growth form and raised rim of the recruit are likely a response to direct competition with the expanding *Lobophora* thallus. Potentially, the recruit also used its mesenterial filaments to combat the algae as it grew over the top, resulting in the circular hole in the algal tissue. Adult *Acropora* have been observed to use their mesenterial filaments to sweep detritus and turf to create space for growth (Roff et al. 2009). While this observation demonstrates that newly settled coral recruits have the capacity to compete with and resist algal overgrowth, it is likely an exception rather than a rule.

References

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Mar Ecol Progr Ser 342:139–149

Doropoulos C, Roff G, Visser M-S, Mumby PJ (2017) Sensitivity of coral recruitment to subtle shifts in early community succession. Ecology 98:304–314

Roff G, Dove SG, Dunn SR (2009) Mesenterial filaments make a clean sweep of substrates for coral growth. Coral Reefs 28:79

C. Doropoulos (✉)
CSIRO Oceans and Atmosphere, Dutton Park, QLD 4102, Australia
e-mail: christopher.doropoulos@csiro.au

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Global warming and recurrent mass bleaching of corals

Terry P. Hughes[1], James T. Kerry[1], Mariana Álvarez-Noriega[1,2], Jorge G. Álvarez-Romero[1], Kristen D. Anderson[1], Andrew H. Baird[1], Russell C. Babcock[3], Maria Beger[4], David R. Bellwood[1,2], Ray Berkelmans[5], Tom C. Bridge[1,6], Ian R. Butler[7], Maria Byrne[8], Neal E. Cantin[9], Steeve Comeau[10], Sean R. Connolly[1,2], Graeme S. Cumming[1], Steven J. Dalton[11], Guillermo Diaz-Pulido[12], C. Mark Eakin[13], Will F. Figueira[14], James P. Gilmour[15], Hugo B. Harrison[1], Scott F. Heron[13,16,17], Andrew S. Hoey[1], Jean-Paul A. Hobbs[18], Mia O. Hoogenboom[1,2], Emma V. Kennedy[12], Chao-yang Kuo[1], Janice M. Lough[1,9], Ryan J. Lowe[10], Gang Liu[13,16], Malcolm T. McCulloch[10], Hamish A. Malcolm[11], Michael J. McWilliam[1], John M. Pandolfi[7], Rachel J. Pears[19], Morgan S. Pratchett[1], Verena Schoepf[10], Tristan Simpson[20], William J. Skirving[13,16], Brigitte Sommer[7], Gergely Torda[1,9], David R. Wachenfeld[19], Bette L. Willis[1,2] & Shaun K. Wilson[21]

During 2015–2016, record temperatures triggered a pan-tropical episode of coral bleaching, the third global-scale event since mass bleaching was first documented in the 1980s. Here we examine how and why the severity of recurrent major bleaching events has varied at multiple scales, using aerial and underwater surveys of Australian reefs combined with satellite-derived sea surface temperatures. The distinctive geographic footprints of recurrent bleaching on the Great Barrier Reef in 1998, 2002 and 2016 were determined by the spatial pattern of sea temperatures in each year. Water quality and fishing pressure had minimal effect on the unprecedented bleaching in 2016, suggesting that local protection of reefs affords little or no resistance to extreme heat. Similarly, past exposure to bleaching in 1998 and 2002 did not lessen the severity of bleaching in 2016. Consequently, immediate global action to curb future warming is essential to secure a future for coral reefs.

The world's tropical reef ecosystems, and the people who depend on them, are increasingly affected by climate change[1–7]. Since the 1980s, rising sea surface temperatures owing to global warming have triggered unprecedented mass bleaching of corals, including three pan-tropical events in 1998, 2010 and 2015/16 (ref. 1). Thermal stress during marine heatwaves disrupts the symbiotic relationship between corals and their algal symbionts (*Symbiodinium* spp.), causing the corals to lose their colour[2,3]. Bleached corals are physiologically damaged, and prolonged bleaching often leads to high levels of coral mortality[5–8]. Increasingly, individual reefs are experiencing multiple bouts of bleaching, as well as the effects of more chronic local stressors such as pollution and overfishing[1–4]. Our study represents a fundamental shift away from viewing bleaching events as individual disturbances to reefs, by focusing on three recurrent bleachings over the past 18 years along the 2,300 km length of the Great Barrier Reef, as well as the potential influence of water quality and fishing pressure on the severity of bleaching.

The geographic footprints of mass bleaching of corals on the Great Barrier Reef have varied markedly during three major events in 1998, 2002 and 2016 (Fig. 1a). In 1998, bleaching was primarily coastal and most severe in the central and southern regions. In 2002, bleaching was more widespread, and affected offshore reefs in the central region that had escaped in 1998 (ref. 8). In 2016, bleaching was even more extensive and much more severe, especially in the northern regions, and to a lesser extent the central regions, where many coastal, mid-shelf and offshore reefs were affected (Fig. 1a, b). In 2016, the proportion of reefs experiencing extreme bleaching (>60% of corals bleached) was over four times higher compared to 1998 or 2002 (Fig. 1f). Conversely, in 2016, only 8.9% of 1,156 surveyed reefs escaped with no bleaching, compared to 42.4% of 631 reefs in 2002 and 44.7% of 638 in 1998. The cumulative, combined footprint of all three major bleaching events now covers almost the entire Great Barrier Reef Marine Park, with the exception of southern, offshore reefs (Fig. 1d).

Explaining spatial patterns

The severity and distinctive geographic footprints of bleaching in each of the three years can be explained by differences in the magnitude and spatial distribution of sea surface temperature anomalies (Fig. 1a, b and Extended Data Table 1). In each year, 61–63% of reefs experienced four or more degree heating weeks (DHWs; °C-weeks). In 1998, heat stress was relatively constrained, ranging from 1–8 DHWs (Fig. 1c). In 2002, the distribution of DHWs was broader, and 14% of reefs encountered 8–10 DHWs. In 2016, the spectrum of DHWs expanded further still, with 31% of reefs experiencing 8–16 DHWs (Fig. 1c). The largest heat stress occurred in the northern 1,000-km-long section of the Great Barrier

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[1]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia. [2]College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia. [3]Commonwealth Science and Industry Research Organization, GPO Box 2583 Brisbane, Queensland 4001, Australia. [4]School of Biology, University of Leeds, Leeds LS2 9JT, UK. [5]24 Hanwood Court, Gilston, Queensland 4211, Australia. [6]Queensland Museum, 70-102 Flinders St, Townsville, Queensland 4810, Australia. [7]Australian Research Council, Centre of Excellence for Coral Reef Studies, School of Biological Sciences, University of Queensland, Brisbane, Queensland 4072, Australia. [8]School of Medical Sciences, University of Sydney, Sydney, New South Wales 2006, Australia. [9]Australian Institute of Marine Science, PMB 3, Townsville, Queensland 4810, Australia. [10]Australian Research Council Centre of Excellence in Coral Reef Studies, Oceans Institute and School of Earth and Environment, University of Western Australia, Crawley, Western Australia 6009, Australia. [11]Fisheries Research, Department of Primary Industries, PO Box 4291, Coffs Harbour, New South Wales 2450, Australia. [12]School of Environment, and Australian Rivers Institute, Griffith University, Brisbane, Queensland 4111, Australia. [13]Coral Reef Watch, US National Oceanic and Atmospheric Administration, College Park, Maryland 20740, USA. [14]School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia. [15]Australian Institute of Marine Science, Indian Oceans Marine Research Centre, University of Western Australia, Crawley, Western Australia 6009, Australia. [16]Global Science & Technology, Inc., Greenbelt, Maryland 20770, USA. [17]Marine Geophysical Laboratory, College of Science, Technology and Engineering, James Cook University, Townsville, Queensland 4811, Australia. [18]Department of Environment and Agriculture, Curtin University, Perth, Western Australia 6845, Australia. [19]Great Barrier Reef Marine Park Authority, PO Box 1379, Townsville, Queensland 4810, Australia. [20]Torres Strait Regional Authority, PO Box 261, Thursday Island, Queensland 4875, Australia. [21]Department of Parks and Wildlife, Kensington, Perth, Western Australia 6151, Australia.

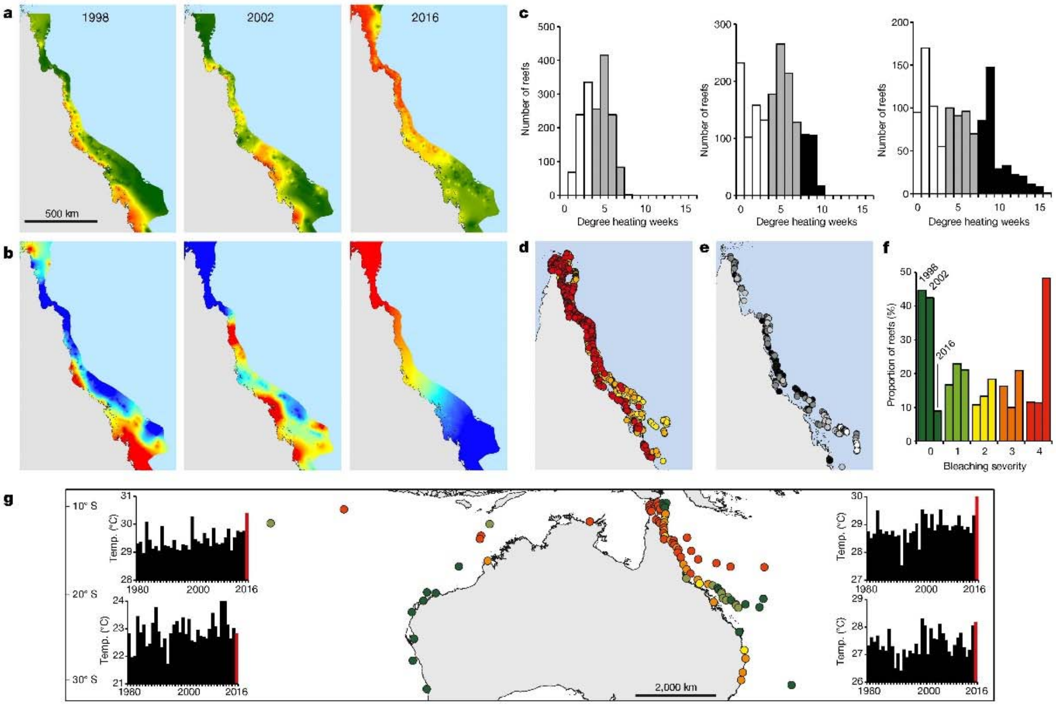

Figure 1 | Geographic extent and severity of recurrent coral bleaching at a regional scale, Australia. a, The footprint of bleaching on the Great Barrier Reef in 1998, 2002 and 2016, measured by extensive aerial surveys: dark green (<1% of corals bleached), light green (1–10%), yellow (10–30%), orange (30–60%), red (>60%). The number of reefs surveyed in each year was 638 (1998), 631 (2002), and 1,156 (2016). **b**, Spatial pattern of heat stress (DHWs; °C-weeks) during each mass-bleaching event. Dark blue indicates 0 DHW, and red is the maximum DHW for each year (7, 10 and 16, respectively). Orange and yellow indicate intermediate levels of heat exposure on a continuous scale. **c**, Frequency distribution of maximum DHWs on the Great Barrier Reef, in 1998, 2002 and 2016. White bars indicate 0–4 °C-weeks; grey bars, 4–8 °C-weeks; black bars, >8 °C-weeks. **d**, Locations of individual reefs that bleached (by >10% or more) in 1998, 2002 and/or 2016, showing the most severe bleaching score for reefs that were surveyed more than once. Yellow, 10–30% bleaching; orange, 30–60%; red, >60%. **e**, Location of reefs that were surveyed in all three years that bleached zero (white), one (light grey), two (dark grey) or three times (black). **f**, Frequency distribution of aerial bleaching scores for reefs surveyed in 1998 (left bars), 2002 (middle), and 2016 (right bars). Colour bleaching scores as in **a**. **g**, Bleaching severity during March to early April 2016 on both sides of Australia, including the Coral Sea and the eastern Indian Ocean. Colour bleaching scores as in **a**. Bar graphs show mean sea surface temperatures during March for each year from 1980 to 2016 for northern and southern latitudes on either side of Australia. The red bar highlights the north–south disparity in 2016. Map templates provided by Geoscience Australia under licence from Creative Commons Attribution 4.0 International Licence.

Reef. Consequently, the geographic pattern of severe bleaching in 2016 matched the strong north–south gradient in heat stress. By contrast, in 1998 and 2002, heat stress extremes and severe bleaching were both prominent further south (Fig. 1a, b). In 2016, severe bleaching (defined as an aerial score of >30% of corals bleached) was correctly predicted by satellite-derived DHWs in a statistical model, in 75% of cases (Extended Data Fig. 1 and Extended Data Table 1), similar to the amount of spatial variation in bleaching explained by temperature stress in 1998 and 2002 (ref. 8).

The geographic pattern of bleaching also demonstrates how marine heatwaves can be ameliorated by local weather[9], even during a global bleaching event. Arguably, southern reefs of the Great Barrier Reef would also have bleached in 2016 if wind, cloud cover and rain from ex-tropical cyclone Winston had not rescued them[10]. Winston passed over Fiji on February 20th, when the southern Great Barrier Reef was only 1 °C cooler than the north. By March 6th, this disparity increased to 4 °C (Extended Data Fig. 2). Corals in the south that had begun to pale in February regained their colour in the south in March, whereas bleaching continued to progress in central and northern sectors (Fig. 2a). Similarly, in western Australia in 2016, tropical cyclone Stan cooled down mid-coast regions in early February[11], and the Leeuwin Current (which transports warm tropical water southwards) was also weakened due to El Niño conditions[12]. Consequently, both sides of tropical and sub-tropical Australia, including offshore atolls in the Coral Sea and Indian Ocean, exhibited continental-scale latitudinal gradients in bleaching (Fig. 1g).

The local (individual reef)-scale pattern of recurrent bleaching on the Great Barrier Reef also reveals the trend of increasing severity and the erosion of potential spatial refugia. Of the 171 individual reefs that were aerially surveyed three times, 43% bleached in 1998, 56% in 2002, and 85% in 2016. Knowing the bleaching history of these well-studied reefs allows us to investigate why they have bleached zero, one, two or three times. Only 9% of these repeatedly surveyed reefs have never bleached, in most cases because they are located near the southern, offshore end of the Great Barrier Reef (Fig. 1e), where they have experienced relatively low temperature anomalies during each event. A further 26% of repeatedly surveyed reefs have bleached only once—10 reefs in 1998, 8 in 2002, and 32 for the first time in 2016. The latter

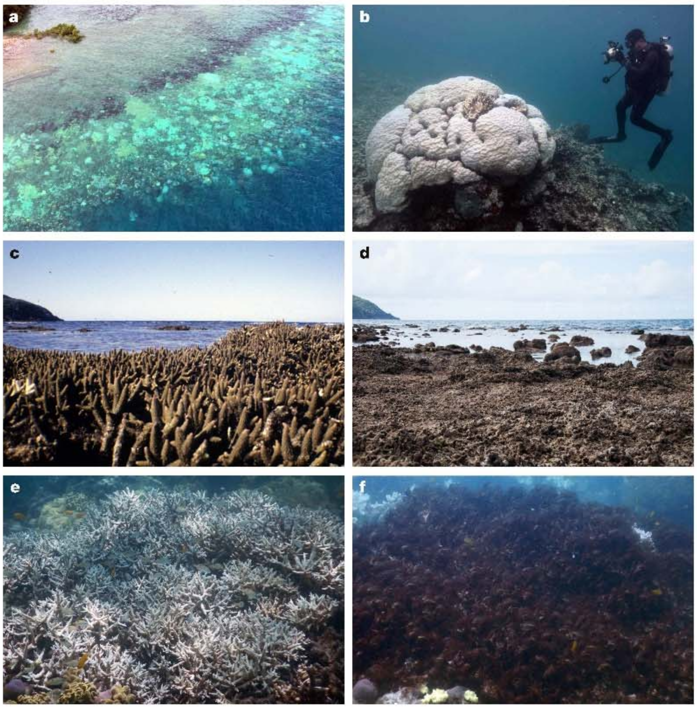

Figure 2 | Recurrent severe coral bleaching. **a**, Aerial view of severe bleaching in Princess Charlotte Bay, northeast Australia, March 2016. Close to 100% of corals are bleached on the reef flat and crest. Bleaching occurs when algal symbionts (*Symbiodinium* spp.) in a coral host are killed by environmental stress, revealing the white underlying skeleton of the coral. **b**, Severe bleaching in 2016 on the northern Great Barrier Reef affected even the largest and oldest corals, such as this slow-growing *Porites* colony. **c**, Large, old beds of clonal staghorn corals, *Acropora pulchra*, on Orpheus Island, Queensland photographed in 1997 were killed by the first major bleaching event on the Great Barrier Reef in 1998. **d**, Eighteen years later in May 2016, corals at this site have never recovered, with the original assemblages still visible as dead, unconsolidated and muddy rubble that is unsuitable for successful colonization by coral larvae. **e**, **f**, Mature stands of clonal staghorn corals were extirpated by heat stress and colonized by algae over a period of just a few weeks in 2016 on Lizard Island, Great Barrier Reef. Before (**e**) and after (**f**) photographs were taken on 26 February and 19 April 2016. Photo credits: **a**, J.T.K.; **b**, J. Marshall; **c**, B.W.; **d**, C.Y.K.; **e**, **f**, R. Streit.

were primarily in the northern sector of the Great Barrier Reef, which largely escaped bleaching in the two earlier events (Fig. 1a). Thirty-five per cent of the reefs have bleached twice, but only one reef bleached in both 1998 and 2002, compared to 58 reefs that bleached either in 1998 or 2002 and for a second time in the severe 2016 event. Finally, 29% of the repeatedly surveyed reefs bleached for a third time in 2016, primarily in central areas of the Great Barrier Reef, because they experienced anomalously warm temperatures during all three events (Fig. 1b, e). We conclude that the overlap of disparate geographic footprints of heat stress explains why different reefs have bleached 0–3 times, that is, the repeated exposure to unusually hot conditions is the primary driver of the likelihood of recurrent bleaching at the scale of both individual reefs and the entire Great Barrier Reef (Fig. 1a, b). We found a similar strong relationship between the amount of bleaching measured underwater, and the satellite-based estimates of heat exposure on individual reefs (Fig. 3). Low levels of bleaching were observed at some locations when DHW values were only 2–3 °C-weeks. Typically, 30–40% of corals bleached on reefs exposed to 4 °C-weeks, whereas an average of 70–90% of corals bleached on reefs that experienced 8 °C-weeks or more (Fig. 3).

Resistance and adaptation to bleaching

Once we account for the amount of heat stress experienced on each reef, adding chlorophyll *a*, a proxy for water quality, to our statistical model yielded no support for the hypothesis that good water quality confers resistance to bleaching[13]. Rather, the estimated effect of chlorophyll *a* was to significantly reduce the DHW threshold for bleaching (Extended Data Table 1). However, despite the statistical significance, the effect in real terms beyond heat stress alone is very small (Extended Data Fig. 1). Similarly, we found no effect of the level of protection (in fished or protected zones) on bleaching ($P > 0.1$: Extended Data Table 1). These results are consistent with the broad-scale pattern of severe bleaching in the northern Great Barrier Reef, which affected hundreds of reefs across inshore–offshore gradients in water quality and regardless of their zoning (protection) status (Fig. 1a, b).

Similarly, we find no evidence for a protective effect of past bleaching (for example, from acclimation or adaptation): reefs with higher bleaching scores in 1998 or 2002 did not experience less severe bleaching in 2016, after accounting for the relationship between the 2016 temperature stress and bleaching propensity ($P > 0.9$ in all cases; Extended Data Fig. 3). Thus, while several studies have indicated that prior exposure can influence the subsequent bleaching responses of corals[14–17], our comprehensive analysis of 171 repeatedly surveyed reefs indicates that any such historical effects on the Great Barrier Reef were masked by the severity of bleaching in 2016 (Fig. 2).

Winners and losers

Individual coral taxa bleached to different extents, especially on less-affected reefs, creating both winners (resistant corals) and losers

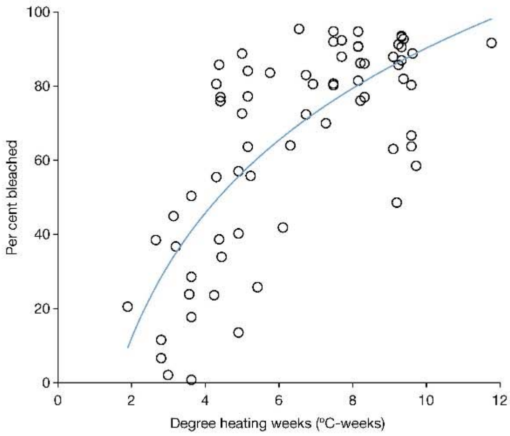

Figure 3 | The relationship between heat exposure (satellite-based DHWs in 2016) and the amount of bleaching measured underwater (per cent of corals bleached) in March/April. Each data point represents an individual reef ($n = 69$). The fitted line is $y = 48.6\ln(x) - 21.6$, $R^2 = 0.545$.

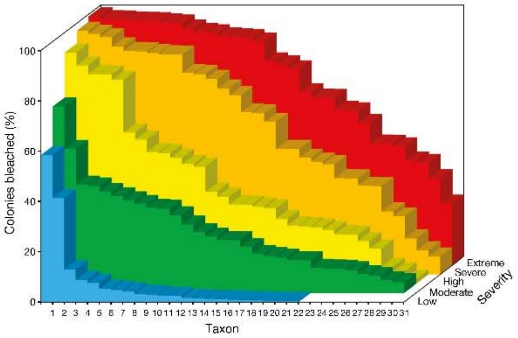

Figure 4 | Spectrum of bleaching responses by coral taxa on the Great Barrier Reef in 2016, with relative winners on the right, and losers on the left. Individual species or genera (58,414 colonies) are plotted in rank descending order along the x axis from high to low levels of bleaching, for different severities of reef bleaching. Reef-scale bleaching severities are: blue, 1–10% of all corals bleached; green, 10–30%; yellow, 30–60%; orange, 60–80%; and red, >80% bleached. See Extended Data Table 2 for taxonomic details.

(susceptible species), but the disparity among species diminished in the worst-affected, northern regions. (Fig. 4). At the population and assemblage level, when and where bleaching is severe, even century-old corals can bleach (Fig. 2b–d). By contrast, where bleaching is less intense, it is highly selective, with a broad spectrum of responses shown by winners versus losers; winners by definition bleach less and have higher survivorship[18–21]. On lightly and moderately bleached reefs (<10% or 10–30% of corals affected), predominantly in the southern Great Barrier Reef, many of the more robust coral taxa escaped with little or no bleaching in 2016. By contrast, on extremely bleached reefs in the north (60–80% or >80% overall bleaching), we found far fewer lightly bleached winners (Fig. 4). The rank order of winners versus losers also changed as the severity of bleaching increased (Extended Data Table 2), reflecting disparate responses by each taxon to the range of bleaching intensities. Thus, even species that are winners on relatively mildly bleached reefs joined the ranks of losers where bleaching was more intense (Fig. 4), creating a latitudinal gradient in the response of the coral assemblages.

The recovery time for coral species that are good colonizers and fast growers is 10–15 years[22–24], but when long-lived corals die from bleaching their replacement will necessarily take many decades. Recovery for long-lived species requires the sustained absence of another severe bleaching event (or other significant disturbance), which is no longer realistic while global temperatures continue to rise[25]. Therefore, the assemblage structure of corals is now likely to be permanently shifted at severely bleached locations in the northern Great Barrier Reef.

Implications for reef management

Our analysis has important implications for the management and conservation of coral reefs. We find that local management of coral reef fisheries and water quality affords little, if any, resistance to recurrent severe bleaching events: even the most highly protected reefs and near-pristine areas are highly susceptible to severe heat stress. On the remote northern Great Barrier Reef, hundreds of individual reefs were severely bleached in 2016 regardless of whether they were zoned as no-entry, no-fishing, or open to fishing, and irrespective of inshore–offshore differences in water quality (Fig. 1a and Extended Data Fig. 1). However, local protection of fish stocks and improved water quality may, given enough time, improve the prospects for recovery[3,4,26–29]. A key issue for all coral reefs is the frequency, or return time, of recurrent disturbance events, and whether there is sufficient time between successive bleachings for the re-assembly of mature coral assemblages. The chances of the northern Great Barrier Reef returning to its pre-bleaching assemblage structure are slim given the scale of damage that occurred in 2016 and the likelihood of a fourth bleaching event occurring within the next decade or two as global temperatures continue to rise.

Identifying and protecting spatial refugia is a common strategy for conservation of threatened species and ecosystems, including coral reefs[30]. However, our analyses indicate that the cumulative footprint of recurrent bleachings is expanding, and the number of potential refugia on the Great Barrier Reef is rapidly diminishing. Indeed, the remote northern region escaped serious damage in 1998 and 2002, but bore the brunt of extreme bleaching in 2016. Rather than relying on the premise of refugia, our results highlight the growing importance of promoting the recovery of reefs to recurrent bleaching events through local management of marine parks and water quality. However, bolstering resilience will become more challenging and less effective in coming decades because local interventions have had no discernible effect on resistance of corals to extreme heat stress, and, with the increasing frequency of severe bleaching events, the time for recovery is diminishing. Securing a future for coral reefs, including intensively managed ones such as the Great Barrier Reef, ultimately requires urgent and rapid action to reduce global warming.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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1. Heron, S. F., Maynard, J. A., van Hooidonk, R. & Eakin, C. M. Warming trends and bleaching stress of the World's coral reefs 1985–2012. *Sci. Rep.* **6**, 38402 (2016).
2. Spalding, M. D. & Brown, B. E. Warm-water coral reefs and climate change. *Science* **350**, 769–771 (2015).
3. Baker, A. C., Glynn, P. W. & Riegl, B. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* **80**, 435–471 (2008).
4. Hughes, T. P. *et al.* Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929–933 (2003).
5. Glynn, P. W. Widespread coral mortality and the 1982–83 El Nino Warming Events. *Environ. Conserv.* **11**, 133–146 (1984).
6. Oliver, J. K., Berkelmans, R. & Eakin, C. M. in *Ecological Studies: Analysis and Synthesis* (eds van Oppen, M. J. H. & Lough, J. M.) 21–39 (2009).
7. Eakin, C. M. *et al.* Global coral bleaching 2014–2017. *Reef Currents* **31**, 1 (2016).

8. Berkelmans, R., De'ath, G., Kininmonth, S. & Skirving, W. J. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. *Coral Reefs* **23,** 74–83 (2004).
9. Carrigan, A. D. & Puotinen, M. Tropical cyclone cooling combats region-wide coral bleaching. *Glob. Change Biol.* **20,** 1604–1613 (2014).
10. Leahy, S. M., Kingsford, M. J. & Steinberg, C. R. Do clouds save the great barrier reef? Satellite imagery elucidates the cloud-SST relationship at the local scale. *PLoS One* **8,** e70400 (2013).
11. Australian Bureau of Meteorology (BOM). Tropical Cyclone Stan Track. http://www.australiasevereweather.com/cyclones/2016/bom/tropical_cyclone_stan.png (2016).
12. Feng, M., Meyeres, G., Pearce, A. & Wijffels, S. Annual and interannual variations of the Leeuwin Current at 32°S. *J. Geophys. Res.* **108,** 2156–2202 (2003).
13. Wooldridge, S. A. *et al.* Excess seawater nutrients, enlarged algal symbiont densities and bleaching sensitive reef locations: 2. A regional-scale predictive model for the Great Barrier Reef, Australia. *Mar. Pollut. Bull.* **114,** 343–354 (2016).
14. Carilli, J., Donner, S. D. & Hartmann, A. C. Historical temperature variability affects coral response to heat stress. *PLoS One* **7,** e34418 (2012).
15. Guest, J. R. *et al.* Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS One* **7,** e33353 (2012).
16. Pratchett, M. S., McCowan, D., Maynard, J. A. & Heron, S. F. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLoS One* **8,** e70443 (2013).
17. Ainsworth, T. D. *et al.* Climate change disables coral bleaching protection on the Great Barrier Reef. *Science* **352,** 338–342 (2016).
18. Loya, Y. *et al.* Coral bleaching: the winners and the losers. *Ecol. Lett.* **4,** 122–131 (2001).
19. Swain, T. D. *et al.* Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. *Glob. Change Biol.* **22,** 2475–2488 (2016).
20. Baird, A. H. & Marshall, P. A. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **237,** 133–141 (2002).
21. Marshall, P. A. & Baird, A. H. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* **19,** 155–163 (2000).
22. Connell, J. H., Hughes, T. P. & Wallace, C. C. A 30-year study of coral community dynamics: influence of disturbance and recruitment on abundance, at several scales in space and time. *Ecol. Monogr.* **67,** 461–488 (1997).
23. Kayanne, H., Harii, S., Ide, Y. & Akimoto, F. Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. *Mar. Ecol. Prog. Ser.* **239,** 93–103 (2002).
24. Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H. & Pratchett, M. S. Recovery of an isolated coral reef system following severe disturbance. *Science* **340,** 69–71 (2013).
25. van Hooidonk, R. *et al.* Local-scale projections of coral reef futures and implications of the Paris Agreement. *Sci. Rep.* **6,** 39666 (2016).
26. Scheffer, M. *et al.* Climate and conservation. Creating a safe operating space for iconic ecosystems. *Science* **347,** 1317–1319 (2015).
27. van de Leemput, I. A., Hughes, T. P., van Nes, E. H. & Scheffer, M. Multiple feedbacks and the prevalence of alternate stable states on coral reefs. *Coral Reefs* **35,** 857–865 (2016).
28. Hughes, T. P., Graham, N. A. J., Jackson, J. B. C., Mumby, P. J. & Steneck, R. S. Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* **25,** 633–642 (2010).
29. Graham, N. A., Jennings, S., MacNeil, M. A., Mouillot, D. & Wilson, S. K. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518,** 94–97 (2015).
30. West, J. M. & Salm, R. V. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv. Biol.* **17,** 956–967 (2003).

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Author Contributions The study was conceptualized by T.P.H. who wrote the first draft of the paper. All authors contributed to writing subsequent drafts. J.T.K. coordinated data compilation, analysis and graphics. Aerial bleaching surveys in 2016 of the Great Barrier Reef and Torres Strait were executed by J.T.K., T.P.H. and T.S., and in 1998 and 2002 by R.B. and D.R.W. Underwater bleaching censuses in 2016 were undertaken on the Great Barrier Reef by M.A.-N., A.H.B., D.R.B., M.B., N.E.C., C.Y.K., G.D.-P., A.S.H., M.O.H., E.V.K., M.J.M., R.J.P., M.S.P., G.T. and B.L.W., in the Coral Sea by T.C.B. and H.B.H., in subtropical Queensland and New South Wales by M.B., I.R.B., R.C.B., S.J.D., W.F.F., H.A.M., J.M.P. and B.S., off western Australia by R.C.B., S.C., J.P.G., J.-P.A.H., M.T.M., V.S. and S.K.W. J.G.A.-R., S.R.C., C.M.E., S.F.H., G.L., J.M.L. and W.J.S. undertook the analysis matching satellite data to the bleaching footprints on the Great Barrier Reef.

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METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Recurrent bleaching on the Great Barrier Reef. For 2016, comprehensive aerial surveys of the Great Barrier Reef Marine Park and Torres Strait reported in Fig. 1a were conducted on ten days between 22 March 2016 and 17 April 2016 when bleaching was particularly visible. We used light aircraft and a helicopter, flying at an elevation of approximately 150m. A total of 1,156 individual reefs from the coast to the edge of the continental shelf were assessed along 14° of latitude (Extended Data Fig. 4). Each reef was assigned by visual assessment to one of five categories of bleaching severity, using the same protocols as earlier aerial surveys conducted in 1998 and 2002 by R.B.[8]: 0, <1% of corals bleached; 1, 1–10%; 2, 10–30%; 3, 30–60%; and 4, >60% of corals bleached. The accuracy of the scores was assessed by underwater ground-truthing (see next section). The aerial scores are presented in Fig. 1a as heat maps (stretch type: minimum–maximum) using inverse distance weighting (IDW; power, 2; cell size, 1,000; search radius, variable; 100 points) in ArcGIS 10.2.1.

Underwater surveys of eastern and western Australia. To ground-truth the accuracy of aerial scores of bleaching on the Great Barrier Reef (Fig. 1a), we conducted in-water surveys on 104 reefs during March and April 2016 (Extended Data Fig. 5). We also measured differential species responses (winners versus losers; Fig. 4) on 83 reefs, spanning the 1,200-km-long central and northern Great Barrier Reef, from 10–19° S. We surveyed two sites per reef, using five 10 × 1 m belt transects placed on the reef crest at a depth of 2 m at each site. Observers identified and counted each coral colony and recorded a categorical bleaching score for each individual: 1, no bleaching; 2, pale; 3, 1–50% bleached; 4, 51–99% bleached; 5, 100% bleached; 6, bleached and recently dead. The site-level amount of bleaching for each taxon in Fig. 4 is the sum of categories 2–5. The number of colonies assessed was 58,414. A similar standardized protocol was used to measure amounts of bleaching for the Coral Sea, on sub-tropical reefs south of the Great Barrier Reef, and across 18° of latitude along the west coast of Australia (Fig. 1g).

Temperature and thermal stress. The spatial pattern of thermal stress on the Great Barrier Reef during each of the three major bleaching events (1998, 2002 and 2016; Fig. 1b, c) was quantified using the well-established DHW metric[31]. The DHW values were calculated using the optimum interpolation sea surface temperature (OISST)[32], because it provides a consistent measure of thermal stress for all three major bleaching events on the Great Barrier Reef. The baseline climatology for the DHW metric was calculated for 1985–2012, following ref. 33. DHW values are presented in Fig. 1b as heat maps (stretch type: minimum–maximum) using inverse distance weighting (IDW; power, 2; cell size, 1,000; search radius, variable; 100 points) in ArcGIS 10.2.1. For Fig. 1g, March temperatures were compiled from HadISST1 (ref. 34) from 1980–2016 for four regions: northwest Australia, 10.5–20.5° S; mid-west Australia, 20.5–30.5° S; northern Great Barrier Reef, 10.5–16.5° S; and southern Great Barrier Reef, 21.5–24.5°S.

Water quality metrics. We considered remotely sensed chlorophyll *a* and Secchi depth proxies as water quality metrics, measured for the Great Barrier Reef[35] over different averaging windows. Specifically, we used four averaging windows with respect to 2016 (1, 2 or 4 years before bleaching, and a long-term 1997–2016 average), and two different time periods (summer months only (December to May inclusive) and the entire year (June to May inclusive)). We also considered derived quantities from these estimates: the proportion of time that reefs exceeded an estimated water quality chlorophyll *a* threshold of $0.45\,\mu g\,l^{-1}$ (ref. 13) and Secchi depth exposure, again for four different averaging windows, and for the full year and for summer only. All of these metrics were significantly correlated with one another. In particular, long-term (1997–2016) average chlorophyll *a* concentration was very highly correlated with all other metrics (absolute value of Spearman's rank correlation coefficient averaged $r=0.81$, and was never lower than 0.7). Therefore, to minimize the risk of type I errors, we used it as the water quality proxy in our analyses of bleaching, log-transformed to obtain a symmetric distribution of values.

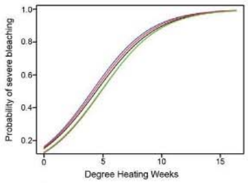
Analysis of spatial patterns, resistance and adaptation. To model the factors affecting bleaching in 2016, we used aerial bleaching scores as a response variable; whether a reef was severely bleached (57% of reefs had a bleaching score of 3–4) or not (the remaining 43% of reefs had a bleaching score of 0–2), for all surveyed reefs in the Great Barrier Reef Marine Park. We considered temperature stress (measured as DHW, described above), water quality (measured as the natural logarithm of long-term chlorophyll *a* concentration), and marine protection status. Reefs in three zones classified as 'Marine National Park', 'Preservation', 'Scientific Research', and 'Buffer' were considered to be protected in the model, whereas all other zones were fished. We repeated our test using other splits of bleaching scores (0 versus 1–4, 0–1 versus 2–4, and 0–3 versus 4), although these led to more uneven splits of the data. Regardless of how the bleaching scores were binned, the severity of bleaching was significantly correlated with DHW, while the additional variables had effects that were similar to our original analysis: small in magnitude or statistically non-significant.

To calibrate the relationship between temperature and bleaching, we fit a generalized linear model (GLM) with binomial error structure, using DHW as the explanatory variable. To test the hypothesis that high water quality confers bleaching resistance[13], we fit a model including both DHW and chlorophyll *a* as explanatory variables, and tested whether the effect of chlorophyll *a* concentration was significantly positive (that is, if reefs with higher chlorophyll *a* concentrations had a higher probability of bleaching). Similarly, to test the hypothesis that fishing increases bleaching resistance, we fit a model including DHW and protection status as explanatory variables, and tested whether the effect of protection was significantly negative (protected reefs had a lower probability of bleaching, at a given level of temperature stress, than fished reefs, see Extended Data Fig. 1 and Extended Data Table 1).

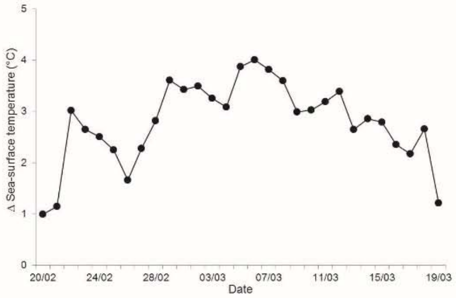
To test for evidence of acclimation or adaptation, we extracted the residuals from our DHW-only generalized linear model (Extended Data Table 1), and we tested for a negative correlation between the residuals and the aerial bleaching scores recorded during prior events: 1998, 2002 or the higher of the two earlier scores (Extended Data Fig. 1). That is, we tested the hypothesis that reefs that bleached more severely in prior events were less likely to bleach at a given temperature stress in 2016, compared to reefs that bleached less in prior events. Because bleaching score is ordered and categorical, we tested this hypothesis with Kendall's τ.

Data and code availability. Data and code available on request from the authors.

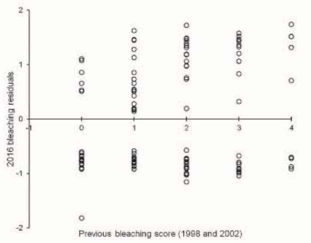
31. Eakin, C. M. *et al.* Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLoS One* **5,** e13969 (2010).
32. Reynolds, R. W. *et al.* Daily high-resolution-blended analyses for sea surface temperature. *J. Clim.* **20,** 5473–5496 (2007).
33. Heron, S.F., *et al.* Climatology development for NOAA Coral Reef Watch's 5-km product suite. NOAA Technical Report NESDIS 145 (NOAA/NESDIS, 2015).
34. Rayner, N. *et al.* Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *J. Geophys. Res.* **108,** 4407 (2003).
35. Globcolour. Remotely-sensed chlorophyll concentration (mg/m³) and Secchi Disk depth (m) based on Sea-Viewing Wide Field of View Sensor (SeaWIFS) imagery. http://hermes.acri.fr/ (2016).



Extended Data Figure 1 | A generalized linear model to explain the severity of coral bleaching. Curves show the estimated relationships between probability of severe bleaching (>30%) on individual reefs of the Great Barrier Reef in 2016 and three explanatory variables (DHWs, chlorophyll *a*, and reef zoning, see Extended Data Table 1). The DHW-only model is shown in black. For the DHW plus chlorophyll *a* model, the blue threshold shows the estimated relationship between probability of severe bleaching and DHW for the 25th percentile of chlorophyll *a*, and the brown threshold shows the same for the 75th percentile of chlorophyll *a*. For the DHW plus reef zoning model, the red threshold shows the relationship for fished reefs, and the green for unfished reefs. Water-quality metrics and level of reef protection make little, if any, difference.

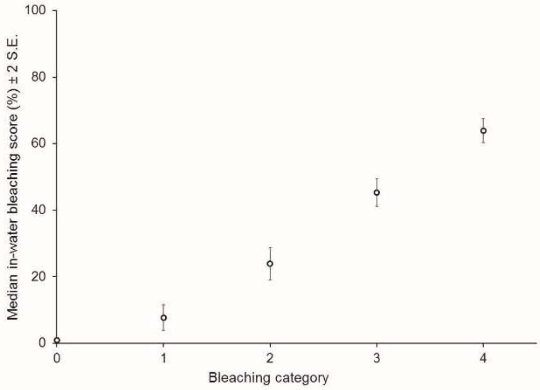


Extended Data Figure 2 | Difference in daily sea surface temperatures between the northern and southern Great Barrier Reef, before and after ex-tropical cyclone Winston. The disparity between Lizard Island (14.67° S) and Heron Island (23.44° S) increased from 1 °C in late February to 4 °C in early March 2016.

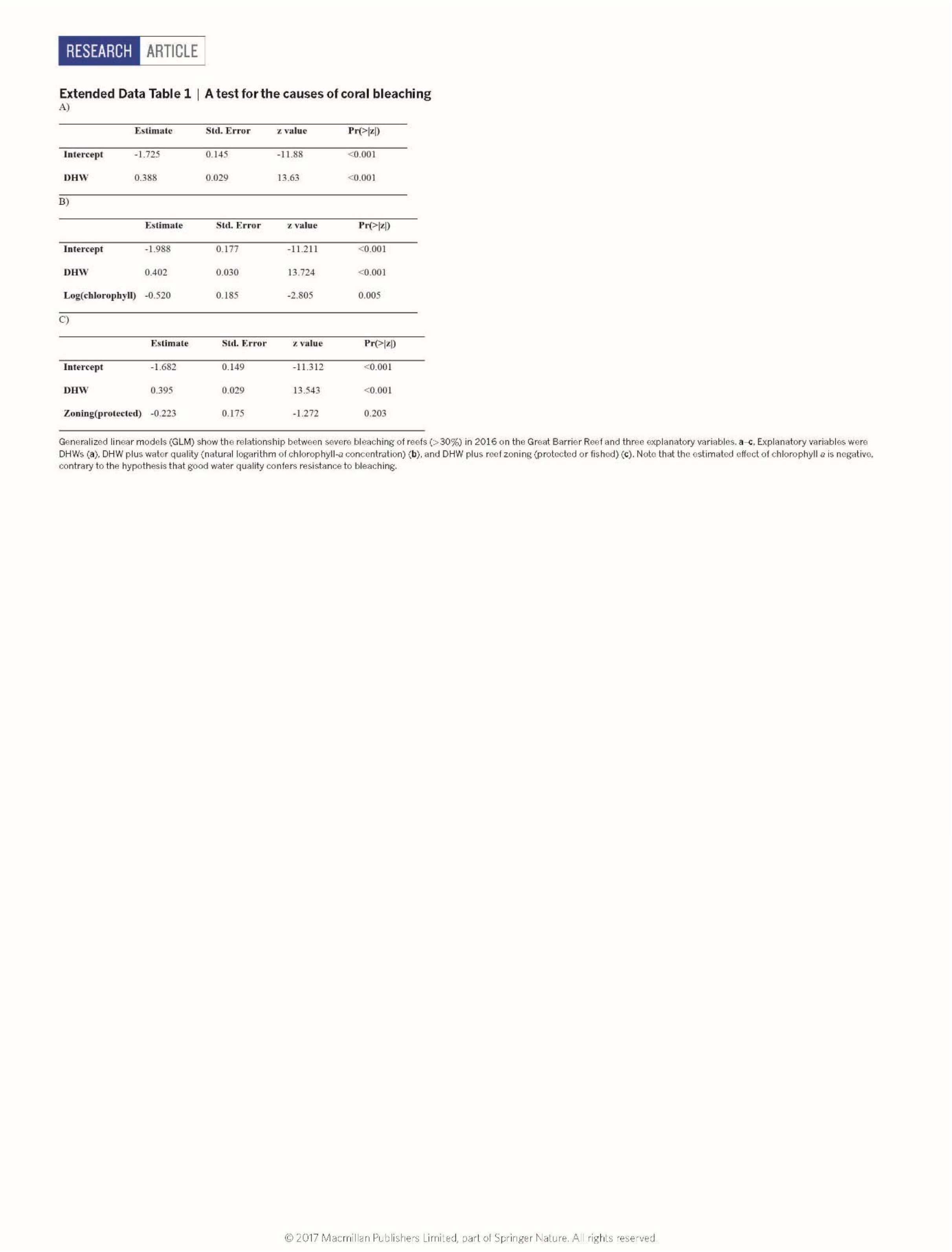


Extended Data Figure 3 | A test for the effect of past bleaching experience on the severity of bleaching in 2016. The relationship between previous bleaching scores (in 1998 or 2002, whichever was higher) and the residuals from the DHW generalized linear model (Extended Data Table 1). Each data point represents an individual reef that was scored repeatedly. There is no negative relationship to support acclimation or adaptation.

Extended Data Figure 4 | Flight tracks of aerial surveys of coral bleaching, conducted along and across the Great Barrier Reef and Torres Strait in March and April 2016. Blue colour represents land, white colour represents open water.



Extended Data Figure 5 | Ground-truthing comparisons of aerial and underwater bleaching scores. Aerial scores are: 0 (<1% of colonies bleached), 1 (1–10%), 2 (10–30%), 3 (30–60%) and 4 (60–100%) on the Great Barrier Reef in 2016 (Fig. 1a). Continuous (0–100%) underwater scores are based on *in situ* observations from 259 sites (104 reefs). Error bars indicate two standard errors both above and below the median underwater score, separately for each aerial category.



Extended Data Table 1 | A test for the causes of coral bleaching

A)

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.725	0.145	-11.88	<0.001
DHW	0.388	0.029	13.63	<0.001

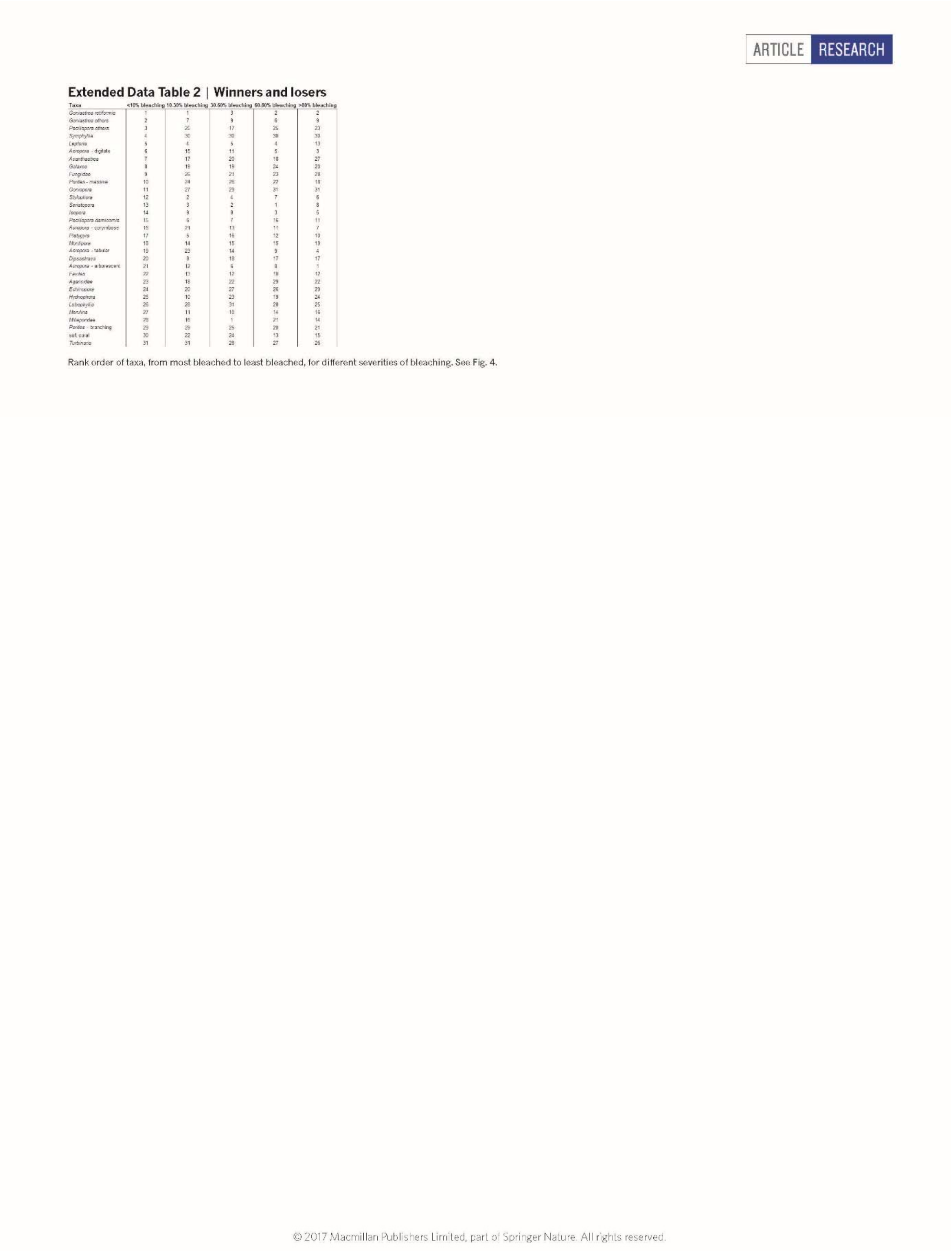
B)

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.988	0.177	-11.211	<0.001
DHW	0.402	0.030	13.724	<0.001
Log(chlorophyll)	-0.520	0.185	-2.805	0.005

C)

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.682	0.149	-11.312	<0.001
DHW	0.395	0.029	13.543	<0.001
Zoning(protected)	-0.223	0.175	-1.272	0.203

Generalized linear models (GLM) show the relationship between severe bleaching of reefs (>30%) in 2016 on the Great Barrier Reef and three explanatory variables. **a**–**c**, Explanatory variables were DHWs (**a**), DHW plus water quality (natural logarithm of chlorophyll-a concentration) (**b**), and DHW plus reef zoning (protected or fished) (**c**). Note that the estimated effect of chlorophyll *a* is negative, contrary to the hypothesis that good water quality confers resistance to bleaching.



Extended Data Table 2 | Winners and losers

Taxa	<10% bleaching	10-30% bleaching	30-60% bleaching	60-80% bleaching	>80% bleaching
Goniastrea retiformis	1	1	3	2	2
Goniastrea others	2	7	9	6	9
Pocillopora others	3	25	17	25	23
Symphyllia	4	30	30	30	30
Leptoria	5	4	5	4	13
Acropora - digitate	6	15	11	5	3
Acanthastrea	7	17	20	18	27
Galaxea	8	19	19	24	20
Fungiidae	9	26	21	23	28
Porites - massive	10	24	26	22	18
Goniopora	11	27	29	31	31
Stylophora	12	2	4	7	6
Seriatopora	13	3	2	1	8
Isopora	14	9	8	3	5
Pocillopora damicornis	15	6	7	16	11
Acropora - corymbose	16	21	13	11	7
Platygyra	17	5	16	12	10
Montipora	18	14	15	15	19
Acropora - tabular	19	23	14	9	4
Dipsastraea	20	8	18	17	17
Acropora - arborescent	21	12	6	8	1
Favites	22	13	12	10	12
Agariciidae	23	18	22	29	22
Echinopora	24	20	27	26	29
Hydnophora	25	10	23	19	24
Lobophyllia	26	28	31	28	25
Merulina	27	11	10	14	16
Milleporidae	28	16	1	21	14
Porites - branching	29	29	25	20	21
soft coral	30	22	24	13	15
Turbinaria	31	31	28	27	26

Rank order of taxa, from most bleached to least bleached, for different severities of bleaching. See Fig. 4.

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Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery

Beverly Z. L. Oh[A,B,C,E], *Michele Thums*[B,C], *Russ C. Babcock*[D], *Jessica J. Meeuwig*[A], *Richard D. Pillans*[D], *Conrad Speed*[B,C] *and Mark G. Meekan*[B,C]

[A]Centre for Marine Futures, School of Biological Sciences and Oceans Institute, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
[B]Australian Institute of Marine Science, The University of Western Australia, 39 Fairway, Crawley WA 6009, Australia.
[C]Indian Ocean Marine Research Centre, The University of Western Australia, 39 Fairway, Crawley WA 6009, Australia.
[D]CSIRO Oceans and Atmosphere, Ecosciences Precinct, GPO Box 2583, Brisbane, Qld 4001, Australia.
[E]Corresponding author. Email: beverly.oh@gmail.com

Abstract. The benefits of marine protected areas are difficult to estimate for mobile species, but their effectiveness can be increased if essential habitats, such as nursery areas, are protected. In the present study we examined movements of juvenile blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks in a coastal nursery in northern Australia. Telemetry-derived data were modelled using Brownian bridges and overlaid with maps of habitats and no-take zones. Juvenile *N. acutidens* were typically residents (≥30 days) of the nursery with small areas of core space use ($<1.9\ \text{km}^2$), whereas juvenile *C. melanopterus* were non-residents (<30 days) and used larger areas ($<5.6\ \text{km}^2$). Both species exhibited positive selection for sandflats and mangroves, and avoidance of deeper lagoonal and slope habitats. Monthly patterns were examined only for resident *N. acutidens*, and residency decreased with increasing shark length and varied seasonally for males but not females. Space use showed weak declines with increasing tidal range, and slight increases with mean air pressure, rainfall and shark length. Protecting sandflat and vegetated habitats may increase the efficacy of no-take zones for juvenile *N. acutidens*, because they exhibit residency and affinity to these features. Conversely, such protection will be of limited benefit for juvenile *C. melanopterus*, because they exhibit low residency and broader movements.

Additional keywords: conservation, elasmobranchs, marine, modelling, protected areas.

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Introduction

Marine protected areas (MPAs) are important tools for addressing the rapid loss of biodiversity resulting from various stressors, including overexploitation by fisheries and habitat degradation (Worm *et al.* 2006). Benefits of MPAs to species are maximised where no-take zones are well enforced, old (>10 years since establishment), large in area ($>100\ \text{km}^2$) and isolated. When these criteria are met, MPAs can support 5-fold more large fish and 14-fold more shark biomass than fished areas (Edgar *et al.* 2014). Small-scale MPAs may also be effective for species that have restricted ranges or key life stages linked to predictable or fixed habitat features (Garla *et al.* 2006; Schofield *et al.* 2013). Because many sharks are highly mobile and tend to make large-scale movements (>100 km; Heupel *et al.* 2010), MPAs are often too small (median size $4.6\ \text{km}^2$; Wood *et al.* 2008) to encompass the range of movements of larger individuals and adults (Green *et al.* 2015). Small MPAs may offer protection for smaller-bodied species that have restricted movements over their full life cycle (Escalle *et al.* 2015; Munroe *et al.* 2015) or species that occupy coastal nurseries for their early life history stages (Heupel *et al.* 2007) but disperse more widely on reaching maturity. This is particularly important for the resilience of shark species, because most tend to grow slowly, mature late and produce few young (Cortés 2002; Heithaus 2007).

Young sharks typically segregate from adults in shallow, coastal nurseries, which are defined as areas that: (1) support higher abundances of neonates (age <1 year); (2) are used over extended periods of time; and (3) are used over multiple years (Heupel *et al.* 2007). Such nurseries are thought to promote the survivorship of young sharks through protection from predators and increased foraging success (Cortés 2002; Heithaus 2007;

Guttridge *et al.* 2012). The former may be facilitated by the increased availability of microhabitats, such as mangroves, sandflats and seagrass beds, in inshore nurseries (Chin *et al.* 2012; Munroe *et al.* 2014; Escalle *et al.* 2015). The use of these shallow habitats may also contribute to the foraging success of sharks, with ebbing high tides forcing smaller fish and other prey off intertidal sandflats (Papastamatiou *et al.* 2009, 2015). For many species, the use of nurseries coincides with warmer water temperatures (e.g. Grubbs and Musick 2007; Conrath and Musick 2008), which may also assist with thermoregulation and increased foraging or digestive efficiency (DiGirolamo *et al.* 2012). Aggregation by juveniles (Guttridge *et al.* 2009) in a nursery may also improve foraging success through social learning (Guttridge *et al.* 2013) or dilution of predation risk (Heupel and Simpfendorfer 2005). Tide-mediated selection for these shallow habitats has also been proposed as a strategy for predator avoidance (Wetherbee *et al.* 2007; Guttridge *et al.* 2012). However, competition for limited food resources could result in habitat partitioning within and between species in communal nurseries (Papastamatiou *et al.* 2006; Kinney *et al.* 2011). Given the susceptibility of inshore coastal habitats to anthropogenic effects and climate change (Field *et al.* 2009; Chin *et al.* 2010), improved knowledge of ecological factors that affect the use of coastal nurseries is required to enhance the management and conservation of sharks.

Although nurseries for coastal sharks have been identified and characterised in the north-western Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Keeney *et al.* 2005; Chapman *et al.* 2009; Conrath and Musick 2010; Norton *et al.* 2012), very limited information about nurseries exists for the Indian Ocean. Ningaloo Reef in the eastern Indian Ocean is the world's largest fringing coral reef system and a United Nations World Heritage Site that supports a wide variety of habitats and is a global hot spot of shark diversity (Lucifora *et al.* 2011). Extensive surveys indicate that Mangrove Bay, a shallow (water depth <10 m), mangrove-lined tidal embayment in the north of the Ningaloo Reef Marine Park (NMP), had the highest sighting rates for six species of shark and rays within the NMP (Stevens *et al.* 2009). There is some evidence that Mangrove Bay is a communal nursery for juveniles, but the delineation of nursery habitats within the Bay remains unclear (Cerutti-Pereyra *et al.* 2014; Speed *et al.* 2016). Furthermore, the zoning plan of the NMP was not developed to protect these species (Escalle *et al.* 2015; Speed *et al.* 2016) and therefore existing spatial management strategies may not be suitable for conservation and management of shark and ray nurseries.

The present study addresses these issues using acoustic telemetry to examine spatial and temporal patterns in the movements of young blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks at Mangrove Bay. We hypothesised that: (1) both species would exhibit patterns of long-term residency (>6 months) and restricted space use, consistent with the use of Mangrove Bay as a shark nursery; (2) residency would decrease and space use increase with increasing shark size, thus decreasing the degree of protection afforded to both species by existing no-take MPAs; (3) because factors such as temperature (Conrath and Musick 2008; Froeschke *et al.* 2010), proximity to tidal inlets (Froeschke *et al.* 2010) and barometric pressure (Heupel *et al.* 2003; Udyawer *et al.* 2013) are known to be important determinants of habitat use by juvenile sharks, the presence of young sharks in Mangrove Bay would be affected by environmental variables (tides, water temperatures, air pressure, wind, etc.); and (4) given the similarities in their dependency on coastal producers (Speed *et al.* 2012), young sharks of these species would be likely to partition habitats within the nursery to coexist and decrease interspecies competition.

Materials and methods

Study site

Ningaloo Reef (21.9°S, 113.9°E) extends for 320 km along the north-west coast of Western Australia (WA) and has been protected by the multiple-use NMP, covering a total area of 4566 km^2, since 1996 (Fig. 1; Leprovost Dames and Moore 2000; CALM and MPRA 2005). Commercial fishing is prohibited within the NMP, but recreational fishing is allowed in all zones with the exception of no-take zones, which comprise 34% of the NMP. Shark capture and tagging for the present study was concentrated at Mangrove Bay within the NMP (Fig. 1), a tidal embayment encompassing small mangrove-lined inlets and a fringing reef at the seaward edge. The bay contains the Mangrove Bay Sanctuary Zone, a no-take area ~11.4 km^2 in size, established to protect a small area of mangrove forest within the NMP and its associated ecosystems (CALM and MPRA 2005; Smallwood *et al.* 2012). Habitats within Mangrove Bay include coral reefs, bare rocky reefs, mangroves, algae and turf-covered reefs interspersed with sandflats (Fig. 1; Bancroft 2003). The mean monthly tidal range is ~2.0 m, with the Bay drying at lowest tide levels. The prevailing wind is from south to south-west (Table 1) and the region is periodically subjected to severe cyclonic wind and floods (Lovelock *et al.* 2011). Mean monthly water temperature is ~25.3°C (Table 1).

Shark tagging and receiver array

Blacktip reef (*C. melanopterus*) and sicklefin lemon (*N. acutidens*) sharks were captured from shore within the Mangrove Bay Sanctuary zone using gill nets or handlines with barbless, 6/0 circle hooks baited with pilchard or squid. Captured sharks were transferred to a holding tank filled with seawater and identified to species, sexed, measured, photographed, assessed for clasper calcification and examined for umbilical scar condition and wounds. We measured fork length (FL; the distance from the snout to the fork of the tail) and stretched total length (TL; the distance from the snout to the tip of the upper lobe of the caudal fin) to the nearest centimetre and classified sharks as either neonate based on the presence of umbilical scars (Chin *et al.* 2015) or juvenile using length-at-age data (Last and Stevens 2009). In total, 13 *C. melanopterus* (8 females, 5 males; Table 2) and 23 *N. acutidens* (11 females, 12 males) were implanted with a uniquely coded microchip (Trovan FDX-A; Microchips Australia Pty Ltd, Melbourne, Vic., Australia) at the base of the left dorsal fin to minimise the possibility of double-tagging with acoustic tags. Sharks were then inverted to induce tonic immobility (Kessel and Hussey 2015) and an acoustic tag (V13-1H; Vemco, Halifax, NS, Canada) was implanted into the abdominal cavity through a 2-cm incision made using a scalpel along the ventral midline that was subsequently closed with

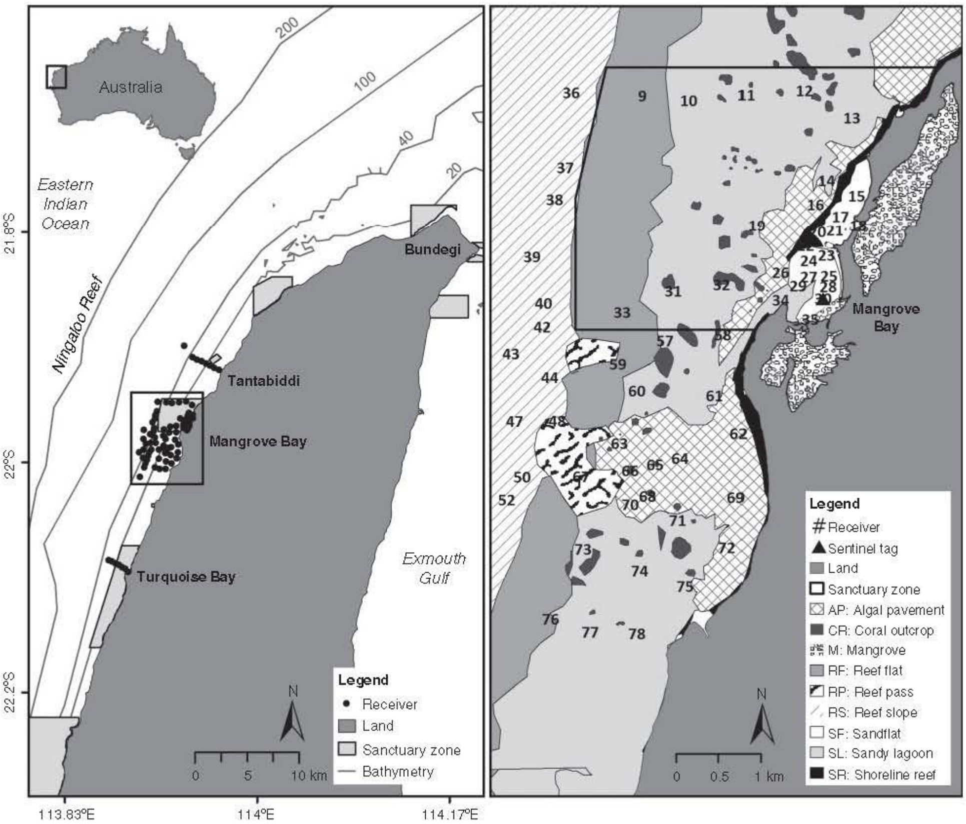

Fig. 1. Map of Mangrove Bay, in the northern Ningaloo Reef Marine Park, showing the location of acoustic receivers (points on the left plot and numbers on the right plot), bathymetry (grey lines), sanctuary zones (solid lines) and inset map of Australia. Benthic habitats are shaded by habitat type.

absorbable surgical sutures (Ethicon 2–0; Johnson and Johnson, Livingstone International Pty Ltd, Sydney, NSW, Australia). Each tag transmitted a unique identification code with a transmission delay that varied randomly from 110 to 250 s and a battery life of 514–540 days. Sharks were held for 5–10 min from capture to completion of surgery, after which individuals were monitored until recovery (i.e. the individual could swim away from gentle restraint, usually 5–15 min) and released at the site of capture. All procedures were permitted under Department of Parks and Wildlife licences (SF009588, 163165, CE004244), Department of Fisheries WA exemptions (2150, 2355) and the University of Western Australia Animal Ethics Committee (UWA AEC; RA 3/100/1168).

An array of 85 acoustic receivers (VR2 and VR2W; Vemco) deployed as part of a national network of receivers (https://animaltracking.aodn.org.au/, accessed 9 March 2016) was used to monitor movements of sharks tagged in Mangrove Bay (Fig. 1; see Table S1, available as Supplementary material for this paper). The array consisted of 71 receivers at Mangrove Bay and two cross-shelf lines of 8 receivers at Tantabiddi and 7 receivers at Turquoise Bay (Fig. 1). Receivers were secured to metal pickets either hammered directly into the reef or mounted in custom-built cement blocks (0.013 m^3) deployed on the reef. The receivers were placed within movement corridors including inlets, natural constrictions and channels. Various factors can affect spatial and temporal variability in the detection range of receivers, including depth, temperature wind and ambient noise (Kessel *et al.* 2014; Huveneers *et al.* 2016). To establish the effective detection range of receivers in intertidal areas of Mangrove Bay, receivers were anchored in a straight line at ~0, 50, 100, 150, 175, 200, 225, 250 and 275 m away from a submersed, fixed-delay interval V13-1H range-test tag (with a mean transmission interval of 10 s). Range tests were conducted in the intertidal zone of Mangrove Bay in March 2013, when wind speeds ranged from 0 to 47.9 km h^{-1} (median 20.3 km h^{-1}), and in the lagoon in August 2012 following the

Table 1. List of explanatory variables included in models of residency index (RI) and core and total kernel areas (50 and 95% KAs respectively) of *Negaprion acutidens* at Mangrove Bay

Details include description, source, range of values calculated from monthly values from March 2013 to May 2015, unit of measure for each continuous variable or category levels for categorical predictors (marked with an asterisk). All variables were included as fixed effects apart from tag number, which was included as a random effect in all models

Variable	Description	Source	Units or levels	Range
Environmental				
PressAV	Mean air pressure	Milyering weather station	hPa	1004.1–1017.1
PressR	Air pressure range	Milyering weather station	hPa	0–14.8
TempAV	Mean water temperature	Temperature logger	°C	23.0–28.2
TempR	Water temperature range	Temperature logger	°C	2.4–7.4
TideAV	Mean tidal height	Regional Oceanic Modelling System	m	1.42–1.66
TideR	Tidal height range	Regional Oceanic Modelling System	m	1.78–2.17
WspeedAV	Mean wind speed	Milyering weather station	km h^{-1}	0–22.7
WspeedR	Wind speed range	Milyering weather station	km h^{-1}	0–49.0
WdireAV	Mean wind direction	Milyering weather station	Degrees	0–257.2
RainAV	Mean cumulative rainfall	Milyering weather station	mm	0–17.8
Biological				
TL	Stretched total length	Observer	mm	63.0–116.9
Tag*	Tag identification number	Observer; Vemco Ltd (Halifax, NS, Canada)	B1–13; L1–23	–
Sex*	Sex	Observer	Female, male	–
Temporal				
Month	Month	Calendar	Month	1–12

methods described by Pillans *et al.* (2014). The detection probability of a receiver was calculated by dividing the number of detections by the expected mean number of transmissions (given a mean transmission interval of 10 s) over the range-testing period. The effective detection range was defined as the distance at which detection probability was 50% (D_{50}) and estimated using a LOESS smoother fitted in R, ver. 3.3.1 (R Foundation for Statistical Computing, Vienna, Austria, see http://www.r-project.org). Range testing showed that the effective detection range (D_{50}) for the receivers in the intertidal bay was 175 m (see Fig. S1) and in the lagoon was 300 m (Pillans *et al.* 2014). Receivers were spaced 150–300 m apart in the intertidal zone adjacent to mangroves (2-m depth) and 200–800 m apart in the lagoon (2–10-m depth), channel (10–15-m depth) and open shelf (15–40-m depth; Fig. 1). Receivers were downloaded every 6–9 months and acoustic monitoring of tagged sharks occurred from March 2013 to May 2015.

To assess temporal variation in receiver performance (Payne *et al.* 2010), we deployed a V13-1H sentinel tag (with a transmission delay of 550–650 s) at fixed distances from two receivers (1 and 153 m) located in areas of greatest shark activity between November 2013 and January 2015 (Fig. 1). We assessed the effect of environmental variables on detection probability of these two receivers using generalised additive models (see the Methods section and Table S2 in the Supplementary material).

Residency and space use

Prior to analysis, false detections were removed from the dataset. False detections were defined as single detections recorded within a 24-h period, or when two detections recorded by different receivers were within too short a time frame for an individual to travel the distance separating the receivers (Pincock 2012). To examine patterns of residency, a shark was considered as present if two or more detections were recorded on a receiver on a given day (Papastamatiou *et al.* 2010). A residency index (RI) was calculated as the number of days a shark was present within the full array as a proportion of the total number of days monitored. Because individuals were released on different days, the projected battery life of each tag was used as a standard reference value for the total number of days monitored. All sharks were likely to have survived the tagging process (Buray *et al.* 2009; Chin *et al.* 2015) and thus sharks not detected by the array were assumed to have departed. RI values ranged from 0 (no residency) to 1 (high residency). Drawing upon descriptions of one of the criteria for a shark nursery (Heupel *et al.* 2007), we classified individuals as either non-residents that were present within the array for days to weeks (<30 days; $RI < 0.06$) or residents that were predictably present within the array for months to years (≥30 days; $RI \geq 0.06$).

To investigate space use patterns the mean geographic position of each shark was estimated every 15 min using the centre of activity (COA) algorithm developed by Simpfendorfer *et al.* (2002). Only sharks that were detected for at least 5 days were included in this analysis to minimise the effect of short detection times on results. The COA positions provide a more accurate representation of movement than the raw receiver locations, and were used in subsequent analysis of kernel utilisation distributions (KUDs) to quantify the spatial area used by tagged sharks. Receiver locations were collected in World Geodetic System 1984 (WGS84) geographic coordinates, but subsequent spatial analysis was conducted in a Lambert conformal conic projection (m). KUD was estimated using the Brownian bridge kernel method in the *adehabitatHR* package (Calenge 2015) in R (R Foundation for Statistical Computing), which applies a conditional random walk to model both the shark positions and the expected path travelled between

Table 2. Tagging and detection details of 13 *Carcharhinus melanopterus* and 23 *Negaprion acutidens* monitored at Mangrove Bay from March 2013 to May 2015

Details include sex (F, female; M, male), life stage (N, neonate; J, juvenile), stretched total length (TL), residency category (RC; R, resident; NR, non-resident), total monitoring days (TMD), days detected (DD), consecutive days detected (CDD), the number of receivers on which a tagged shark was detected, residency index (RI) and core and total kernel areas (50 and 95% KA respectively). Sharks L5 and L19 were moving around the array until 26 May 2013 and 20 January 2014 respectively. After these dates, the tags were stationary close to one receiver. The RI for these sharks was calculated from data before the tags became stationary. Shark L3 was recaptured by fishermen in the recreational-use zone within the array on 21 July 2013 and its tag was subsequently implanted into Shark L9. NA, not available

Tag	Sex	Stage	TL (cm)	RC	Date tagged	Date last detected	TMD	DD	CDD	Number of receivers	RI	50% KA	95% KA
C. melanopterus													
B1	F	N	88	R	27 November 2013	16 February 2015	540	395	148	39	0.73	1.70	22.89
B2	F	N	56	R	4 December 2013	31 May 2015	540	407	90	5	0.75	0.16	0.95
B3	M	N	74	R	2 December 2013	4 November 2014	540	45	6	13	0.08	4.14	27.21
B4	F	N	53.5	NR	25 November 2013	2 December 2013	540	8	8	15	0.01	0.36	1.41
B5	F	J	107	NR	29 November 2013	4 December 2013	540	6	6	10	0.01	5.51	31.47
B6	F	N	55.5	NR	14 December 2013	15 December 2013	514	2	2	13	0.00	0.65	2.76
B7	F	N	55	NR	15 December 2013	12 January 2014	514	9	4	2	0.02	0.07	0.33
B8	F	N	51	NR	17 December 2013	23 December 2013	514	7	7	16	0.01	3.00	18.72
B9	F	N	55.5	NR	17 December 2013	21 December 2013	514	5	5	8	0.01	4.89	17.92
B10	M	N	56	NR	27 November 2013	NA	NA	NA	NA	NA	NA	NA	NA
B11	M	N	59	NR	5 December 2013	23 December 2013	514	16	11	4	0.03	0.09	0.45
B12	M	N	52	NR	10 December 2013	3 January 2014	514	12	10	15	0.02	1.05	7.80
B13	M	N	68	NR	17 December 2013	11 January 2014	514	9	8	12	0.02	0.15	0.94
N. acutidens													
L1	F	N	70.5	R	21 March 2013	17 October 2013	540	185	156	18	0.34	0.20	1.18
L2	F	N	67	R	21 March 2013	29 June 2013	540	101	101	29	0.19	0.12	1.10
L3	F	N	70	R	24 March 2013	21 July 2013	120	105	57	17	0.88	0.19	2.15
L4	M	N	75	R	21 March 2013	12 November 2013	540	230	223	12	0.43	0.11	0.57
L5	M	N	65	R	21 March 2013	2 August 2013	65	65	67	19	1.00	0.86	11.33
L6	M	N	69.5	R	22 March 2013	5 August 2013	540	136	135	30	0.25	0.33	2.77
L7	M	N	63	R	23 November 2013	8 January 2014	540	47	8	8	0.09	0.13	0.70
L8	M	N	72	R	26 November 2013	23 December 2014	540	391	327	17	0.72	0.43	2.22
L9	M	N	70	R	27 November 2013	1 August 2014	248	75	11	9	0.30	0.73	7.29
L10	M	N	81	R	27 November 2013	21 May 14	540	159	80	20	0.29	0.99	5.60
L11	M	N	90	R	30 November 2013	11 April 2014	540	131	129	16	0.24	0.19	1.06
L12	M	N	90.5	R	11 December 2013	27 May 15	514	512	470	21	1.00	0.34	2.40
L13	F	N	75.5	R	25 November 2013	5 August 2014	540	236	112	30	0.44	1.81	13.91
L14	F	N	74.5	R	28 November 2013	27 July 2014	540	242	242	15	0.45	0.20	0.75
L15	F	N	101	R	2 December 2013	10 March 2015	540	440	370	20	0.81	0.63	3.76
L16	F	N	69	R	17 December 2013	31 May 15	514	517	123	15	1.00	0.32	1.71
L17	F	N	73	NR	12 December 2013	3 January 2014	514	23	23	16	0.04	0.42	1.94
L18	F	N	64.5	NR	12 December 2013	15 December 2013	514	4	4	14	0.01	0.23	1.47
L19	F	N	74	NR	16 December 2013	5 June 2014	514	37	37	4	0.07	0.13	0.86
L20	F	N	91.5	NR	16 December 2013	24 December 2013	514	8	6	16	0.02	2.19	13.02
L21	M	N	85	NR	25 November 2013	30 November 2013	540	4	3	8	0.01	0.58	2.01
L22	M	N	66.5	NR	10 December 2013	24 February 2014	514	28	7	19	0.05	2.50	24.15
L23	M	N	72	NR	14 December 2013	23 December 2013	514	10	10	16	0.02	0.59	1.97

successive positions. We set two smoothing parameters: sig1, which controlled the width of the 'bridge' connecting successive positions; and sig2, which was related to the imprecision of the positions (Horne *et al.* 2007). Values of sig1 were selected using the *liker* function (Calenge 2015), which implemented the maximum likelihood approach (Horne *et al.* 2007). A fixed sig2 value of 175 m was used as the mean positional error around each receiver location and calculated from the effective detection range (D_{50}) established from range tests (see Fig. S1). Utilisation distribution increases with increasing sig2 values (positional error), with low and high values under- and overestimating space use (Calenge 2015; see Table S2). Therefore, we used the mean positional error for sig2 because it is considered the best trade-off to over- and underestimation and is likely to be more robust to variations in detection range that are likely in shallow environments and allowed for a more conservative assessment of the relative use of a MPA by tagged sharks. We subtracted the area where the 50 and 95% KUD contours overlapped with land to determine core and total space use (50 and 95% kernel areas respectively) over the total period each shark was detected. Individual kernel areas were then overlaid in ArcGIS, ver. 10.3 (ESRI, Redlands, CA, USA), to produce relative densities (i.e. the sum of the number of individuals in each overlapping area) of core kernel area and contours of total kernel area per species. Kernel areas were then overlaid with shapefiles of no-take zones and benthic habitat categories (Bancroft 2003) in ArcGIS, ver. 10.3 (ESRI), to calculate the relative proportion (0–1) of total space use within no-take zones and each benthic habitat type respectively (Fig. 1). Chi-squared goodness-of-fit and multiple comparison tests with Bonferroni corrections were used to assess whether sharks used any habitat type significantly more often than expected based on availability. To determine whether individuals were selecting or avoiding habitats, selectivity indices (S_i) were calculated for each habitat type as:

$$S_i = o_i - \pi_i$$

where o_i is the proportion of habitat type i used by each individual and π_i is the proportion of habitat type i used by all sharks, as described by (Strauss 1979). Selection was indicated with values greater than zero, whereas avoidance was indicated by values less than zero.

We first tested for differences in shark length and number of days detected between species (*C. melanopterus* and *N. acutidens*) and sexes using generalised linear models (GLMs) and an information theoretic approach to model selection (Burnham and Anderson 2002). For each response variable (shark length and number of days detected), a Gaussian error distribution with identity link was used and the slope model was compared with the intercept-only (null) model according to Akaike's information criterion corrected for small sample size and corresponding AIC_C weight (wAIC_C), which assigns relative strengths of evidence to the different competing models. The information theoretic approach uses a multimodel framework to provide a more robust method than standard regression techniques for comparing alternative hypotheses (Burnham and Anderson 2002) and was used in all subsequent model evaluation. The residuals of the models within 2 AIC_C points of the top-ranked model were examined to verify that the appropriate distribution was applied.

A suite of generalised additive models (GAMs) was used to evaluate the effects of shark length and sex and possible two-way interactions on three response variables, namely RI and, core and total kernel area (50 and 95% KA respectively), separately for each species. RI was modelled as the frequency of presence (i.e. the number of days a shark was present or absent) using a binomial error distribution with logit link and 50 and 95% KA using Gaussian error distributions with identity link. For the GAMs of RI, both binomial and β error distributions were tested with diagnostic plots showing that the former was more appropriate. Shark TL was modelled using a cubic regression spline (bs = 'cr'), with the basis dimension 'k' restricted to <4 to avoid overfitting. A maximum of one term per model was specified for *C. melanopterus* due to the small sample size (n = 10) and three terms were specified for *N. acutidens* due to the relatively larger sample size (n = 21). Hence, a candidate set of three models was used for *C. melanopterus* and five models were used for *N. acutidens* that included all possible combinations of variables, which were ranked according to AIC_C and wAIC_C (Table 3). For each response variable, a confidence set of models that were within 2 AIC_C points of the top-ranked model were considered equivalent and if these models did not include the null model, we used model averaging to calculate relative variable importance (RVI; Burnham and Anderson 2002) from the sum of wAIC_C across the confidence set. Models containing only highly influential variables (i.e. determined as those preceding a sharp decline in RVI) were used for graphical representation of variable effects.

Monthly patterns of residency and space use

Monthly metrics of residency and space use were calculated and analysed only for *N. acutidens* that were resident within the receiver array for over 30 days (n = 16). It was not possible to perform temporal analysis for *C. melanopterus* due to the low number of resident individuals (n = 3). To examine biological and environmental effects on monthly patterns of residency and space use, a suite of relevant explanatory variables was compiled, including water temperature, air pressure, rainfall, tidal height, wind speed and direction, month, sex and the TL of shark (Table 1). Multicollinearity was assessed between pairs of variables using Pearson correlation coefficients (r) and one variable was retained from correlated pairs ($r > 0.6$) to minimise the possibility of over-fitting models (Dormann *et al.* 2013). To account for the growth of tagged sharks over the monitoring period, monthly TL was estimated based on the initial size at capture and published growth rates of juvenile *N. acutidens* reported in the Indian Ocean (Stevens 1984). Water temperature was recorded at Tantabiddi using data loggers (U22-001; HOBO Data Loggers Australia, Adelaide, SA, Australia) calibrated at the Australian Institute of Marine Science (AIMS) and sampling at 30-min intervals, which were periodically downloaded and replaced every 3–12 months. Daily values for air pressure (hPa), rainfall totals (mm) and wind speed (m s^{-1}) and direction (degrees) were obtained from a weather station at Milyering (10 m elevation; 22.03°S, 113.92°E) situated 6.8 km south of Mangrove Bay (http://data.aims.gov.au/, accessed 7 October 2015). Predicted tidal height data were obtained through the Regional Oceanic Modelling System (https://www.myroms.org/, accessed 4 November 2015). Monthly mean values and range were computed for all variables from March 2013 to May 2015 and chronologically matched with shark movement data across the monitoring period.

Generalised additive mixed-effect models (GAMMs) with binomial error distributions and logit link were used to model RI. To model square root-transformed (to normalise distribution) 50 and 95% KAs, GAMMs with Gaussian error distributions and identity link were used. To account for repeated observations made for each shark, tag number was included as a random effect in the models (Bolker *et al.* 2009). All explanatory variables were modelled with a cubic regression spline, except for month and wind direction, which were modelled with a cyclic cubic regression spline (i.e. a penalised cubic regression spline whose ends match, up to second derivative). Because the latter smoother includes shrinkage by default, the shrinkage version of the cubic regression spline was also implemented here. The basis dimension 'k' was restricted to <4 to avoid overfitting. A maximum of four fixed effects per model was specified due to small sample sizes and the rule of marginality was applied such that interactions were included only in models

Table 3. Ranked additive models (m1, model 1, etc.) of residency index (RI), core and total kernel area (50 and 95% KA respectively) and the proportion of total kernel area within no-take zones (p95% KA in no-take) of *Carcharhinus melanopterus* and *Negaprion acutidens* explained by the biological variables (see Table 1 for explanations of each variable)

All models fitted for each response are shown; the best-supported model is highlighted in bold. Details include the estimated degrees of freedom (d.f.$_e$), Akaike's information criterion corrected for small sample size (AICc), increase in AIC$_C$ relative to the model with the lowest AIC$_C$ value (ΔAIC$_C$), relative AIC$_C$ weight (wAIC$_C$) and goodness of fit (adjusted R^2). TL, total length; sqrt, square root

Model number	Response	Model	d.f.$_e$	AIC$_C$	ΔAIC$_C$	wAIC$_C$	Adjusted R^2
C. melanopterus							
m3	RI	TL	3.00	331.26	0.00	1	88.0
m2	RI	Sex	1.00	1471.35	1140.09	0	6.1
m1	RI	1	0.00	1665.93	1334.67	0	0.0
m1	sqrt (50% KA)	1	0.00	26.20	0.00	0.90	0.0
m2	sqrt (50% KA)	Sex	1.00	30.60	4.40	0.10	9.3
m3	sqrt (50% KA)	TL	2.78	36.08	9.88	0.01	54.2
m1	sqrt (95% KA)	1	0.00	43.85	0.00	0.86	75.3
m2	sqrt (95% KA)	Sex	1.00	48.20	4.35	0.10	8.7
m3	sqrt (95% KA)	TL	2.92	49.94	6.09	0.04	0.00
m3	p95% KA in no-take	TL	2.99	159.68	0.00	1	59.7
m2	p95% KA in no-take	Sex	0.00	456.49	296.81	0	10.8
m1	p95% KA in no-take	1	1.00	463.76	304.08	0	0.0
N. acutidens							
m5	RI	Sex × TL	6.96	3526.32	0.00	1	0.7
m4	RI	Sex + TL	4.00	4244.19	717.87	0	4.0
m3	RI	TL	3.00	4244.21	717.89	0	1.8
m2	RI	Sex	1.00	4906.25	1379.93	0	4.2
m1	RI	1	0.00	4946.41	1420.09	0	0.0
m1	sqrt (50% KA)	1	0.00	21.84	0.00	0.33	0.0
m3	sqrt (50% KA)	TL	0.00	21.84	0.00	0.33	0.0
m5	sqrt (50% KA)	Sex × TL	2.67	23.25	1.42	0.16	16.1
m2	sqrt (50% KA)	Sex	1.00	24.50	2.66	0.09	4.8
m4	sqrt (50% KA)	Sex + TL	1.00	24.50	2.66	0.09	4.8
m1	sqrt (95% KA)	1	0.00	69.02	0.00	0.35	0.0
m3	sqrt (95% KA)	TL	0.00	69.02	0.00	0.35	0.0
m2	sqrt (95% KA)	Sex	1.00	71.46	2.44	0.10	3.7
m4	sqrt (95% KA)	Sex + TL	1.00	71.46	2.44	0.10	3.7
m5	sqrt (95% KA)	Sex × TL	1.87	71.55	2.53	0.10	3.8
m5	p95% KA in no-take	Sex × TL	5.59	630.86	0.00	1	23.8
m4	p95% KA in no-take	Sex + TL	3.85	664.67	33.81	0	20.9
m3	p95% KA in no-take	TL	2.69	667.37	36.51	0	13.2
m1	p95% KA in no-take	1	0.00	676.48	45.62	0	0.0
m2	p95% KA in no-take	Sex	1.00	677.49	46.63	0	5.0

with both main effects. This resulted in a set of 96 candidate models, with model selection and averaging undertaken using the same approach described for GAMs. Standard diagnostic plots were made to assess the validity of the models in the confidence set and we checked for temporal autocorrelation in the residuals. The top six models for each response were then presented, except when more than six models were within 2 AIC$_C$ points, in which case all models within the confidence set were presented. All models were implemented using the *lme4, MuMIn, mgcv* and *gamm4* packages in R (R Foundation for Statistical Computing). Unless specified otherwise, all data are presented as the mean (±s.d) values.

Results

Tagged sharks were monitored for 2–544 days between March 2013 and May 2015 (Table 2; Fig. 2). All the tagged sharks were neonates with umbilical scars in various stages of healing (age <1 year), with the exception of one *C. melanopterus* that was a juvenile female. The mean TL of *N. acutidens* was slightly larger than that of *C. melanopterus* (75.2 ± 10.0 ($n = 23$) *v.* 63.9 ± 16.7 cm ($n = 13$) respectively), with higher statistical support for the generalised linear model (GLM) that included species (wAICc = 0.59) than the intercept-only model (wAIC$_C$ = 0.41). We found no evidence for a difference in TL between sexes for either *C. melanopterus* (65.2 ± 20.6 and 61.8 ± 9.0 cm in females and males respectively; wAIC$_C$ = 0.89 for the intercept-only model) or *N. acutidens* (75.5 ± 11.0 and 75.0 ± 9.5 cm in females and males respectively; wAIC$_C$ = 0.77 for the intercept-only model).

Residency and space use

Nine *C. melanopterus* and five *N. acutidens* were detected within the array between 2 and 23 days after tagging, but ceased to be detected after January 2014 (Table 2). The remaining three

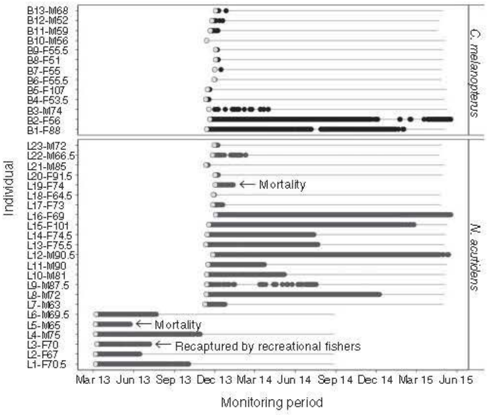

Fig. 2. Daily presence of individual *Carcharhinus melanopterus* (black circles) and *Negaprion acutidens* (dark grey circles) released with acoustic transmitters in Mangrove Bay from March 2013 to May 2015. Individuals are identified by species (B, blacktip reef shark; L, sicklefin lemon shark), tag identification number, sex (M, male; F, female), followed by stretched total length (cm). The tagging dates are indicated by light grey circles and grey lines represent the availability of the shark for detection based on tagging date and battery life of the tag.

C. melanopterus were detected for a maximum of 45–407 days (77 ± 152 days) and 18 *N. acutidens* were detected for between 47 and 517 days (166 ± 160 days), with higher statistical support for the model that included species (wAICc = 0.84) relative to the intercept-only model ($\mathrm{wAIC_C} = 0.16$). We found no evidence for differences in the number of days detected between the sexes in both species ($\mathrm{wAIC_C} = 0.80$ and 0.77 for the intercept-only model for *C. melanopterus* and *N. acutidens* respectively). One of the tagged *C. melanopterus* (B10) was not detected following its release (Fig. 2). Two of the 18 *N. acutidens* (L5 and L19) were assumed to have died close to a receiver after 65 and 37 days respectively, resulting in the tag being continuously detected by one or more overlapping receivers (Fig. 2). We retrieved a tag from one *N. acutidens* (L3) that was recaptured by a recreational fisher outside the Mangrove Bay no-take zone, and subsequently deployed it into another *N. acutidens* (L9). Throughout the detection period, 74% of tagged sharks were detected on more than 10 receivers (15 ± 8 receivers; Table 2). One *C. melanopterus* (B1) and three *N. acutidens* (L13, L15 and L22) were detected by the receiver curtains off Tantabiddi (~10 km north) and Turquoise Bay (~15 km south), a part of the array that was designed to detect such long-range movement (Fig. 1). We found strong evidence for an effect of species on RI, with the slope model having highest statistical support (wAICc = 1) and *N. acutidens* having higher residency than *C. melanopterus* (0.42 ± 0.34 *v.* 0.17 ± 0.30 respectively).

For *C. melanopterus* residency, the additive model including TL had the highest statistical support (GAM, $\mathrm{wAIC_C} = 1$; Table 3) and accounted for 88% of the variance in the response, indicating a positive trend in residency when TL increased from 60 to 90 cm (Fig. 3*a*). For *N. acutidens* residency, we found highest support for the model including sex, TL and the interaction between sex and TL (GAM, $\mathrm{wAIC_C} = 1$; Table 3), indicating increased residency among smaller (≤70 cm TL) neonate females and decreased residency with increasing TL of larger (>70 cm TL) neonate females (Fig. 3*b*). In contrast, there was no apparent change in residency with increasing TL for males (Fig. 3*c*), but this model accounted for less than 1% of the variance in the response ($R^2 = 0.7$).

Core and total kernel areas (50 and 95% KA respectively) of 10 *C. melanopterus* and 21 *N. acutidens* largely overlapped within nearshore waters of Mangrove Bay (Fig. 4). We found evidence that 50% KAs differed between species, with the slope model having higher statistical support (wAICc = 0.72) than the intercept-only model ($\mathrm{wAIC_C} = 0.28$; mean (±s.d.), 1.6 ± 2.0 and 0.6 ± 0.7 km^2 for *C. melanopterus* and *N. acutidens* respectively; Table 2). There was also evidence for a species difference in 95% KAs, with the slope model having higher statistical support (wAICc = 0.66) than the intercept-only model ($\mathrm{wAIC_C} = 0.34$). The 95% KAs were larger for *C. melanopterus* than for *N. acutidens* (11.2 ± 12.5 *v.* 4.8 ± 6.1 km^2 respectively).

We found no evidence for a difference in overall core space use of *C. melanopterus* with either shark sex or TL with the intercept-only model having majority support ($\mathrm{wAIC_C} = 0.80$). Similarly, there was little evidence for an effect of TL or sex on total space use, because the intercept-only model ranked highest (Table 3). There was also no evidence for a difference in core and total space use of *N. acutidens* in response to either shark sex or TL, with the intercept-only model most parsimonious (Table 3). The proportion of total space use within no-take zones was higher for *N. acutidens* relative to *C. melanopterus* (0.86 ± 0.19 *v.* 0.71 ± 0.30 respectively), with the slope model having complete support ($\mathrm{wAIC_C} = 1$) over the intercept-only model.

In terms of the proportion of 95% KA within no-take zones, the additive mixed model including TL had the highest statistical support for *C. melanopterus* ($\mathrm{wAIC_C} = 1$; Table 3). This model accounted for 60% of the variance in the response, and indicated a negative trend in the protection of total space use when TL exceeded 60 cm for *C. melanopterus* (Fig. 3*d*). For *N. acutidens*, the highest statistical support was for the model including sex, TL and the interaction between sex and TL ($\mathrm{wAIC_C} = 1$; Table 3) and accounted for 24% of the variance. The proportion of total space use within no-take zones was marginally higher for females between 65 and 75 cm TL, but was consistent for males across the range of TL sampled (Fig. 3*e, f*). There was no difference in the proportion of habitat types used between species (50% KA, $\chi^2_8 = 1.14$, $P = 1.00$; 95% KA, $\chi^2_8 = 13.21$, $P = 0.10$) and across space use metrics within species (*C. melanopterus*, $\chi^2_8 = 5.22$, $P = 0.73$; *N. acutidens*, $\chi^2_8 = 1.71$, $P = 0.99$). Core and total space use of both species primarily focused on sandflats (>34 and >21% respectively) and sandy lagoon habitats (>30 and >26% respectively). We found that neonates selected disproportionately for inshore sandflats, followed by mangroves, algal pavement and shoreline reefs (*C. melanopterus*, $\chi^2_8 = 29.57$, $P < 0.001$; *N. acutidens*, $\chi^2_8 = 106.78$, $P < 0.001$; Fig. 5). Mean selection values revealed that reef slope and sandy lagoon habitats were consistently avoided by *C. melanopterus* and *N. acutidens* (Fig. 5).

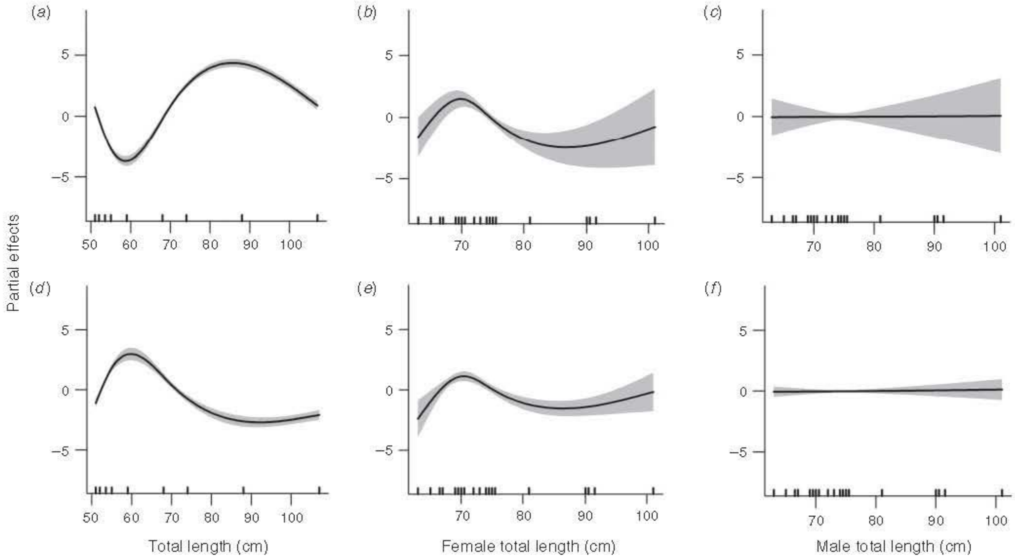

Fig. 3. Partial residual plots showing the relationships of the dependent variables of (*a*–*c*) residency index and (*d*–*f*) the relative proportion of 95% kernel area in no-take marine protected areas with that of the independent variable of total length in the top-ranked additive models for *Carcharhinus melanopterus* (*a*, *d*) and *Negaprion acutidens* (*b*, *c*, *e* and *f*). Black lines represent the fitted line and grey shaded areas represent 95% confidence intervals.

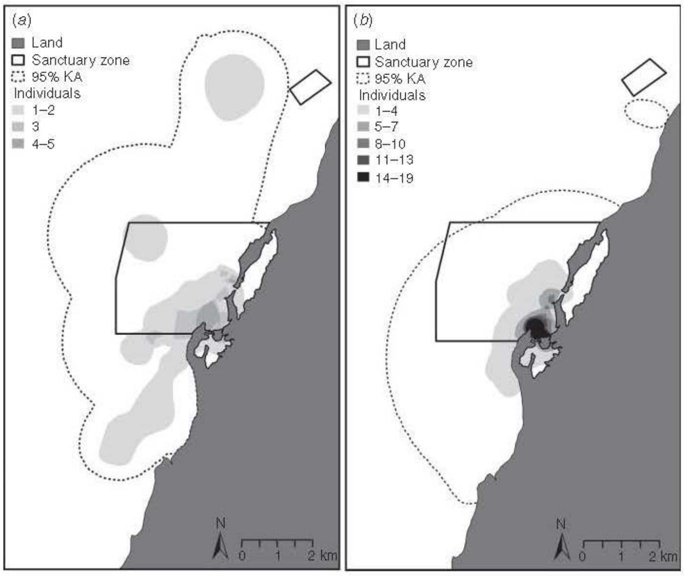

Fig. 4. Maps of 50 and 95% kernel areas (KAs) for (*a*) *Carcharhinus melanopterus* and (*b*) *Negaprion acutidens* monitored within Mangrove Bay for at least 5 days. Contours of 95% KA (dashed lines) and relative densities of 50% KA (shaded areas) are shown for combined individuals.

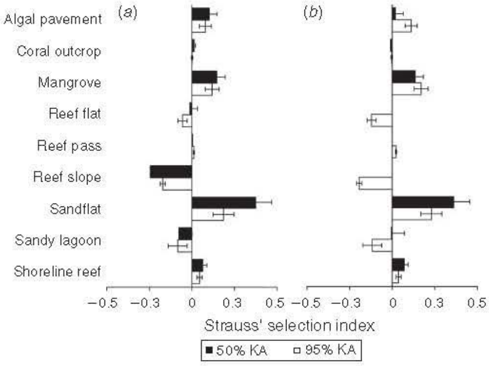

Fig. 5. Mean (±s.e.) Strauss' selection index values based on 50 and 95% kernel areas (KAs) of (*a*) *Carcharhinus melanopterus* and (*b*) *Negaprion acutidens* across the habitat types detailed in Fig. 1.

Monthly patterns of residency and space use

A detection span sufficient (>30 days) to allow the estimation of monthly RI and space use (50 and 95% KAs) was obtained for three *C. melanopterus* and 16 *N. acutidens* (Table 2). However, the GAMMs described were only fitted for *N. acutidens* and not *C. melanopterus* due to the small sample size. Mean values of water temperature were strongly correlated with those of tidal height ($r - 0.86$), and mean values of air pressure was strongly correlated with those of wind direction ($r -\quad 0.73$). Therefore, predictors from each correlated pair ($r > 0.6$) were used in separate candidate models. The modelling revealed that the confidence set (<2 ΔAIC_C) included one model where RI was the response, 13 models where 50% KA was the response and two models where 95% KA was the response (Table 4). For RI, the model containing TL and the interaction between month and sex had the highest statistical support ($wAIC_c - 1$, $R^2 - 4.8\%$; Figs 6, 7*a*–*c*). We found only weak relationships between 50% KA and explanatory variables for all 13 models within the confidence set (R^2 ranging from 0.2 to 2.8%; Table 4). Of these,

Table 4. Ranked additive mixed models (m1, model 1, etc.) of monthly residency index (RI), core and total kernel area (50 and 95% KA respectively) of *Negaprion acutidens* explained by the independent variables

The top six models for each response are shown; if more than six models are within 2 Akaike's information criterion corrected for small sample size (AICc) points, all these models are shown. Tag number was treated as a random effect in all models; the model(s) containing the most influential variables and used for graphical representation are highlighted in bold. Details for each model include the estimated degrees of freedom ($d.f._e$), AIC_C, increase in AIC_C relative to the model with the lowest AIC_C value (ΔAIC_C), relative AIC_C weight ($wAIC_C$) and goodness of fit (adjusted R^2). TL, total length; sqrt, square root; PressAV, mean air pressure; PressR, air pressure range; TideR, tidal height range; WdireAV, mean wind direction; RainAV, mean cumulative rainfall

Model number	Response	Model	$d.f._e$	AIC_C	ΔAIC_C	$wAIC_C$	Adjusted R^2
50% KA							
m11	RI	TL + month × sex	17.88	592.67	0.00	1.00	4.8
m7	RI	TL + month	11.81	661.58	68.91	0.00	4.3
m10	RI	TL + sex	12.81	663.47	70.80	0.00	4.5
m12	RI	Month + sex × TL	14.43	666.71	74.04	0.00	4.4
m23	RI	TL + pressAV	4.90	696.62	103.95	0.00	4.1
m43	RI	Sex × TL + pressAV	5.90	698.58	105.91	0.00	4.2
50% KA							
m84	sqrt (50% KA)	TempAV + tideR	3.62	236.03	0.00	0.06	0.6
m19	sqrt (50% KA)	TideR	2.65	235.98	0.05	0.06	0.2
m13	sqrt (50% KA)	PressAV	1.21	235.61	0.42	0.05	1.5
m66	sqrt (50% KA)	PressAV + tideR	3.39	235.43	0.60	0.05	1.2
m4	sqrt (50% KA)	Month	3.04	235.24	0.79	0.04	2.0
m29	sqrt (50% KA)	TL + tideR	3.41	235.17	0.86	0.04	2.8
m79	sqrt (50% KA)	RainAV + tideR	3.59	235.12	0.91	0.04	1.1
m7	sqrt (50% KA)	TL + month	3.98	235.06	0.97	0.04	1.5
m23	sqrt (50% KA)	TL + pressAV	3.17	234.97	1.06	0.04	1.8
m92	sqrt (50% KA)	TideR + wdireAV	3.39	234.80	1.24	0.03	0.4
m2	sqrt (50% KA)	TL	2.37	234.72	1.31	0.03	2.4
m64	sqrt (50% KA)	PressAV + pressR	2.95	234.45	1.58	0.03	1.5
m63	sqrt (50% KA)	PressAV + rainAV	3.09	234.15	1.88	0.03	2.4
95% KA							
m25	sqrt (95% KA)	TL + rainAV	3.07	129.39	0.00	0.26	8.2
m45	sqrt (95% KA)	TL + sex + rainAV	4.08	130.83	1.44	0.13	12.7
m15	sqrt (95% KA)	RainAV	1.58	131.65	2.26	0.08	2.4
m35	sqrt (95% KA)	Sex + rainAV	2.58	133.14	3.75	0.04	6.2
m76	sqrt (95% KA)	RainAV + tempAV	2.3	133.16	3.77	0.04	3.2
m79	sqrt (95% KA)	RainAV + tideR	2.13	133.61	4.22	0.03	2.9

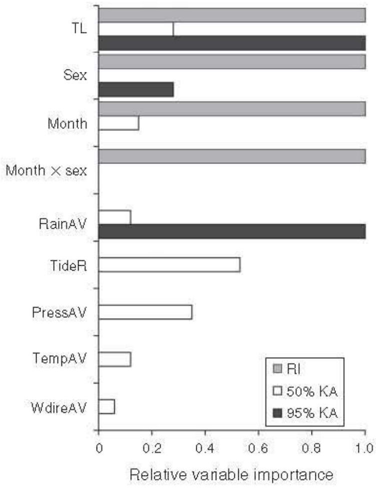

Fig. 6. Relative variable importance values of the independent variables in additive mixed models of monthly patterns of residency index (RI) and 50 and 95% kernel areas (KAs) of *Negaprion acutidens*. Variables that were common within the confidence set (i.e. models with values <2-point change in Akaike's information criterion corrected for small sample size) have a relative variable importance value of 1.0. RainAV, mean rain accumulation; TideR, tidal height range; PressAV, mean air pressure; TempAV, mean water temperature; WdireAV, mean wind direction.

relative variable importance (RVI) values derived from model averaging indicated that tidal height range, mean air pressure and TL had the most effect on core space use (Fig. 6) and the models containing these variables (Models 19, 13 and 2; Table 4) are shown in Fig. 7*d–f*. For 95% KA, model averaging indicated that TL and mean rain accumulation had the most effect on total space use (Fig. 6) and the model containing these variables (Model 25; wAICc − 0.26, R^2 − 8.2%; Table 4) is shown in Fig. 7*g*, *h*. Estimated TLs of *N. acutidens* at the end of the detection period ranged from 64.8 to 114.8 cm, indicating that all resident individuals were still immature. There was a negative trend in the monthly residency of immature *N. acutidens* across the range of TL sampled (Fig. 7*a*). Monthly residency indices of *N. acutidens* were sex specific (Fig. 7*b*, *c*). Females were resident throughout the year (Fig. 7*b*), whereas males were found to have longer residency in winter and spring (June–September) than in summer and autumn (Fig. 7*c*). Core space used by *N. acutidens* increased by 0.02 km^2 when mean air pressure was greater than 1012 hPa, and decreased by 0.05 km^2 when monthly tidal height range exceeded 2.0 m (Fig. 7*d*, *f*). Core and total space used by *N. acutidens* increased by 0.1 and 0.5 km^2 respectively when TL exceeded 88 cm (Fig. 7*e*, *h*). Total space use of *N. acutidens* increased marginally as mean rainfall increased from 0 to 7 mm and then stabilised (Fig. 7*g*).

Discussion

The present study is the first to quantify long-term residency and patterns of space use of neonate *C. melanopterus* and *N. acutidens* in the eastern Indian Ocean. Differences in the residency patterns between these species imply that for *N. acutidens*, the nearshore waters of Mangrove Bay meet the proposed criteria of Heupel *et al.* (2007) for a nursery, but it is apparent that additional data are required for *C. melanopterus*. Neonates of *N. acutidens* had small activity spaces (mean 95% KA − 4.5 km^2), which is consistent with patterns in earlier studies both at Ningaloo (Speed *et al.* 2011, 2016) and elsewhere (Filmalter *et al.* 2013). We also found evidence of ontogenetic expansions in space use among neonates of this species.

Although the present study does not provide quantitative data on increased neonate abundance in Mangrove Bay (one of the criteria for a nursery area), our high capture rates and extensive in-water surveys from Stevens *et al.* (2009) suggest that Mangrove Bay supports a higher abundance of both species. The presence of open and partially healed umbilical scars (age <1 week; Chin *et al.* 2015) on both *C. melanopterus* and *N. acutidens* captured between November and March over two seasons indicates that neonates of these species are pupped in or near to Mangrove Bay in autumn and summer, and some remain there for up to 17 months. We found highly variable patterns in the residency of neonate and juvenile *C. melanopterus* (mean RI (±s.d.), 0.14 ± 0.3), consistent with reported variability in the residency of juveniles of this species (0.3 ± 0.3) in eastern Australia (Chin *et al.* 2016). The findings for *C. melanopterus* in the present study contrast with patterns of long-term residency observed in *N. acutidens*, and corroborate increasing evidence that although extended residency in shark nurseries is common (DeAngelis *et al.* 2008; Chapman *et al.* 2009; Knip *et al.* 2011; Legare *et al.* 2015), it is not universal in juvenile sharks (Chin *et al.* 2016; Munroe *et al.* 2016). The results of the present study suggest that although Mangrove Bay may provide suitable pupping grounds for *C. melanopterus*, it does not appear to function as a long-term nursery habitat for this species. Prolonged residency and site attachment has been recorded for adult *C. melanopterus* on isolated coral atolls (Papastamatiou *et al.* 2009; Mourier *et al.* 2012), whereas large-scale dispersal (>80 km) has been documented for neonates and juveniles in archipelagic systems (Chin *et al.* 2013, 2016). The shallow depth of the lagoon at Mangrove Bay (<4 m) and availability of contiguous reef habitat along Ningaloo Reef may facilitate the dispersal of neonate *C. melanopterus* along the reef system. Two of the nine *C. melanopterus* (B5 and B9) that permanently departed the array were last recorded on the receivers at the northern limit of the array at Tantabiddi, indicating a minimum linear dispersal distance of 10 km. Alternatively, or in addition, low apparent residencies of neonate *C. melanopterus* could also reflect high mortality rates of juveniles, as have been documented in populations of blacktip (Heupel and Simpfendorfer 2002), lemon (Gruber *et al.* 2001) and scalloped hammerhead (*Sphyrna lewini*) (Duncan and Holland 2006) sharks elsewhere. In contrast, 70% of tagged *N. acutidens* had high residency and exhibited repeated use of nearshore, shallow sandflats, consistent with patterns reported for this species at atolls in the western Indian Ocean (Filmalter *et al.* 2013) and habitat selection in other similar-sized carcharhinids (Papastamatiou *et al.* 2009; Chin *et al.* 2012; Rizzari *et al.* 2014).

As expected, our temporal models revealed a progressive decline in monthly residency and increase in monthly space use

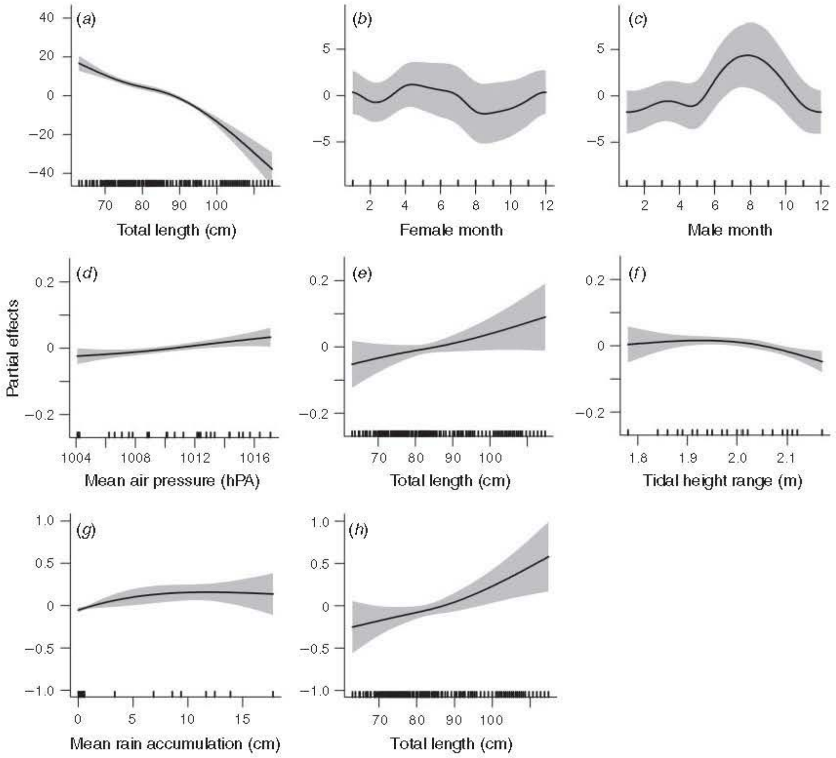

Fig. 7. Partial residual plots relative to the independent variables in the top-ranked additive mixed models for (*a c*) residency index, (*d f*) 50% kernel area (KA) and (*g*, *h*) 95% KA of *Negaprion acutidens* (see Table 4 for an explanation of each model). Each vertical plane represents the effect of a variable on each response. Black lines represent fitted lines and grey shaded areas represent 95% confidence intervals.

with ontogeny for resident individuals of *N. acutidens*. Ontogenetic expansion in space use (Garla *et al.* 2006; Dicken *et al.* 2007; Knip *et al.* 2011), followed by reduced nursery residency (Hussey *et al.* 2009; Conrath and Musick 2010) has been observed in many sharks, and is thought to reflect foraging optimisation in association with reduced predation risk as sharks grow in size (Heupel *et al.* 2004; Matich and Heithaus 2015). The relationship between TL and overall residency of *N. acutidens* showed the opposite trend to monthly residency, with an increase in overall residency for the larger neonates. These differences may suggest that other factors in addition to ontogeny drive residency, but it would seem that our temporal modelling approach, which incorporated monthly increases in shark TL, was more appropriate for examining the relationship between ontogeny and residency.

Estimates of total space use by neonate and juvenile *C. melanopterus* in Mangrove Bay (95% KA; 0.3–31.5 km^2) were consistent with estimates in east Australia (95% KA; 10.9–30.1 km^2; Chin *et al.* 2016) and larger than those found in older juveniles (minimum convex polygons (MCP); 5.8–8.5 km^2) and adults (MCP; 3.5–21.8 km^2) in this region (Speed *et al.* 2016). The findings of the present study support recent evidence that coastal habitat use by *C. melanopterus* (Chin *et al.* 2016) differs from conspecifics on coral reefs (Papastamatiou *et al.* 2011; Mourier *et al.* 2013*b*) and does not conform to the characteristic patterns of classical nursery use where neonates demonstrate highly restricted movements before undergoing ontogenetic expansions in space use. The results of the present study, combined with previous studies, reflect the ecological flexibility of *C. melanopterus* in being able to adapt movement patterns to optimise the use of local environments and suggest that this behaviour may be innate. In any event, the results of the present study must be treated with caution because of the low sample size ($n - 10$) of tagged *C. melanopterus* and the fairly short duration of monitoring.

Consistent with previous observations of overlap in nursery habitat use by *C. melanopterus* and *N. acutidens* in the Pacific Ocean (Papastamatiou *et al.* 2009; Mourier *et al.* 2013*a*), both species in the present study showed positive selection for nearshore sandflat and vegetated (mangrove and algal pavement) habitats, indicating low levels of habitat partitioning. This absence of habitat partitioning and space use overlap between and within species may reflect opportunistic use of abundant refuges or prey resources (Frisch *et al.* 2016) within sandflats and vegetated habitats where parturition occurs (Papastamatiou *et al.* 2009; Mourier *et al.* 2013*a*). Alternatively, strong selection for inshore sandflats and mangroves may relate to reduced predation risk within physical refuges (Guttridge *et al.* 2012), increased chances of finding prey on shallow sandflats (Papastamatiou *et al.* 2009) or behavioural thermoregulation (Papastamatiou *et al.* 2015). Avoidance of deeper lagoonal and reef slope habitats by neonate sharks may reduce predation risk or competition with other species, because larger predators, such as adult *C. melanopterus*, grey reef Carcharhinus *amblyrhynchos* and tiger sharks *Galeocerdo cuvier*, frequent these habitats (Ferreira *et al.* 2015; Speed *et al.* 2016).

Our modelling of temporal patterns indicated that environmental variables affected the space use of *N. acutidens* on a monthly basis, but had no effect on monthly residency. Along with expansions in space use with ontogeny, we found a weak negative effect of tidal range on core space use of neonate *N. acutidens,* consistent with the hypothesis of tide-mediated selection of shallow or familiar habitats as a strategy for predator avoidance, as seen in juvenile lemon sharks *Negaprion brevirostris* (Wetherbee *et al.* 2007; Guttridge *et al.* 2012). At Mangrove Bay, the high-use area at the southern part of the Bay contained a shallow sandflat adjacent to a mangrove-fringed inlet that remained flooded at low tides. Our telemetry data and capture locations confirmed that at high tide neonate *N. acutidens* often remained within the complex of mangrove root systems that probably afforded a physical refuge for these juveniles from larger predators. Alternatively, or in addition, reduced space use may be a strategy for optimising foraging efficiency as a consequence of tidally driven prey migrations via discrete corridors (Friedlander and Monaco 2007; Papastamatiou *et al.* 2009). We detected slight increases in core space use of *N. acutidens* with increases in barometric pressure, which is consistent with evidence of behavioural responses of a range of Carcharhinid shark species to changing barometric pressure (Heupel *et al.* 2003; Udyawer *et al.* 2013). Increases in total space use of *N. acutidens* with increasing rainfall may reflect avoidance of freshwater inflows or the redispersion of prey from core parts of the habitat. Alternatively, freshwater inflows were hypothesised to contribute to increased niche separation of juvenile sharks from adults (Heupel and Simpfendorfer 2008) and to expand available habitat for juvenile bull sharks *Carcharhinus leucas* (Matich and Heithaus 2015). The minimal effect of environmental variables on residency suggests that local conditions and the availability of prey resources may be favourable year-round for this species in the nursery. The lack of seasonality in the residency of neonate *N. acutidens* females was consistent with patterns seen in older juveniles (Filmalter *et al.* 2013), but we found increases in the residency of neonate *N. acutidens* males in winter months. Differences in residency patterns between sexes in adults sharks may be driven by sex-specific differences in thermoregulatory requirements (Hight and Lowe 2007), avoidance of sexual harassment in females (Wearmouth *et al.* 2012) or sex-specific dietary preferences (McCord and Campana 2003), and the results of the present study suggest that sex-specific behaviour may be innate. The latter hypothesis could be verified by future studies examining differences in diet between the sexes.

Analysis of movements based on acoustic telemetry requires several assumptions to be made regarding equipment performance and cessation of detections from tagged animals. In contrast with other studies (Gjelland and Hedger 2013; Mathies *et al.* 2014; Huveneers *et al.* 2016), we found no evidence of temporal variations in receiver performance due to ambient noise from wind or rain or changes in air pressure or water temperature. Because movement and behaviour were not observed directly, an abrupt end in detections could have resulted from premature transmitter failure, tagging-associated mortality (predation or transmitter expulsion), natural or fishing mortality and dispersal of the tagged animal from the study area. Characteristic detection patterns indicated natural mortality of two *N. acutidens*, which were assumed to have died or been consumed close to a receiver after 65 and 17 days of tagging, resulting in the tag being continuously detected by one or more overlapping receivers. There was also one instance of fishing mortality, with one *N. acutidens* recaptured by recreational fishers. High rates of wound healing and survival of internally tagged individuals of our two focal species (Buray *et al.* 2009; Filmalter *et al.* 2013; Chin *et al.* 2015) and multiple recaptures of sharks between 2 and 19 days from release (17%) indicated that declines in detections of tagged sharks likely reflect dispersal to other sites, high rates of natural or fishing mortality or a combination of both, rather than tagging mortality.

Conservation and management

No-take zones in the present study encompassed large proportions (>70%) of total space use areas for neonate populations of *N. acutidens* and, to a lesser extent, *C. melanopterus* and provide some support for the use of small-scale no-take MPAs for effective management of the vulnerable, early life stages of carcharhinids (Garla *et al.* 2006; Heupel *et al.* 2010). To effectively protect mobile species, no-take zones should ideally be at least twice the size of the 95% KA of focal species (Green *et al.* 2015). Although total space use estimates of both species are largely encompassed by existing no-take zones, there was evidence of short-term residency and declining spatial protection for neonate *C. melanopterus* when their TL exceeded 60 cm, thus supporting our hypothesis of lower protection for larger-sized sharks of this species. Conversely, protection afforded by no-take zones was fairly consistent with increasing TL of neonate *N. acutidens.* A previous study suggested considerable rates of recapture (4.2%) of tagged reef sharks by recreational fishers in the NMP (Speed *et al.* 2016), indicating that areas within (Smallwood *et al.* 2012) or adjacent to no-take zones may still be vulnerable to anthropogenic effects. A southward extension of the Mangrove Bay no-take zone would enhance protection for neonate populations of *C. melanopterus* and *N. acutidens*. The results of the present study indicate that similar scale no-take zones may provide some protection for other neonate populations of *C. melanopterus* along the Ningaloo Reef coast and increase species resilience at seascape scales (Mumby 2006).

Given that Ningaloo Reef extends over 320 km of coastline, it is unlikely that Mangrove Bay is the only potential nursery, although equivalent habitats with fringing mangroves are rare along this coastline (Smallwood *et al.* 2012). Future work should focus on the identification of other potential nursery or pupping locations and possible connectivity between these nurseries.

The short-term residency and higher dispersal capacity of *C. melanopterus* seen in this study and elsewhere (Chin *et al.* 2013, 2016) suggest that this species is able to use a wider variety of habitats for development than *N. acutidens*, particularly shallow reef environments within the region (Vanderklift *et al.* 2014). In contrast, the intensive use of small areas by *N. acutidens* has implications for the vulnerability of the species due to increased exposure to coastal threats, such as fisheries, pollution and habitat loss or degradation (Knip *et al.* 2010). The International Union for the Conservation of Nature has currently classified *C. melanopterus* as 'Near Threatened' globally (Heupel 2009) and *N. acutidens* as 'Least Concern' in Australia but 'Vulnerable' globally (Pillans 2003), providing opportunity to protect one of the last strongholds for the species. Although we have identified potential drivers of space use and residency for *C. melanopterus* and *N. acutidens* in their natal environments, further studies of reef shark movement and behaviour involving an expanded acoustic array, active tracking in shallow microhabitat, standardized surveys and genetic assessment of parentage (Mourier and Planes 2013; Mourier *et al.* 2013*b*) will help clarify the significance of particular nursery habitats for population maintenance in contiguous coastal systems.

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References

Bancroft, K. P. (2003). A standardised classification scheme for the mapping of shallow-water marine habitats in Western Australia. Report MCB-05/2003, Department of Conservation and Land Management, Perth, WA, Australia.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., and White, J. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**, 127–135. doi:10.1016/J.TREE.2008.10.008

Buray, N., Mourier, J., Planes, S., and Clua, E. (2009). Underwater photo-identification of sicklefin lemon sharks, *Negaprion acutidens*, at Moorea (French Polynesia). *Cybium* **33**, 21–27.

Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach.' (Springer: New York, NY, USA.)

Calenge, C. (2015). Home range estimation in R: the adehabitatHR package, ver. 1-60. Available at https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf [Verified 1 March 2017].

CALM and MPRA (2005).Western Australia Management plan for the Ningaloo Marine Park and Muiron Islands marine managament area 2005–2015. Management Plan 52, Department of Conservation and Land Management and Marine Parks and Reserves Authority, Perth, WA, Australia.

Cerutti-Pereyra, F., Thums, M., Austin, C. M., Bradshaw, C. J. A., Stevens, J. D., Babcock, R., Pillans, R., and Meekan, M. G. (2014). Restricted movements of juvenile rays in a nursery area at Ningaloo Reef, Western Australia – evidence for the existence of a nursery. *Environmental Biology of Fishes* **97**, 371–383. doi:10.1007/S10641-013-0158-Y

Chapman, D. D., Babcock, E. A., Gruber, S. H., Dibattista, J. D., Franks, B. R., Kessel, S. A., Guttridge, T., Pikitch, E. K., and Feldheim, K. A. (2009). Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. *Molecular Ecology* **18**, 3500–3507. doi:10.1111/J.1365-294X.2009.04289.X

Chin, A., Kyne, P. M., Walker, T. I., and McAuley, R. B. (2010). An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology* **16**, 1936–1953. doi:10.1111/J.1365-2486.2009.02128.X

Chin, A., Tobin, A., Simpfendorfer, C., and Heupel, M. (2012). Reef sharks and inshore habitats: patterns of occurrence and implications for vulnerability. *Marine Ecology Progress Series* **460**, 115–125. doi:10.3354/MEPS09722

Chin, A., Heupel, M., Simpfendorfer, C., and Tobin, A. (2013). Ontogenetic movements of juvenile blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and coral reefs. *Aquatic Conservation* **23**, 468–474. doi:10.1002/AQC.2349

Chin, A., Mourier, J., and Rummer, J. L. (2015). Blacktip reef sharks (*Carcharhinus melanopterus*) show high capacity for wound healing and recovery following injury. *Conservation Physiology* **3**(1), cov062. doi:10.1093/CONPHYS/COV062

Chin, A., Heupel, M. R., Simpfendorfer, C. A., and Tobin, A. J. (2016). Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. *Marine Ecology Progress Series* **544**, 197–211. doi:10.3354/MEPS11545

Conrath, C. L., and Musick, J. A. (2008). Investigations into depth and temperature habitat utilization and overwintering grounds of juvenile sandbar sharks, *Carcharhinus plumbeus*: the importance of near shore North Carolina waters. *Environmental Biology of Fishes* **82**, 123–131. doi:10.1007/S10641-007-9263-0

Conrath, C. L., and Musick, J. A. (2010). Residency, space use and movement patterns of juvenile sandbar sharks (*Carcharhinus plumbeus*) within a Virginia summer nursery area. *Marine and Freshwater Research* **61**, 223–235. doi:10.1071/MF09078

Cortés, E. (2002). Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology* **16**, 1048–1062. doi:10.1046/J.1523-1739.2002.00423.X

DeAngelis, B. M., McCandless, C. T., Kohler, N. E., Recksiek, C. W., and Skomal, G. B. (2008). First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. *Marine Ecology Progress Series* **358**, 257–271. doi:10.3354/MEPS07308

Dicken, M., Booth, A., Smale, M., and Cliff, G. (2007). Spatial and seasonal distribution patterns of juvenile and adult raggedtooth sharks (*Carcharias taurus*) tagged off the east coast of South Africa. *Marine and Freshwater Research* **58**, 127–134. doi:10.1071/MF06018

DiGirolamo, A. L., Gruber, S. H., Pomory, C., and Bennett, W. A. (2012). Diel temperature patterns of juvenile lemon sharks *Negaprion brevirostris*, in a shallow-water nursery. *Journal of Fish Biology* **80**, 1436–1448. doi:10.1111/J.1095-8649.2012.03263.X

Dormann, C., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J., Gruber, B., Lafourcade, B., Leitão, P., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., and Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46. doi:10.1111/J.1600-0587.2012.07348.X

Duncan, K. M., and Holland, K. N. (2006). Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. *Marine Ecology Progress Series* **312**, 211–221. doi:10.3354/MEPS312211

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T. F., Berkhout, J., Buxton, C. D., Campbell, S. J., Cooper, A. T., Davey, M., Edgar, S. C., Försterra, G., Galván, D. E., Irigoyen, A. J., Kushner, D. J., Moura, R., Parnell, P. E., Shears, N. T., Soler, G. A., Strain, E. M. A., and Thomson, R. J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220. doi:10.1038/NATURE13022

Escalle, L., Speed, C. W., White, W. T., Babcock, R. B., Pillans, R. P., and Huveneers, C. (2015). Restricted movements and mangrove dependency of the nervous shark *Carcharhinus cautus* in nearshore coastal waters. *Journal of Fish Biology* **87**, 323–341. doi:10.1111/JFB.12724

Ferreira, L. C., Thums, M., Meeuwig, J. J., Vianna, G. M. S., Stevens, J., McAuley, R., and Meekan, M. G. (2015). Crossing latitudes – long-distance tracking of an apex predator. *PLoS One* **10**(2), e0116916. doi:10.1371/JOURNAL.PONE.0116916

Field, I. C., Meekan, M. G., Buckworth, R. C., and Bradshaw, C. J. A. (2009). Chapter 4. Susceptibility of sharks, rays and chimaeras to global extinction. *Advances in Marine Biology* **56**, 275–363. doi:10.1016/S0065-2881(09)56004-X

Filmalter, J. D., Dagorn, L., and Cowley, P. D. (2013). Spatial behaviour and site fidelity of the sicklefin lemon shark *Negaprion acutidens* in a remote Indian Ocean atoll. *Marine Biology* **160**(9), 2425–2436. doi:10.1007/S00227-013-2237-1

Friedlander, A. M., and Monaco, M. E. (2007) Acoustic tracking of reef fishes to elucidate habitat utilization patterns and residence times inside and outside marine protected areas around the Island of St John, USVI. Technical Memorandum NOS NCCOS 61, National Oceanic and Atmospheric Administration, Silver Spring, MD, USA.

Frisch, A. J., Ireland, M., Rizzari, J. R., Lönnstedt, O. M., Magnenat, K. A., Mirbach, C. E., and Hobbs, J.-P. A. (2016). Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs* **35**(2), 459–472. doi:10.1007/S00338-016-1415-2

Froeschke, J., Stunz, G. W., and Wildhaber, M. L. (2010). Environmental influences on the occurrence of coastal sharks in estuarine waters. *Marine Ecology Progress Series* **407**, 279–292. doi:10.3354/MEPS08546

Garla, R. C., Chapman, D. D., Wetherbee, B. M., and Shivji, M. (2006). Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. *Marine Biology* **149**, 189–199. doi:10.1007/S00227-005-0201-4

Gjelland, K. O., and Hedger, R. D. (2013). Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods in Ecology and Evolution* **4**, 665–674. doi:10.1111/2041-210X.12057

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., Gleason, M. G., Mumby, P. J., and White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews of the Cambridge Philosophical Society* **90**, 1215–1247. doi:10.1111/BRV.12155

Grubbs, R. D., and Musick, J. A. (2007). Spatial delineation of summer nursery areas for juvenile sandbar sharks in Chesapeake Bay, Virginia. *American Fisheries Society Symposium* **50**, 63–85.

Gruber, S. H., de Marignac, J. R. C., and Hoenig, J. M. (2001). Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. *Transactions of the American Fisheries Society* **130**, 376–384. doi:10.1577/1548-8659(2001)130<0376:SOJLSA>2.0.CO;2

Guttridge, T., Gruber, S., Gledhill, K., Croft, D., Sims, D., and Krause, J. (2009). Social preferences of juvenile lemon sharks, *Negaprion brevirostris. Animal Behaviour* **78**, 543–548. doi:10.1016/J.ANBEHAV.2009.06.009

Guttridge, T. T. L., Gruber, S. H., Franks, B. R., Kessel, S. T., Gledhill, K. S., Uphill, J., Krause, J., and Sims, D. W. (2012). Deep danger: intraspecific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris. Marine Ecology Progress Series* **445**, 279–291. doi:10.3354/MEPS09423

Guttridge, T. L., van Dijk, S., Stamhuis, E. J., Krause, J., Gruber, S. H., and Brown, C. (2013). Social learning in juvenile lemon sharks, *Negaprion brevirostris. Animal Cognition* **16**, 55–64. doi:10.1007/S10071-012-0550-6

Heithaus, M. R. (2007). Nursery areas as essential shark habitats: a theoretical perspective. *American Fisheries Society Symposium* **50**, 3–13.

Heupel, M. (2009). *Carcharhinus melanopterus* (blacktip reef shark). In 'The IUCN Red List of Threatened Species', ver. 3.1, e.T39375A10219032. (International Union for Conservation of Nature and Natural Resources.) Available at http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T39375A10219032.en [Verified 29 March 2017].

Heupel, M., and Simpfendorfer, C. (2002). Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 624–632. doi:10.1139/F02-036

Heupel, M. R., and Simpfendorfer, C. A. (2005). Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology* **147**, 1239–1249. doi:10.1007/S00227-005-0004-7

Heupel, M. R., and Simpfendorfer, C. A. (2008). Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology* **1**, 277–289. doi:10.3354/AB00030

Heupel, M. R., Simpfendorfer, C. A., and Hueter, R. E. (2003). Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. *Journal of Fish Biology* **63**, 1357–1363. doi:10.1046/J.1095-8649.2003.00250.X

Heupel, M. R., Simpfendorfer, C. A., and Hueter, R. E. (2004). Estimation of shark home ranges using passive monitoring techniques. *Environmental Biology of Fishes* **71**, 135–142. doi:10.1023/B:EBFI.0000045710.18997.F7

Heupel, M. R., Carlson, J. K., and Simpfendorfer, C. A. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* **337**, 287–297. doi:10.3354/MEPS337287

Heupel, M. R., Simpfendorfer, C. A., and Fitzpatrick, R. (2010). Large-scale movement and reef fidelity of grey reef sharks. *PLoS One* **5**, e9650. doi:10.1371/JOURNAL.PONE.0009650

Hight, B. V., and Lowe, C. G. (2007). Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? *Journal of Experimental Marine Biology and Ecology* **352**, 114–128. doi:10.1016/J.JEMBE.2007.07.021

Horne, J. S., Garton, E. O., Krone, S. M., and Lewis, J. S. (2007). Analyzing animal movements using Brownian bridges. *Ecology* **88**, 2354–2363. doi:10.1890/06-0957.1

Hussey, N. E., Mccarthy, I. D., Dudley, S. F. J., and Mann, B. Q. (2009). Nursery grounds, movement patterns and growth rates of dusky sharks, *Carcharhinus obscurus*: a long-term tag and release study in South African waters. *Marine and Freshwater Research* **60**, 571–583. doi:10.1071/MF08280

Huveneers, C., Simpfendorfer, C. A., Kim, S., Semmens, J. M., Hobday, A. J., Pederson, H., Stieglitz, T., Vallee, R., Webber, D., Heupel, M. R., Peddemors, V., and Harcourt, R. G. (2016). The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution* **7**, 825–835. doi:10.1111/2041-210X.12520

Keeney, D. B., Heupel, M. R., Hueter, R. E., and Heist, E. J. (2005). Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. *Molecular Ecology* **14**, 1911–1923. doi:10.1111/J.1365-294X.2005.02549.X

Kessel, S. T., and Hussey, N. E. (2015). Tonic immobility as an anaesthetic for elasmobranchs during surgical implantation procedures. *Canadian Journal of Fisheries and Aquatic Sciences* **72**, 1287–1291. doi:10.1139/CJFAS-2015-0136

Kessel, S., Chapman, D., Franks, B., Gedamke, T., Gruber, S., Newman, J., White, E., and Perkins, R. (2014). Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). *Marine Ecology Progress Series* **514**, 175–190. doi:10.3354/MEPS10966

Kinney, M. J., Hussey, N. E., Fisk, A. T., Tobin, A. J., and Simpfendorfer, C. A. (2011). Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. *Marine Ecology Progress Series* **439**, 263–276. doi:10.3354/MEPS09327

Knip, D. M., Heupel, M. R., and Simpfendorfer, C. A. (2010). Sharks in nearshore environments: models, importance, and consequences. *Marine Ecology Progress Series* **402**, 1–11. doi:10.3354/MEPS08498

Knip, D. M., Heupel, M. R., Simpfendorfer, C. A., Tobin, A. J., and Moloney, J. (2011). Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. *Marine Ecology Progress Series* **425**, 233–246. doi:10.3354/MEPS09006

Last, P. R., and Stevens, J. D. (2009) 'Sharks and Rays of Australia.' (CSIRO Publishing: Melbourne, Vic., Australia.)

Legare, B., Kneebone, J., DeAngelis, B., and Skomal, G. (2015). The spatiotemporal dynamics of habitat use by blacktip (*Carcharhinus limbatus*) and lemon (*Negaprion brevirostris*) sharks in nurseries of St. John, United States Virgin Islands. *Marine Biology* **162**, 699–716. doi:10.1007/S00227-015-2616-X

Leprovost Dames, N., and Moore, N. (2000). Ningaloo Marine Park (Commonwealth Waters) - Literature review. Environment Australia, Department of the Environment, Canberra, ACT, Australia.

Lovelock, C. E., Feller, I. C., Adame, M. F., Reef, R., Penrose, H. M., Wei, L., and Ball, M. C. (2011). Intense storms and the delivery of materials that relieve nutrient limitations in mangroves of an arid zone estuary. *Functional Plant Biology* **38**, 514–522. doi:10.1071/FP11027

Lucifora, L. O., García, V. B., and Worm, B. (2011). Global diversity hotspots and conservation priorities for sharks. *PLoS One* **6**, e19356. doi:10.1371/JOURNAL.PONE.0019356

Mathies, N. H., Ogburn, M. B., McFall, G., and Fangman, S. (2014). Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Marine Ecology Progress Series* **495**, 27–38. doi:10.3354/MEPS10582

Matich, P., and Heithaus, M. R. (2015). Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). *Oecologia* **178**, 347–359. doi:10.1007/S00442-015-3253-2

McCord, M. E., and Campana, S. E. (2003). A quantitative assessment of the diet of the blue shark (*Prionace glauca*) off Nova Scotia, Canada. *Journal of Northwest Atlantic Fishery Science* **32**, 57–63. doi:10.2960/J.V32.A4

Mourier, J., and Planes, S. (2013). Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. *Molecular Ecology* **22**, 201–214. doi:10.1111/MEC.12103

Mourier, J., Vercelloni, J., and Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. *Animal Behaviour* **83**, 389–401. doi:10.1016/J.ANBEHAV.2011.11.008

Mourier, J., Buray, N., Schultz, J. K., Clua, E., and Planes, S. (2013*a*). Genetic network and breeding patterns of a sicklefin lemon shark (*Negaprion acutidens*) population in the Society Islands, French Polynesia. *PLoS One* **8**, e73899. doi:10.1371/JOURNAL.PONE.0073899

Mourier, J., Mills, S. C., and Planes, S. (2013*b*). Population structure, spatial distribution and life-history traits of blacktip reef sharks *Carcharhinus melanopterus. Journal of Fish Biology* **82**, 979–993. doi:10.1111/JFB.12039

Mumby, P. J. (2006). Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. *Biological Conservation* **128**, 215–222. doi:10.1016/J.BIOCON.2005.09.042

Munroe, S. E. M., Simpfendorfer, C. A., and Heupel, M. R. (2014). Habitat and space use of an abundant nearshore shark, *Rhizoprionodon taylori. Marine and Freshwater Research* **65**, 959–968. doi:10.1071/MF13272

Munroe, S. E. M., Simpfendorfer, C. A., Moloney, J., and Heupel, M. R. (2015). Nearshore movement ecology of a medium-bodied shark, the creek whaler *Carcharinus fitroynensis*. *Animal Biotelemetry* **3**, 10. doi:10.1186/S40317-015-0026-Y

Munroe, S. E. M., Simpfendorfer, C. A., and Heupel, M. R. (2016). Variation in blacktip shark movement patterns in a tropical coastal bay. *Environmental Biology of Fishes* **99**, 377–389. doi:10.1007/S10641-016-0480-2

Norton, S. L., Wiley, T. R., Carlson, J. K., Frick, A. L., Poulakis, G. R., and Simpfendorfer, C. A. (2012). Designating critical habitat for juvenile endangered smalltooth sawfish in the United States. *Marine and Coastal Fisheries* **4**, 473–480. doi:10.1080/19425120.2012.676606

Papastamatiou, Y. P., Wetherbee, B. M., Lowe, C. G., and Crow, G. L. (2006). Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series* **320**, 239–251. doi:10.3354/MEPS320239

Papastamatiou, Y. P., Lowe, C. G., Caselle, J. E., and Friedlander, A. M. (2009). Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology* **90**, 996–1008. doi:10.1890/08-0491.1

Papastamatiou, Y. P., Friedlander, A. M., Caselle, J. E., and Lowe, C. G. (2010). Long-term movement patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll. *Journal of Experimental Marine Biology and Ecology* **386**, 94–102. doi:10.1016/J.JEMBE.2010.02.009

Papastamatiou, Y. P., Cartamil, D. P., Lowe, C. G., Meyer, C. G., Wetherbee, B. M., and Holland, K. N. (2011). Scales of orientation, directed walks and movement path structure in sharks. *Journal of Animal Ecology* **80**, 864–874. doi:10.1111/J.1365-2656.2011.01815.X

Papastamatiou, Y. P., Watanabe, Y. Y., Bradley, D., Dee, L. E., Weng, K., Lowe, C. G., and Caselle, J. E. (2015). Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? *PLoS One* **10**, e0127807. doi:10.1371/JOURNAL.PONE.0127807

Payne, N. L., Gillanders, B. M., Webber, D. M., and Semmens, J. M. (2010). Interpreting diel activity patterns from acoustic telemetry: the need for controls. *Marine Ecology Progress Series* **419**, 295–301. doi:10.3354/MEPS08864

Pillans, R. (2003). *Negaprion acutidens* (sharptooth lemon shark). In 'The IUCN Red List of Threatened Species', ver. 3.1, e.T41836A10576957. (International Union for Conservation of Nature and Natural Resources.) Available at http://dx.doi.org/10.2305/IUCN.UK.2003.RLTS.T41836A10576957.en [Verified 23 February 2017].

Pillans, R. D., Bearham, D., Boomer, A., Downie, R. A., Patterson, T. A., Thomson, D. P., and Babcock, R. C. (2014). Multi year observations reveal variability in residence of a tropical demersal fish, *Lethrinus nebulosus*: implications for spatial management. *PLoS One* **9**, e105507. doi:10.1371/JOURNAL.PONE.0105507

Pincock, D. G. (2012). False detections: what they are and how to remove them from detection data. Application Note DOC-004691–03, Amirix Systems Inc., Halifax, NS, Canada.

Rizzari, J. R., Frisch, A. J., and Magnenat, K. A. (2014). Diversity, abundance, and distribution of reef sharks on outer-shelf reefs of the Great Barrier Reef, Australia. *Marine Biology* **161**, 2847–2855. doi:10.1007/S00227-014-2550-3

Schofield, G., Scott, R., Dimadi, A., Fossette, S., Katselidis, K. A., Koutsoubas, D., Lilley, M. K. S. S., Pantis, J. D., Karagouni, A. D., Hays, G. C., Katselidis, K. A., Koutsoubas, D., Lilley, M. K. S. S., Pantis, J. D., Karagouni, A. D., and Hays, G. C. (2013). Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. *Biological Conservation* **161**, 101–109. doi:10.1016/J.BIOCON.2013.03.004

Simpfendorfer, C. A., Heupel, M. R., and Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 23–32. doi:10.1139/F01-191

Smallwood, C. B., Beckley, L. E., and Moore, S. A. (2012). Influence of zoning and habitats on the spatial distribution of recreational activities in a multiple-use marine park. *Coastal Management* **40**, 381–400. doi:10.1080/08920753.2012.692312

Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., Stevens, J. D., McGregor, F., Huveneers, C., Berger, Y., and Bradshaw, C. J. A. (2011). Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Marine Ecology Progress Series* **429**, 261–275. doi:10.3354/MEPS09080

Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., Abrantes, K., and Bradshaw, C. J. A. (2012). Trophic ecology of reef sharks determined using stable isotopes and telemetry. *Coral Reefs* **31**, 357–367. doi:10.1007/S00338-011-0850-3

Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., Harcourt, R. G., Stevens, J. D., Babcock, R. C., Pillans, R. D., and Bradshaw, C. J. A. (2016). Reef shark movements relative to a coastal marine protected area. *Regional Studies in Marine Science* **3**, 58–66. doi:10.1016/J.RSMA.2015.05.002

Stevens, J. D. (1984). Life-history and ecology of sharks at Aldabra atoll, Indian Ocean. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **222**, 79–106. doi:10.1098/RSPB.1984.0050

Stevens, J. D., Last, P. R., White, W. T., Mcauley, R. B., and Meekan, M. G. (2009). Diversity, abundance and habitat utilisation of sharks and rays. Final Report, Western Australian Marine Science Institute, Perth, WA, Australia.

Strauss, R. E. (1979). Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* **108**, 344–352. doi:10.1577/1548-8659(1979)108<344:REFIEI>2.0.CO;2

Udyawer, V., Chin, A., Knip, D. M., Simpfendorfer, C. A., and Heupel, M. R. (2013). Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. *Marine Ecology Progress Series* **480**, 171–183. doi:10.3354/MEPS10244

Vanderklift, M., Boschetti, F., Roubertie, C., Pillans, R., Haywood, M., and Babcock, R. (2014). Density of reef sharks estimated by applying an agent-based model to video surveys. *Marine Ecology Progress Series* **508**, 201–209. doi:10.3354/MEPS10813

Wearmouth, V. J., Southall, E. J., Morritt, D., Thompson, R. C., Cuthill, I. C., Partridge, J. C., and Sims, D. W. (2012). Year-round sexual harassment as a behavioral mediator of vertebrate population dynamics. *Ecological Monographs* **82**, 351–366. doi:10.1890/11-2052.1

Wetherbee, B. M., Gruber, S. H., and Rosa, R. S. (2007). Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. *Marine Ecology Progress Series* **343**, 283–293. doi:10.3354/MEPS06920

Wood, L. J., Fish, L., Laughren, J., and Pauly, D. (2008). Assessing progress towards global marine protection targets: shortfalls in information and action. *Oryx* **42**, 340–351. doi:10.1017/S003060530800046X

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J., and Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**, 787–790. doi:10.1126/SCIENCE.1132294

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https://doi.org/10.1071/MF16131_AC

Supplementary material

Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery

Beverly Z. L. Oh[A,B,C,E], *Michele Thums*[B,C], *Russ C. Babcock*[D], *Jessica J. Meeuwig*[A],
Richard D. Pillans[D], *Conrad Speed*[B,C] *and Mark G. Meekan*[B,C]

[A]Centre for Marine Futures, School of Biological Sciences and Oceans Institute,
The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.

[B]Australian Institute of Marine Science, The University of Western Australia, 39 Fairway,
Crawley WA 6009, Australia.

[C]Indian Ocean Marine Research Centre, The University of Western Australia, 39 Fairway,
Crawley WA 6009, Australia.

[D]CSIRO Oceans and Atmosphere, Ecosciences Precinct, GPO Box 2583,
Brisbane, Qld 4001, Australia.

[E]Corresponding author. Email: beverly.oh@gmail.com

Methods

Variables influencing receiver efficiency

To examine environmental effects on monthly patterns of detection efficiency of two acoustic receivers placed 1 and 153 m from a V13–1H sentinel transmitter, we compiled a suite of explanatory variables including water temperature, air pressure, rainfall, tidal height, wind speed and direction, month, sex and total length of shark (Table 1 in the main paper). Water temperature was recorded at Tantabiddi using HOBO Pro V2 data loggers (U22-001; HOBO Data Loggers Australia, Adelaide, South Australia) calibrated at the Australian Institute Marine Science; AIMS and sampling at 30-min intervals, which were periodically downloaded and replaced every 3–12 months. Daily values for air pressure (hPa), rainfall totals (mm), wind speed (m s^{-1}) and direction (degrees) were obtained from a weather station at Milyering (10-m elevation; 22.03°S, 113.92°E) situated 6.8 km south of Mangrove Bay (http://data.aims.gov.au/, accessed 7 October 2015). Predicted tidal height data were obtained through the Regional Oceanic Modelling System (https://www.myroms.org/, accessed 4 November 2015). Values of monthly mean and range were computed for all variables from November 2013 to January 2015 and chronologically matched with detection data of the sentinel tag across the monitoring period. We used generalized additive mixed models (GAMMs) with binomial error distributions to model detection probability. We modelled month as a random effect in all models and fitted all environmental variables with a cubic regression spline, restricting the basis dimension 'k' to < 4 to avoid overfitting. A maximum of one fixed term per model was specified due to fairly small sample sizes ($n = 12$). This resulted in a set of 11 candidate models (Table S2) which were ranked according to the sample-corrected Akaike's Information Criterion (AIC_C) and relative AIC_C weight ($wAIC_C$).

Results

Variables influencing receiver efficiency

Atmospheric pressure, water temperature, rainfall, wind speed and direction were not found to be important drivers of receiver performance (Table S2). Therefore, we found no evidence that the monthly patterns in residency and space use of tagged sharks in our study were an artefact of ambient noise from wind or rain or changes in air pressure or water temperature. We found the highest statistical support for model 7 ($wAIC_C = 1$), which showed a negative influence of tidal height on detection probabilities of the station located 1 m from the sentinel tag, and model 8 ($wAIC_C = 1$), which showed negative influence of tidal range on detection probabilities of the station located 153 m from the sentinel tag (Table S2; Fig. S2).

Table S1. Summary of the location, habitat type and detections of the acoustic receivers deployed in the Mangrove Bay array

Receiver	Longitude	Latitude	Deployment		Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
			Start	End					
Tantabiddi									
1	–21.899	113.937	01-Mar-14	01-Jun-15	Coral reef		1	1	0.00
2	–21.909	113.944	19-Mar-13	01-Jun-15	Coral reef		1	17	0.00
3	–21.911	113.948	19-Mar-13	01-Jun-15	Coral reef		1	4	0.00
4	–21.915	113.956	01-Mar-14	19-Oct-14	Sandflat		1	0	0.00
5	–21.912	113.952	19-Mar-13	01-Jun-15	Rocky reef		1	1	0.00
6	–21.916	113.959	19-Mar-13	01-Jun-15	Sandflat		1	4	0.00
7	–21.918	113.963	19-Mar-13	01-Jun-15	Rocky reef		1	4	0.00
8	–21.920	113.967	19-Mar-13	01-Jun-15	Rocky reef		1	12	0.00
Mangrove bay									
9	–21.948	113.921	19-Mar-13	01-Jun-15	Coral reef	SZ	2	20	0.00
10	–21.949	113.926	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	0	0.00
11	–21.948	113.933	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	0	0.00
12	–21.948	113.939	19-Mar-13	01-Jun-15	Coral reef	SZ	2	0	0.00
13	–21.950	113.944	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	65	0.01
14	–21.957	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	970	0.19
15	–21.959	113.944	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	1845	0.36
16	–21.960	113.940	25-Mar-13	01-Jun-15	Algal reef	SZ	2	764	0.15
17	–21.961	113.943	25-Mar-13	31-May–15	Rocky reef	SZ	2	2322	0.46
18	–21.962	113.945	26-Mar-13	31-May–15	Rocky reef	SZ	2	4615	0.91
19	–21.962	113.934	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	231	0.05
20	–21.963	113.940	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	6707	1.33
21	–21.963	113.942	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	30593	6.05
22	–21.964	113.939	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	2018	0.40
23	–21.965	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	4006	0.79
24	–21.966	113.939	08-Dec-14	31-May–15	Rocky reef	SZ	2	112	0.02
25	–21.967	113.941	19-Mar-13	31-May–15	Rocky reef	SZ	2	5673	1.12
26	–21.967	113.936	19-Mar-13	01-Jun-15	Algal reef	SZ	2	2729	0.54

Receiver	Longitude	Latitude	Deployment		Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
			Start	End					
27	–21.968	113.939	19-Mar-13	01-Jun-15	Sandflat	SZ	2	4407	0.87
28	–21.969	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	39054	7.72
29	–21.969	113.938	19-Mar-13	31-May–15	Sandflat	SZ	2	135477	26.79
30	–21.974	113.941	19-Mar-13	31-May–15	Sandflat	SZ	2	75768	14.98
31	–21.969	113.925	19-Mar-13	01-Jun-15	Coral reef	SZ	2	1582	0.31
32	–21.969	113.930	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	156	0.03
33	–21.972	113.919	19-Mar-13	01-Jun-15	Coral reef	SZ	2	92	0.02
34	–21.970	113.936	19-Mar-13	01-Jun-15	Sandflat	SZ	2	161182	31.87
35	–21.972	113.939	26-Mar-13	31-May–15	Mangrove	SZ	2	18401	3.64
36	–21.948	113.914	19-Mar-13	01-Jun-15	Coral reef		3	1	0.00
37	–21.956	113.913	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
38	–21.959	113.912	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
39	–21.966	113.910	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
40	–21.971	113.911	19-Mar-13	01-Jun-15	Coral reef		3	2	0.00
41	–21.972	113.902	19-Mar-13	24-May–13	Rocky reef		3	0	0.00
42	–21.973	113.911	19-Mar-13	01-Jun-15	Coral reef		3	1	0.00
43	–21.976	113.907	08-Mar-14	24-Oct-14	Rocky reef		3	0	0.00
44	–21.979	113.912	19-Mar-13	01-Jun-15	Coral reef		3	5	0.00
45	–21.980	113.902	08-Mar-14	01-Jun-15	Rocky reef		3	1	0.00
46	–21.984	113.904	08-Mar-14	24-Oct-14	Rocky reef		3	0	0.00
47	–21.983	113.908	08-Mar-14	01-Jun-15	Coral reef		3	0	0.00
48	–21.983	113.912	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
49	–21.989	113.902	19-Mar-13	02-Mar-14	Rocky reef		3	26	0.01
50	–21.989	113.909	19-Mar-13	22-Oct-14	Coral reef		3	1	0.00
51	–21.991	113.898	19-Mar-13	19-Oct-14	Rocky reef		3	6	0.00
52	–21.992	113.907	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
53	–21.998	113.905	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
54	–22.001	113.903	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
55	–22.005	113.902	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00

Receiver	Longitude	Latitude	Deployment Start	End	Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
56	−22.013	113.899	19-Mar-13	26-Oct-14	Coral reef		3	0	0.00
57	−21.975	113.924	19-Mar-13	01-Jun-15	Coral reef		4	763	0.15
58	−21.974	113.930	19-Mar-13	01-Jun-15	Algal reef		4	3144	0.62
59	−21.977	113.919	19-Mar-13	01-Jun-15	Coral reef		4	23	0.00
60	−21.980	113.921	19-Mar-13	01-Jun-15	Coral reef		4	13	0.00
61	−21.980	113.929	19-Mar-13	01-Jun-15	Sandflat		4	2119	0.42
62	−21.985	113.932	19-Mar-13	01-Jun-15	Coral reef		4	509	0.10
63	−21.986	113.919	19-Mar-13	01-Jun-15	Coral reef		4	1	0.00
64	−21.987	113.925	19-Mar-13	01-Jun-15	Coral reef		4	12	0.00
65	−21.988	113.923	02-Mar-14	01-Jun-15	Coral reef		4	0	0.00
66	−21.989	113.920	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
67	−21.989	113.915	19-Mar-13	01-Jun-15	Coral reef		4	2	0.00
68	−21.991	113.922	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
69	−21.991	113.931	19-Mar-13	01-Jun-15	Algal reef		4	183	0.04
70	−21.992	113.920	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
71	−21.994	113.925	19-Mar-13	01-Jun-15	Algal reef		4	13	0.00
72	−21.997	113.931	19-Mar-13	01-Jun-15	Rocky reef		4	45	0.01
73	−21.997	113.915	19-Mar-13	01-Jun-15	Coral reef		4	15	0.00
74	−21.999	113.921	19-Mar-13	01-Jun-15	Coral reef		4	6	0.00
75	−22.001	113.926	19-Mar-13	01-Jun-15	Coral reef		4	5	0.00
76	−22.005	113.912	19-Mar-13	01-Jun-15	Coral reef		4	4	0.00
77	−22.006	113.916	19-Mar-13	01-Jun-15	Rocky reef		4	12	0.00
78	−22.006	113.921	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
Turquoise bay									
79	−22.085	113.871	19-Mar-13	01-Jun-15	Rocky reef		6	0	0.00
80	−22.086	113.874	19-Mar-13	01-Jun-15	Rocky reef		6	0	0.00
81	−22.088	113.877	19-Mar-13	01-Jun-15	Coral reef		6	0	0.00
82	−22.089	113.880	19-Mar-13	01-Jun-15	Coral reef	SZ	5	0	0.00
83	−22.091	113.883	19-Mar-13	01-Jun-15	Coral reef	SZ	5	0	0.00

Receiver	Longitude	Latitude	Deployment Start	End	Habitat	MPA zoning	Site zoning	Total detections	Percentage detections
84	−22.093	113.886	19-Mar-13	01-Jun-15	Coral reef	SZ	5	4	0.00
85	−22.095	113.888	19-Mar-13	01-Jun-15	Coral reef	SZ	5	3	0.00

Table S2. Summary of the effects of environmental variables on detection probabilities recorded on acoustic receivers placed 1 m (receiver #30) and 153 m (receiver #28) from a sentinel transmitter used to monitor detection efficiency in Mangrove bay

Month was treated as a random effect in all models (m1, model 1; etc.); details for each model include the estimated degrees of freedom (d.f.$_e$), the Akaike's Information Criterion for small sample size (AIC$_C$), relative AICC weight (wAIC$_C$) and goodness of fit (Adjusted R^2). PressAV, mean air pressure; RainAV, mean cumulative rainfall; TempAV, mean water temperature; TempR, water temperature range; TideAV, mean tidal height; TideR, tidal height range; WdireAV, mean wind direction; WspeedAV, mean wind speed; WspeedR, wind speed range

Model number	Model	Receiver #30 d.f.$_e$	AIC$_C$	wAIC$_C$	Adjusted R^2	Receiver #28 d.f.$_e$	AIC$_C$	wAIC$_C$	Adjusted R^2
m1	1	0.00	5244.06	0	0	0	3938.69	0	0
m2	days.detected	9.87	4768.45	0	2.6	9.22	3853.48	0	21.4
m3	pressAV	2.76	5065.04	0	7.8	2.83	3892.54	0	5.1
m4	rainAV	1.90	5209.43	0	0.6	2.19	3852.26	0	0
m5	tempAV	2.89	5026.28	0	12.4	2.45	3931.24	0	1.8
m6	tempR	2.91	5189.72	0	0.4	0.43	3940.56	0	0.1
m7	tideAV	2.92	4185.76	0	27.6	2.96	3724.17	1	5.4
m8	tideR	2.92	3860.27	1	31.8	2.7	3770.69	0	2.4
m9	wdireAV	1.95	5186.17	0	0.8	1.74	3934.78	0	5.4
m10	wspeedAV	2.66	5238.57	0	0.4	2.9	3809.00	0	8.6
m11	wspeedR	2.31	5206.21	0	0.7	2.84	3925.91	0	0

Table S3. Summary of the effects of varying sig2 values on estimates of 50 and 95% kernel areas of one *N. acutidens* individual

Monthly tracks of the shark #L1, which had the median value for 50% kernel area, were used to estimate kernel area range

Sig2 value	Detection probability	Kernel area (KA) range	
		50% KA (km²)	95% KA (km²)
285.2	0.20	0.24–0.51	0.96–1.84
263.2	0.25	0.22–0.49	0.9–1.75
252.3	0.30	0.21–0.47	0.84–1.67
229.8	0.40	0.18–0.44	0.73–1.51
175.0	0.50	0.12–0.36	0.51–1.56
129.6	0.60	0.08–0.34	0.36–2.77
106.7	0.70	0.07–0.34	0.34–3.85
97.0	0.75	0.07–0.34	0.34–4.33
87.5	0.80	0.06–0.34	0.33–4.8

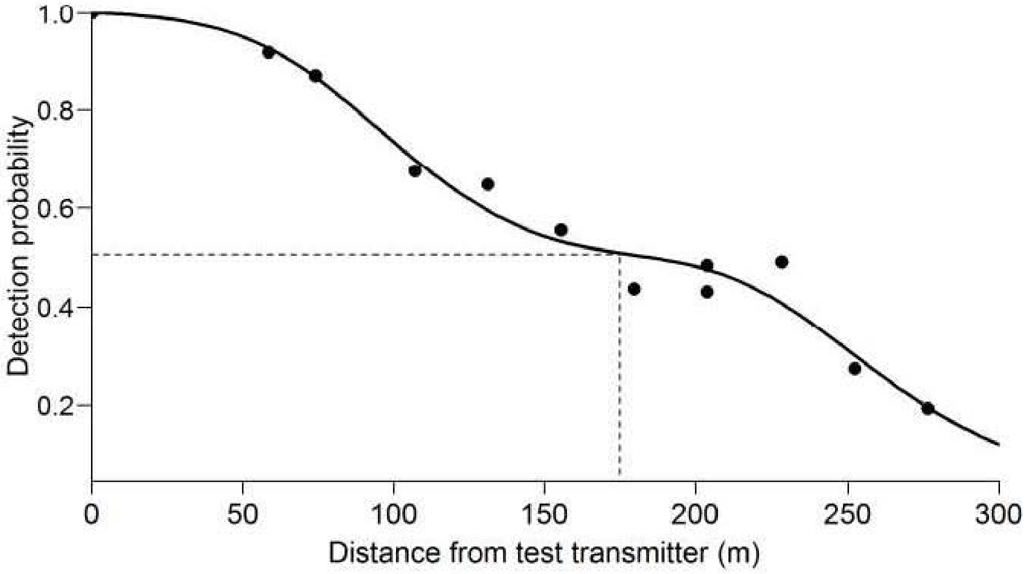

Fig. S1. Detection probabilities recorded on acoustic receivers placed at increasing distances from a test transmitter at Mangrove Bay in March 2013. Data were fitted using a loess smoothing curve and dashed lines represent the effective detection range at which 50% of the transmissions were detected (D_{50} = 175.0 m).

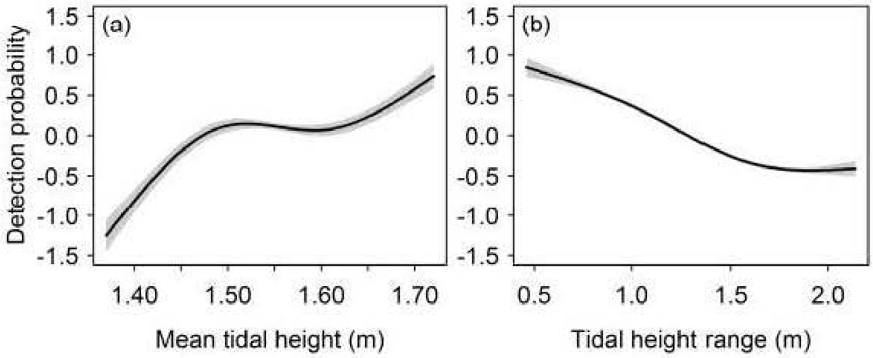

Fig. S2. Summary of the effects of explanatory variables on detection probabilities recorded on acoustic receivers located (*a*) 1 m and (*b*) 153 m from a sentinel tag placed within an area with highest shark activity. Dashed lines and error bars represent 95% confidence intervals.

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Habitat effects on home range and schooling behaviour in a herbivorous fish (*Kyphosus bigibbus*) revealed by acoustic tracking

R. D. Pillans[A], *R. C. Babcock*[A,D], *D. P. Thomson*[B], *M. D. E. Haywood*[A],
R. A. Downie[C], *M. A. Vanderklift*[B] *and W. A. Rochester*[A]

[A]CSIRO Marine and Atmospheric Research, GPO Box 2583, Brisbane, Qld 4001, Australia.
[B]CSIRO Marine and Atmospheric Research, Private Bag 5, Wembley, WA 6913, Australia.
[C]CSIRO Marine and Atmospheric Research, GPA Box 1538, Hobart, Tas. 7001, Australia.
[D]Corresponding author. Email: russ.babcock@csiro.au

Abstract. Large mobile herbivorous fish that specialise in browsing large brown algae are particularly important on coral reefs because their activities mediate algal–coral competition. Despite this important ecological role, we have a poor understanding of the movement patterns of such large herbivorous fish, including *Kyphosus bigibbus*. Nineteen *K. bigibbus* captured near adjacent but distinct patch reefs were tagged with internal acoustic tags and their movements monitored for up to 20 months by an array of 60 acoustic receivers. Home-range estimates showed that movements of individuals from each patch reef encompassed different spatial extents and resulted in differences in habitat used by the two groups of fish. The average 50 and 95% kernel utilisation distribution for long-term resident fish was 0.27 ± 0.03 and $1.61 \pm 0.30\ \text{km}^2$ respectively, ranges that represent the largest values for a herbivorous coral reef fish recorded to date. There was a significantly higher degree of fidelity among fish from the same school, and to particular patch reefs, despite the proximity of the reefs and substantial overlap between schools of conspecifics. A coefficient of sociality was used on pairs of fish and showed that there was no evidence that individuals were consistently detected together when they were detected by receivers away from their home reef. The variability of movement patterns among individuals of *K. bigibbus* results in an increased niche footprint for this important browser, potentially increasing reef resilience.

Additional keywords: acoustic telemetry, algae, coral reef, herbivorous fish, marine protected area, movement, Ningaloo Reef.

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Introduction

The removal of algae by herbivorous coral reef fish has been identified as a key process in maintaining reef resilience (Bellwood *et al.* 2004; Mumby *et al.* 2006; Hughes *et al.* 2007). Herbivorous coral reef fish are often classified into two functional groups, grazers and browsers (Horn 1989), but diet does not always reflect taxonomic relationships (Choat *et al.* 2002). Grazers primarily consume epilithic algal matrix (EAM), organic detritus and calcareous sediments and include scrapers, excavators and detritivores (Bellwood and Choat 1990; Choat *et al.* 2002). Browsers consume large brown algae and small foliose and filamentous red and green algae (Choat *et al.* 2002). Grazers and browsers play important roles in preventing phase shifts on coral reefs by consuming algae that would otherwise compete with corals. Grazers typically consume early life history stages of algae, like newly settled spores or zygotes and new recruits, and through this they can prevent the establishment of adult plants, whereas browsers consume adult plants and can prevent the overgrowth and shading of corals by large erect stands of macroalgae (McCook *et al.* 2001). Browsers may also reverse phase shifts if feeding intensity is sufficiently high (Bellwood *et al.* 2004).

Although the critical role that herbivorous fish play in maintaining or restoring high abundances of corals has been clearly demonstrated (McCook 1997; Bellwood *et al.* 2004; Hughes *et al.* 2007; Burkepile and Hay 2010; Vergés *et al.* 2011), the intensity of algal consumption by fish on coral reefs varies considerably. Habitat complexity, habitat type, the species composition of the fish assemblage, fish behaviour and the area studied can all affect rates of consumption (McCook 1997; Hoey and Bellwood 2008, 2010; Vergés *et al.* 2011; Michael *et al.* 2013). Studies investigating long-term movement patterns and habitat use of key herbivorous species are only recently beginning to provide insights into the spatial extents of movements and home ranges, and their relative importance in shaping coral reef ecosystems (Marshell *et al.* 2011; Welsh and Bellwood 2012*a*, 2012*b*, 2014). This information is essential to understanding how movements of individuals among different habitat types within and among reefs affect the relative abundance of corals and macroalgae, and ultimately the resilience of coral reefs to disturbance. However, compared with studies on coral reef predatory fish, there remain relatively few data on the movement patterns of large herbivorous species on coral reefs.

Rates of algal consumption, and by extension the abundance of erect macroalgae on both the Great Barrier Reef and Ningaloo Reef, is affected by the structural complexity of the surrounding reef, which appears to be a consequence of the availability of refugia from predatory fish (McCook 1997; Vergés *et al.* 2011; Downie *et al.* 2013). Vergés *et al.* (2011) and Downie *et al.* (2013) demonstrated that rates of consumption of tethered algae declined rapidly with distance from corals; the latter study demonstrated how this yields emergent patterns across the landscape, showing that algal biomass decreases rapidly with increasing distance from structurally complex *Porites*-dominated patch reefs. Therefore, the movement patterns and habitat use of herbivorous fish on coral reefs can have important implications to the functional processes at a landscape level.

Large-scale landscape changes in the form of areas largely devoid of macroalgae (termed 'halos') around patch reefs along the Ningaloo Reef system have been attributed primarily to *Kyphosus bigibbus* (previously identified as *Kyphosus sydneyanus*; Downie *et al.* 2013). The relatively small scale of these halos, together with video evidence showing that *K. bigibbus* are rarely observed at distances greater than 30 m from the patch reefs, suggest that this species may be confined to the protection offered by patch reefs (Downie *et al.* 2013). However, during underwater visual census (UVC) surveys of fish at Ningaloo Reef, this species has frequently been observed on the reef flat and reef slope (R. D. Pillans and R. C. Babcock, unpubl. data). These incongruent observations may indicate that there are separate schools of fish occupying distinct habitats, or that the fish that occupy the patch reefs move across greater distances than those implied by the size of the halos and video observations.

Ningaloo Reef hosts a high diversity and abundance of herbivorous fish (Vergés *et al.* 2011; Downie *et al.* 2013) and, of the few species that specialise in eating brown algae, the grey drummer *Kyphosus bigibbus* is among the most abundant (R. D. Pillans and R. C. Babcock, unpubl. data). *K. bigibbus* is a large species found on rocky and coral reefs, and is widespread in the tropical and subtropical Indo-west Pacific from South Africa to Australia and northern and southern Japan (Sakai 2003). Its diet consists primarily of brown algae, and diet composition is largely determined by the availability of algae in the surrounding habitat (Yatsuya *et al.* 2015). The species reaches a maximum size of 75-cm fork length (FL) and, along Ningaloo Reef, it is frequently observed in large schools of up to 200–400 individuals of similar size (50–65 cm FL). To further elucidate the role of this species in the resilience of tropical coral reefs, the aim of the present study was to investigate residency and movement patterns of *K. bigibbus* within the Ningaloo Reef, Western Australia. Specifically we aimed to: (1) investigate whether individuals tagged around patch reefs were resident or nomadic, and determine whether resident fish moved at scales greater than those implied by tethering experiments and algal biomass adjacent to these patch reefs; (2) estimate the home range of resident animals and compare home range estimates with other herbivorous coral reef fish; (3) investigate the effects of tide, time of day and season on home range and maximum linear distance (MLD) moved between receivers; (4) investigate the degree of overlap between fish tagged on adjacent patch reefs; (5) investigate the degree of schooling among individuals; and (6) investigate the relative importance of available habitat.

Materials and methods

Acoustic monitoring system

An array of acoustic receivers was located within and adjacent to the Mangrove Bay Sanctuary Zone in the Ningaloo Marine Park (695 ha). The array extended from ~1-m water depth near the shoreline to ~50-m water depth beyond the reef slope (Fig. 1). Receivers were spaced 200–800 m apart and detection ranges generally did not overlap (for a detailed description, see Pillans *et al.* 2014). The array encompassed multiple habitats, including mangrove-lined shores, limestone pavement, patch reefs dominated by *Porites* spp., extensive shallow coral reefs dominated by *Acropora* spp., sand and rock dominated by macroalgae (predominantly *Sargassum* spp. and other fucalean algae) within the lagoon. A near-continuous fringing reef creates a barrier to movement out of the lagoon at low tide and during times of high swell, but an adjacent reef pass provides direct access for fish to deeper reef slope waters. Several large *Porites*-dominated patch reefs are present within ~1 km of the reef pass (for a detailed description, see Downie *et al.* 2013). The reef slope consists of coral-dominated spur-and-groove habitat and limestone reef interspersed with sand. Beyond 35-m depth, the substratum is predominantly sandy sediment with occasional low relief limestone reef.

The Mangrove Bay array consisted of 50 acoustic receivers (VR2 and VR2W; VEMCO) from December 2007 to May 2008, and 60 acoustic receivers from May 2008 to May 2010 (see Pillans *et al.* 2014). In addition to the Mangrove Bay array, there were three cross-shelf lines of acoustic receivers extending from the reef slope (~12 m) to the 200-m isobath located along the Ningaloo Reef (http://animaltracking.aodn.org.au, accessed 8 December 2016; Fig. 1). Individual *K. bigibbus*, ranging in size from 49 to 66 cm TL, were internally tagged with VEMCO coded transmitters (tags; either V13-1H, V13-1L or V16-4H transmitters). The pulse rate of transmitters was either 60 or 180 s and battery life varied from 450 to 820 days. Range tests were conducted with the V9, V13 and V16 tags with power outputs encompassing the range used on grey drummer. Power output had little effect on detection range during testing and Pillans *et al.* (2014) demonstrated that tag type and power output (encompassing the range used on grey drummer) had negligible effects on movement parameters of spangled emperor tracked within the same array of receivers. Each successfully decoded pulse train was recorded as a single detection in the memory of the individual VR2 as the transmitter's identification number, date and time. Receivers were downloaded every 3–4 months throughout the study, and the batteries were changed at least every 6 months.

Capture and tagging

Capture and tagging of fish was conducted under CSIRO Brisbane Animal Ethics Permit (Permit A2/07). Fish were captured on

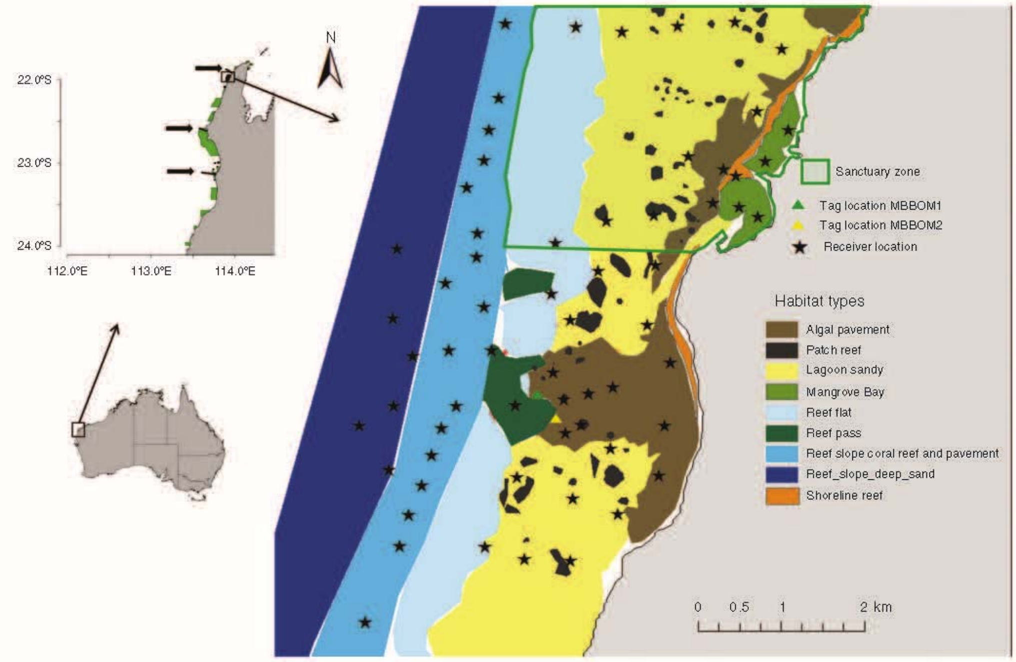

Fig. 1. Map showing Mangrove Bay array in relation to Australia and Ningaloo Marine Park Sanctuary Zones (green shading). All acoustic receivers are plotted as black dots, with the three cross shelf lines highlighted by arrows. The tag location of the two groups of fish is shown, with tag locations referring to the name of the receiver that fish were tagged at.

SCUBA using a 50-m-long barrier net with 44-mm stretched mesh between October 2008 and January 2009. Fish chosen for tagging were placed in a 120-L tub containing 30 mg L^{-1} of AQUI-S aquatic anaesthetic (Primo Aquaculture) in seawater. Fish remained in the tub until they reached Stage III anaesthesia (Iwama *et al.* 1989), at which time they were placed on their dorsal surface into a V-shaped piece of foam lined with plastic. After removing a few scales, a small incision was made slightly off the mid-line between the pelvic fins and anus. Transmitters that had been soaking in an antiseptic bath (povidone iodine and distilled water, 5 : 100) for at least 30 min were then inserted into the peritoneal cavity. Three dissolving sutures were used to close the wound. Following surgery, fish were measured and injected with a mass-dependent dose of Engemycin (MSD Animal Health; 100 mg mL^{-1} oxytetracycline) in the dorsal surface. Fish were allowed to recover in a 120-L tub filled with continuously replenished seawater. The average time from capture to completion of surgery was 6–7 min, whereas recovery times ranged from 15 to 30 min. Once fully recovered, fish were released at the site of capture.

Detection span and residency

For acoustic tags, the detection span of each tag was calculated as the date from first detection to last detection, whereas days detected was the total number of days on which each individual was detected. The percentage of days detected was calculated by dividing detection span by days detected multiplied by 100. The residency index (RI) was calculated as the number of days an individual was detected at least once in the array as a proportion of the total number of days over which it was monitored.

Home range measures

Kernel distribution was calculated for nine individuals that were detected for more than 30 days. (B1-08-01 was excluded from the analysis because it appeared to have died, being detected for 10 months but only by one receiver at the tagging location). Area utilisation was estimated using the utilisation distribution (Van Winkle 1975), which is a probability density function that quantifies an individual's relative use of space (Kernohan *et al.* 2001); it quantifies the probability of an animal occurring at a location within its home range based on a set of relocation points (data obtained from receiver detections; White and Garrott 1990). Kernel utilisation distribution (KUD) has been widely used to investigate animal movements from acoustic telemetry of a range of species ranging from marine turtles (Makowski *et al.* 2006; MacDonald *et al.* 2012) to dugongs (Zeh *et al.* 2015) and fish (Pillans *et al.* 2014). The bandwidth (or smoothing parameter; *h*) can greatly affect the shape and size of the kernel (Gitzen *et al.* 2006; Pillans *et al.* 2014). There is no single *a priori* method for determining the most appropriate bandwidth. Choice of bandwidth may vary depending on the study goals, sample size and patterns of space use by the study species (Worton 1989; Gitzen *et al.* 2006). In the present study, we set the bandwidth to 200 m ($h = 200$) based on range test data from stationary tags of varying power outputs within the array and compared this with the least-squares cross-validation function (h_{lscv}; Silverman 1986). This smoothing parameter ($h = 200$) provided the most realistic representation of space use, with h_{lscv} tending to produce unrealistic multiple kernels that were fragmented and clustered around receivers, excluding important areas occupied by grey drummer. KUD (50 and 95%) was calculated using the adehabitatHR package (Calenge 2011) in R (R Foundation for Statistical Computing, Vienna, Austria).

The behaviour of individuals was characterised by the 50% (core area) and 95% (total area) KUDs, which were calculated for all months combined, as well as for each month–year combination in which an individual was detected. To determine the effects of tide on movement and habitat use, 50 and 95% KUDs of each individual and all individuals combined were calculated during a period spanning 1 h each side of high and low tide for each month–year combination for the entire monitoring period. High and low tide times were obtained from the Western Australian Department of Transport. Diel differences were investigated by comparing the degree of overlap in 50 and 95% KUDs for day and night using local time of sunrise and sunset. The utilisation distribution overlap index (UDOI; Fieberg and Kochanny 2005) was used to measure the degree of overlap between KUDs of individual fish, the degree of overlap between day and night and high and low tide. In addition, as an index of the daily spatial extent of linear movement, we calculated maximum linear dispersal (MLD) as the distance between the two most widely separated receivers that individuals were detected on during each day. Differences in MLD during the day and night, and between seasons, were also evaluated. Season was classified as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November).

To investigate whether fish tagged at distinct patch reefs had overlapping home ranges, the UDOI for all individuals was compared. To investigate schooling behaviour, we calculated the coefficient of sociality (S_C; Kenward *et al.* 1993) for pairs of fish to indicate the extent to which they stayed close to each other as they moved around. Sociality differs from home range overlap because it considers whether fish visit the same locations together rather than independently. The S_C for a pair of individuals is defined as follows:

$$S_C = (D_E - D_O) \div (D_E + D_O)$$

where D_O is the observed mean distance between the two individuals (m) and D_E is the expected mean distance between them (m). The observed mean distance is the mean distance between simultaneous detections of the two individuals. The expected mean distance is the mean distance between random pairs of detections of the two individuals. The S_C varies from −1 to 1 and values above and below 0 indicate cohesion and avoidance respectively. For example, a value of 0.33 indicates that the average observed distance between two individuals is half that expected when they move independently. To calculate S_C, we required the locations of each pair of fish at a series of matching times; however, in the acoustic array data a single detection of a fish often included multiple locations (of the nearest receivers) and the detections of different fish were staggered in time. To create data suitable for calculating S_C, we calculated the average (receiver) location of the detections of each fish in each 20-min interval. The S_C was calculated for all pairs of the six fish that had detection spans of at least 1 year. To investigate cohesion during short- and long-term changes in habitat utilisation, we calculated the S_C on time intervals ranging from 1 day to the entire study period.

To determine habitat use of fish tagged at distinct patch reefs, habitat types were classified based on aerial imagery and a spatial habitat database collected over 10 years of extensive surveys. Habitat polygons were generated in Google Earth. The degree of overlap between the utilisation distribution (all months combined) and different habitat types was calculated as the proportion of the utilisation distribution corresponding with each habitat (i.e. probability density integrated over the area of each habitat). The total area of each habitat was calculated as the total area within a 1-km buffer of the extent of the acoustic array. Ivlev's electivity (E; Ivlev 1961) was calculated using these proportions and areas as follows:

$$E = (r_i - p_i) \div (r_i + p_i)$$

where r_i is the relative use of habitat i in the study area (i.e. the proportion of the utilisation distribution corresponding to a particular habitat) and p_i is the proportion of the entire study area corresponding to that habitat.

Comparisons among times and individuals were made with the monthly KUD areas for the individual animals. Average KUD area or MLD over all individuals was calculated on the averages (over months) for the individuals. All averages are presented as the mean ± s.e. unless stated otherwise. Significance tests for effects of day or night, season and tide were made with linear models of KUD area or MLD on the factor of interest. (The present-values were calculated by analysis of variance (ANOVA) of the nested models with and without the factor.) When the test was over all individuals, tag was included as a factor. For day or night and tide, time (month) was included as a factor (crossed with tag in tests over all individuals). Because tag is nested within tagging location, significance tests for the effects of tagging location were made with mixed-effects models of KUD area or MLD on the factor of interest and with a tag random effect. With mixed-effects models, the effect of a factor was determined to be significant if the 95% confidence interval (CI) of the effect did not include zero. Mixed-effects models were fitted with the lme4 package in R (R Project for Statistical Computing, Vienna, Austria) and CIs were estimated with the confint.merMod function using the default (likelihood profile) option.

Results

Nineteen *K. bigibbus* ranging in size from 49 to 67 cm FL were captured and tagged adjacent to two isolated patch reefs

(MBBOM1 and MBBOM2) within the Mangrove Bay array (Fig. 1). These two patch reefs were located in ~4–6-m depth adjacent to the reef pass and were 360 m apart. Both patch reefs were dominated by large *Porites* spp. colonies (~4 m high and 10 m in diameter) and large schools (200–1000 fish) of *K. bigibbus* were observed throughout the year. The size and habitat available within and around patch reefs at MBBOM1 and MBBOM2 were very similar. The area adjacent to these patch reefs was dominated by algal reef (limestone pavement with varying algal biomass and overlying sand; Downie *et al.* 2013). In October 2008, six individuals were tagged at MBBOM1 and three were tagged at MBBOM2; in January 2009, four and six individuals were tagged at MBBOM1 and MBBOM2 respectively (Table 1). When fish were tagged in January 2009, all fish tagged in October 2008 were still being detected at or adjacent to their original tagging location.

Detection span and residency

The detection span and RI of tagged fish were in the range 1–569 days and 0.002–0.99, with fish tagged in October 2008 detected for significantly longer (detection span, days detected and RI) than fish tagged in January 2009. Fish tagged in the same month had similar detection spans, regardless of the patch reef at which they were captured. However, for fish tagged in October 2008, the average number of days fish were detected in the array was 426.3 ± 54.3, which was significantly longer than for fish tagged in January 2009 (20.7 ± 13.7 days). Only one individual tagged in January 2009 (B1_09_01) was detected for more than 30 days. There was no apparent pattern in residence related to size, and the sex of individuals could not be determined externally or based on size.

Home range, linear dispersal and space use

For the nine individuals that were selected for statistical analysis (see 'Materials and methods'), the average (over individuals) 50 and 95% KUD areas were 0.27 ± 0.03 and $1.61 \pm 0.30\ \text{km}^2$ respectively (Table 1). The average MLD of these long-term residents was 0.75 ± 0.09 km. The 50% KUD or core areas of individuals were centred on the patch reefs where they were captured with individuals most frequently detected on receivers adjacent to the tagging location (Fig. 2). Average KUD areas and MLD were generally larger for fish tagged at MBBOM1 than for those tagged at MBBOM2, but only significantly so for MLD. For fish tagged at MBBOM1 and MBBOM2, the 50% KUD area was 0.30 ± 0.05 and $0.230 \pm 0.003\ \text{km}^2$ respectively, whereas the 95% KUD area was 1.89 ± 0.45 and $1.14 \pm 0.04\ \text{km}^2$ respectively. The MLD of fish tagged at MBBOM1 was significantly larger than that of fish tagged at MBBOM2 (0.88 ± 0.10 *v.* 0.53 ± 0.08 km respectively; significance test: mixed-effects regression of MLD on tagging location with a tag random effect; MBBOM2 effect: -0.34, 95% CI -0.62, -0.07 (excludes zero); $n = 135$). Some individuals (B1_08_04, B1_08_05, B1_08_06) made less frequent movements to the reef slope via the reef pass, with these movements represented in the 95% KUDs (total area) of some fish (Fig. 2). Of the fish that departed the array within 30 days, six of eight were detected primarily from reef pass and reef slope habitats, as well as adjacent to the patch reefs where they were tagged.

Effects of tide, time of day and season

Average (over individuals) KUDs and MLDs were not significantly different between periods of high and low tide (significance tests: linear regression of each quantity on tide, tag, time (month) and tag–time interaction; high tide effects: 50% KUD area effect $= 0.017$, $t = 1.90$, d.f. $= 133$, $n = 269$, $P = 0.06$; 95% KUD area effect $= 0.031$, $t = 0.58$, d.f. $= 133$, $n = 269$, $P = 0.6$; MLD effect $= 0.22$, $t = 1.17$, d.f. $= 130$, $n = 266$, $P = 0.2$). There was a high degree of overlap, with UDOI ranging from 0.27 to 0.33 for long-term residents. Average (over individuals) 50 and 95% KUD areas and MLD were higher during the day than during the night (Table 2; Fig. 3). The day and night 50% KUD areas were 0.27 ± 0.03 and $0.24 \pm 0.02\ \text{km}^2$ respectively, the 95% KUD areas were 1.59 ± 0.30 and $1.23 \pm 0.12\ \text{km}^2$ respectively and the MLDs were 0.60 ± 0.09 and 0.26 ± 0.04 km respectively. These differences were all significant (significance tests: linear regression of each quantity on day or night, tag, time (month) and tag–time interaction; day effects: 50% KUD area effect $= 0.039$, $t = 3.60$, d.f. $= 134$, $n = 270$, $P < 0.001$; 95% KUD area effect $= 0.371$, $t = 4.74$, d.f. $= 134$, $n = 270$, $P < 0.001$; MLD effect $= 0.32$, $t = 10.34$, d.f. $= 130$, $n = 256$, $P < 0.001$). In the majority of tagged fish, average (over months) KUD areas were larger during the day than during the night. In cases where day area was significantly different to night area, day area was always larger than night areas in all (four cases for 50% KUDs and six cases for 95% KUDs; Table 2). The degrees of overlap between day and night 50 and 95% KUDs were 0.14–0.30 and 0.53–2.0 respectively (Table 2).

Monthly 50 and 95% KUDs were relatively stable, with no statistically significant pattern in size during the detection period (significance tests: linear regression of each of 50 and 95% KUD area on season and tag; ANOVA for addition of season: 50% KUD area $F_{3,124} = 1.65$, $n = 135$, $P = 0.2$; 95% KUD area $F_{3,124} = 1.15$, $n = 135$, $P = 0.3$). There was no significant difference in MLD between autumn and winter or between spring and summer; however, MLD was significantly higher in winter than in summer (0.94 ± 0.11 *v.* 0.61 ± 0.11 km respectively; significance test: linear regression of MLD on season and tag; ANOVA for addition of season; $F_{3,124} = 4.00$, $n = 135$, $P = 0.009$; summer–winter contrast effect $= 0.28$, $t = 3.265$, d.f. $= 124$, $n = 135$, $P = 0.0014$; other pairwise season comparisons not significant or (in one case) not significant after Bonferroni correction).

Home range overlap

For individuals that were tagged in October 2008 and detected on more than 30 days, the UDOIs of the two adjacent patch reefs were compared (Fig. 4). There was high overlap in the core area (50% KUD) among individuals tagged at MBBOM1, with an average UDOI of 0.26 ± 0.05. Similarly, for individuals tagged at MBBOM2, average UDOI was 0.33 ± 0.07. Individuals captured at MBBOM1 had very little overlap with those captured at MBBOM2, with average core area UDOI of 0.03 ± 0.03. Only one fish tagged in February 2009 was detected on more than 30 days. This individual was tagged at MBBOM1 and had a higher degree of overlap with individuals tagged at this patch reef in October 2008 (average UDOI 0.24 ± 0.02) than with individuals tagged at the same location on the same day in

Table 1. Fish ID, fork length (FL), date tagged and name of closest receiver for 19 *Kyphosus bigibbus* tagged within the Mangrove Bay array

The tag power output, minimum predicted range of the tag, average ping frequency, detection span, number of days each individual was detected and the percentage of days detected (detection span ÷ days detected since tagged × 100) are also shown. RI, residence index; NA, not applicable; KUD, kernel utilisation distribution (given as the mean ± s.e.)

ID	FL (cm)	Date tagged	Receiver name	Tag power output (dB)	Minimum predicted range of tag (m)	Average ping frequency (s)	Detection span	Number days detected	Percentage of days detected	RI	50% KUD	95% KUD
B1_08_01	57	16-Oct-08	MBBOM1	153	406	60	282	275	98	NA	NA	NA
B1_08_02	58	16-Oct-08	MBBOM1	153	406	60	576	568	99	0.984	0.180 ± 0.002	0.87 ± 0.04
B1_08_03	55	16-Oct-08	MBBOM1	153	406	60	572	569	99	0.986	0.190 ± 0.002	0.89 ± 0.02
B1_08_04	55	19-Oct-08	MBBOM1	153	406	60	180	134	74	0.232	0.310 ± 0.05	2.05 ± 0.38
B1_08_05	51	19-Oct-08	MBBOM1	153	406	60	572	444	78	0.769	0.38 ± 0.05	2.40 ± 0.27
B1_08_06	54	19-Oct-08	MBBOM1	147	282	60	572	490	86	0.849	0.42 ± 0.05	3.22 ± 0.24
B1_09_01	54	22-Jan-09	MBBOM1	147	282	60	473	137	29	0.285	0.32 ± 0.05	1. 79 ± 0.31
B1_09_02	57	22-Jan-09	MBBOM1	147	282	60	4	4	100	0.008	NA	NA
B1_09_03	54	22-Jan-09	MBBOM1	147	282	60	17	7	41	0.015	NA	NA
B1_09_04	59	22-Jan-09	MBBOM1	150	351	180	11	11	100	0.023	NA	NA
B2_08_01	56	16-Oct-08	MBBOM2	153	406	60	573	567	99	0.983	0.23 ± 0.01	1.07 ± 0.06
B2_08_02	66	16-Oct-08	MBBOM2	153	406	60	577	569	99	0.986	0.24 ± 0.01	1.14 ± 0.08
B2_08_03	56	16-Oct-08	MBBOM2	153	406	60	224	221	99	0.383	0.22 ± 0.035	1.19 ± 0.25
B2_09_01	63	21-Jan-09	MBBOM2	147	282	60	6	3	50	0.006	NA	NA
B2_09_02	57	21-Jan-09	MBBOM2	147	282	60	1	1	100	0.002	NA	NA
B2_09_03	61	21-Jan-09	MBBOM2	147	282	60	93	12	13	0.025	NA	NA
B2_09_04	57	21-Jan-09	MBBOM2	147	282	60	12	8	67	0.017	NA	NA
B2_09_05	57	21-Jan-09	MBBOM2	147	282	60	320	17	5	0.035	NA	NA
B2_09_06	49	21-Jan-09	MBBOM2	147	282	60	213	7	3	0.015	NA	NA

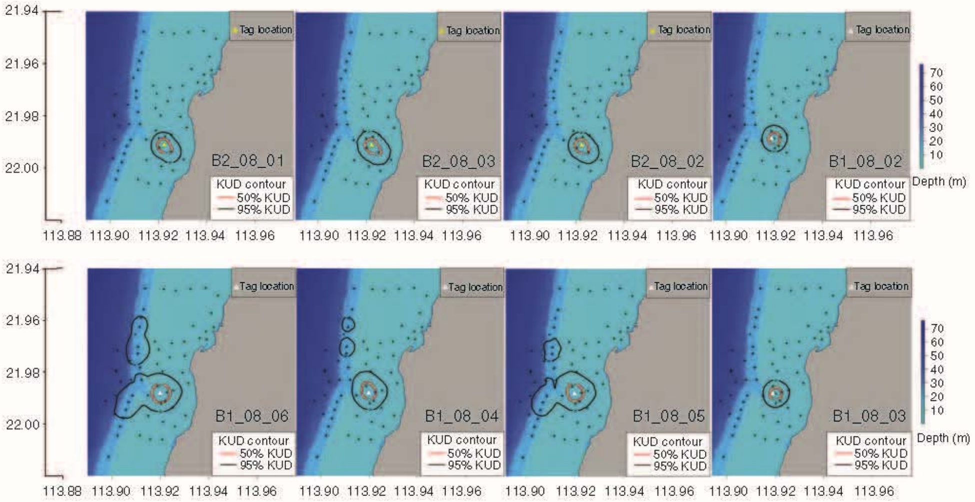

Fig. 2. Map showing tag location and 50 and 95% kernel utilisation distribution (KUD) contours of eight individual *Kyphosus bigibbus*. Tag ID code of each animal is shown in the top right-hand corner of each panel. Fish B2_08_01, B2_08_03 and B2_08_02 were tagged at MBBOM2 (see Fig. 1), whereas Fish B1_08_02, B1_08_06, B1_08_04, B1_08_05 and B1_08_03 were tagged at MBBOM2.

Table 2. Mean (±s.e.) of day and night 50 and 95% kernel utilisation distribution (KUD) area for individual fish detected on more than 30 days
Asterisks indicate significance of differences between day and night (from linear regressions of KUD area on day or night and time (month)): *, $P < 0.05$; **, $P < 0.01$. The overlap of day and night 50 and 95% KUD contours was determined using the utilisation distribution overlap index (UDOI)

Fish ID	50% KUD area		95% KUD area		UDOI	
	Day	Night	Day	Night	50% KUD	95% KUD
B2_08_01	0.23 ± 0.01	0.24 ± 0.01	1.02 ± 0.04	1.13 ± 0.10	0.19	1.06
B2_08_02	0.24 ± 0.01	0.23 ± 0.01	1.09 ± 0.06	1.19 ± 0.12	0.15	1.12
B2_08_03	0.19 ± 0.01	0.26 ± 0.04	1.02 ± 0.17	1.41 ± 0.30	0.23	0.41
B1_09_01	0.32 ± 0.05	0.22 ± 0.02	1.69 ± 0.28	1.06 ± 0.12*	0.14	1.06
B1_08_04	0.32 ± 0.06	0.25 ± 0.05	2.14 ± 0.39	1.18 ± 0.18*	0.24	0.53
B1_08_05	0.37 ± 0.05	0.30 ± 0.04*	2.24 ± 0.25	1.77 ± 0.19*	0.23	2.00
B1_08_06	0.44 ± 0.05	0.27 ± 0.03**	3.22 ± 0.26	1.52 ± 0.15**	0.15	1.66
B1_08_02	0.19 ± 0.01	0.170 ± 0.001**	1.04 ± 0.08	0.78 ± 0.01**	0.30	1.15
B1_08_03	0.190 ± 0.003	0.180 ± 0.001**	0.93 ± 0.03	0.84 ± 0.02*	0.30	1.84

February 2009 that departed the array within a few weeks (average UDOI 0.03 ± 0.03).

Schooling behaviour

The average monthly S_C was low for all pairs of the six fish with detection spans of at least 1 year (Fig. 5). S_C was significantly positive for pairs of fish tagged at the same reef and near (and not significantly different from) zero for all pairs tagged at different reefs. The pair of fish with the strongest cohesion (B1_08_05 and B1_08_06; mean $S_C - 0.24$) was the pair with broad utilisation distributions that shifted around over the study period (Table 1). For this pair, S_C increased with the calculation time interval from 0.11 for 1 day to 0.29 for the whole dataset (576 days; e.g. difference from 3 to 60 days, Wilcoxon rank sum test, $S_C - 0.13, 0.24$; $n - 130, 10$; $W - 301$; $P - 0.004$). This indicates that although the fish did not follow each other particularly closely (average distance apart 545 m), they tended to move to the same general areas as they used different parts of their home ranges over the period of the study.

Habitat overlap

Because individuals from the two patch reefs exhibited different habitat use, we compared Ivlev's E of individuals from these reefs. All individuals spent more time in algal pavement than expected from its proportional availability, with E values of individuals from both patch reefs more than 0.74 (Fig. 6). Fish tagged at MBBOM1 had higher *E* scores for reef slope and reef pass areas dominated by coral and pavement. Fish tagged at MBBOM2 spent very little time in these habitats, but demonstrated an increased preference for patch reefs. Fish were very rarely recorded in bare sand within the lagoon, or in reef slope, shoreline pavement, Mangrove Bay and the reef flat.

Discussion

Herein we demonstrate the existence of both resident and nomadic individuals of *K. bigibbus*. This study provides the first estimates of movement and home range in *K. bigibbus* and strengthens our knowledge of the role of kyphosids as mobile herbivorous trophic links on coral reefs (cf. Welsh and Bellwood 2014). The home ranges of resident *K. bigibbus* were centred around the patch reefs at which individuals were captured, providing additional evidence that low algal biomass adjacent to these reefs (see Downie *et al.* 2013) is a result of high rates of herbivory. The lack of food resources around these heavily grazed areas presumably forces resident individuals to forage more widely around their home reef, with individuals detected up to 7.6 km away. Fish that departed shortly after tagging presumably forage more widely and can be classified as transients, with these fish only detected within the array for up to 17 days after tagging. We also demonstrated strong partitioning of groups of fish tagged in large schools of conspecifics less than 400 m apart. This highlights the diversity and complexity of fish movements and the need for long-term studies that tag animals in a range of habitats and at different times of the year. The different size and shape of the home range in groups of fish tagged less than 400 m apart suggest that resident fish at adjacent patch reefs are potentially foraging in different areas, which increases the spatial scale and range of habitats over which this species exerts its functional role. This partitioning of habitat has important ecological consequences with regard to algal removal and reef resilience and highlights the need for spatial closures to encompass the range of habitats used by individuals within a population.

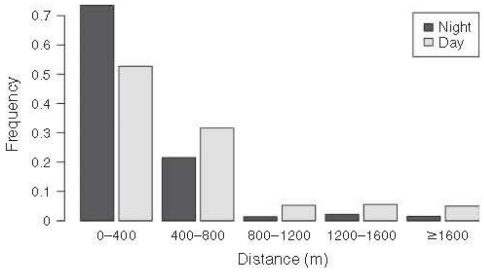

Fig. 3. Frequency of movements between the most distant receivers visited each day (maximum linear distance) for all long-term resident *Kyphosus bigibbus* during the day and night. Distance was measured as the distance between the two most widely separated receivers individuals were detected on each day.

Short-term residents

Tagged fish exhibited multiple behaviours, with 47% of the fish tagged departing the array within 17 days, whereas the remaining fish were all detected over long periods. All the surviving fish tagged in October 2008 were detected for more than 130 days, whereas 9 of 10 fish tagged in January 2009 departed the array within 17 days. Although mortality or capture of the fish tagged in January 2009 cannot be ruled out, given that identical capture and tagging procedures were used the rapid departure of individuals tagged in January 2009 was attributed to transient fish leaving the area. Rapid departure of tagged fish from the capture site has been demonstrated for several herbivorous fish species (Meyer *et al.* 2010; Marshell *et al.* 2011; Garcia *et al.* 2014), as well as more broadly in coral reef fish (Garcia *et al.* 2015; Pillans *et al.* 2014). In several of these studies, individuals were subsequently recorded several kilometres away, with differences in site attachment attributed to behaviour. A plausible explanation for *K. bigibbus* tagged in January 2009 is that these individuals were part of schools of fish that were using the patch reefs as temporary refugia while undertaking more widespread movements. Indeed, one fish (B1_09_03) that departed after 7 days was detected 8 months after tagging by acoustic receivers 138 km south of where it was tagged, adding further support to the nomadic and more wide-ranging movement of individuals within the population. Similar

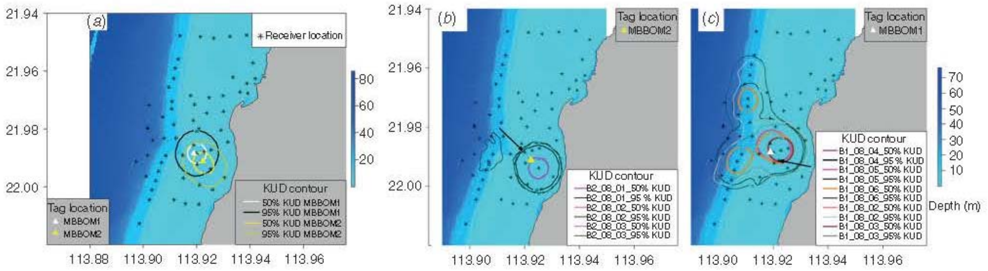

Fig. 4. Kernel utilisation distribution (KUD) contours of all long-term resident *Kyphosus bigibbus* tagged at MBBOM1 and MBBOM2 (see Fig. 1) respectively. (*a*) KUD contours from all detections for all fish combined. (*b*, *c*) KUD contours of all detections, excluding those at the site, of tagging for MBBOM1 (*b*) and MBBOM2 (*c*). Arrows indicate the location of the adjacent patch reef where other fish were tagged.

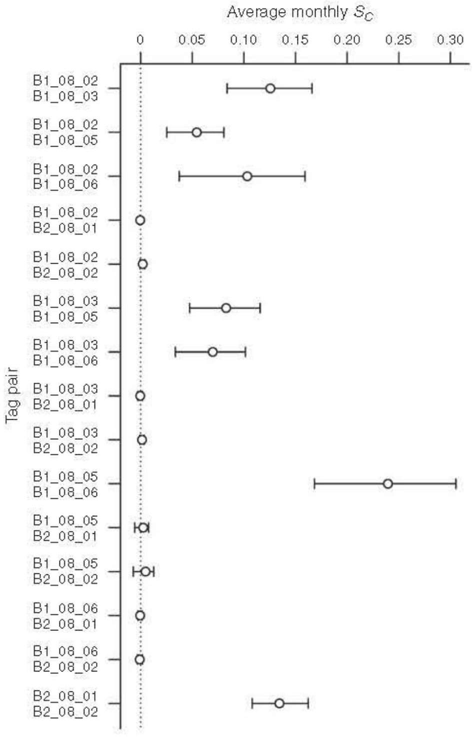

Fig. 5. Average monthly coefficient of sociality (S_C) for each pair of the six fish with the longest detection spans. The error bars indicate 95% bootstrap confidence intervals.

long-distance movements by some individuals, high site fidelity and small home ranges in others have been recorded in the herbivorous *Girella tricuspidata* (Gray *et al.* 2012; Ferguson *et al.* 2013). As more long-term research into fish movements is conducted, there is increasing evidence of this behaviour (see Attwood and Bennett 1994; Egli and Babcock 2004; Parsons *et al.* 2011; Koeck *et al.* 2013; Pillans *et al.* 2014).

Home range of long-term residents

Long-term residents were detected for up to 569 days, and although individuals were detected up to 7.4 km away from the patch reefs where they were tagged, home range was centred around these patch reefs with a core area of 0.27 ± 0.03 km^2. These estimates of core area home range were larger than those reported for other kyphosids, such as *Kyphosus vaigiensis* (50% KUD – 0.16 km^2) on the Great Barrier Reef (Welsh and Bellwood 2014) and for *Kyphosus sectatrix* (total home range 0.03 km^2) in the West Indies (Eristhee and Oxenford 2001). However, our home range area is possibly an overestimate because this area (equivalent radius 0.29 km^2) is too small to be resolved accurately by our receiver array (receiver spacing generally 0.35–0.5 km). With our choice of smoothing parameter (200 m), the smallest possible area is 0.17 km^2 (when all detections are by one receiver). The lower estimates of home range in *K. vaigiensis* may represent species-specific differences, but the arrangement of receivers along a linear depth contour (~5 m) on a narrow reef slope with no receivers in deep water off the slope or in the narrow lagoon inshore (Welsh and Bellwood 2014) may have resulted in smaller home range estimates in *K. vaigiensis*. Compared with other tropical herbivorous fish species studied to date, the home range of *K. bigibbus* was significantly larger, with estimates in surgeon fish (Meyer and Holland 2005; Marshell *et al.* 2011) and parrotfish (Welsh and Bellwood 2012*a*, 2012*b*; Howard *et al.* 2013) ranging from 0.001 to 0.13 km^2.

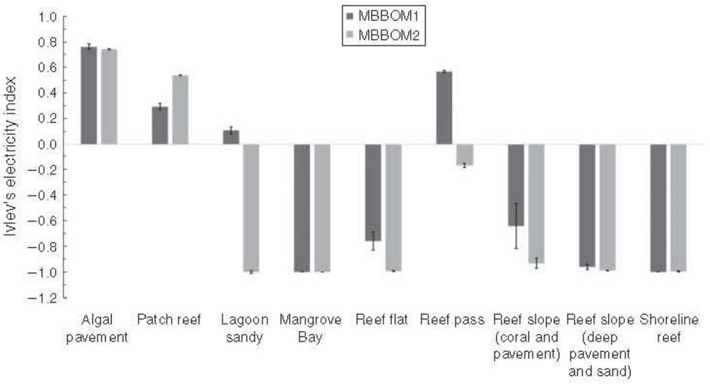

Fig. 6. Mean (±s.e.) habitat selection (Ivlev's 1961 electivity index) of long-resident *Kyphosus bigibbus* tagged at MBBOM1 and MBBOM2 (for locations, see Fig. 1).

Direct comparisons between studies can be confounded by array design (number of receivers and area or habitat covered by receivers), as well as the length of time animals were monitored (e.g. Stocks *et al.* 2015). However, it is clear that *K. bigibbus* tagged on patch reefs within the Ningaloo Reef have the largest reported home ranges of herbivorous fish species studied to date. Additional research that investigates the home range and linear dispersal of *K. bigibbus* tagged within aggregations on the reef slope as well as the reef flat are required to determine the effects of habitat on the size and shape of home range and dispersal patterns. *K. sectatrix* tagged in two different habitats exhibited marked differences in the linear extent and shape of their home ranges, which was attributed to the availability of habitat adjacent to the areas where fish were tagged (Eristhee and Oxenford 2001). *K. sectatrix* tagged along a narrow reef slope covered a linear distance of up to ~800 m, whereas fish tagged on fringing reef had home range covering a linear distance of up to ~300 m. The long, narrow home range and small, circular home range at the two areas resulted in similar home range areas. In the case of *K. bigibbus*, despite the similarity in habitat at the two patch reefs, differences in the size and shape of home range were apparent. Our results illustrate that resident *K. bigibbus* regularly travelled up to 1 km away from the home reef on a daily basis, with individuals tagged at MBBOM1 regularly being recorded up to 3.5 km from their home reef. These linear movements combined with larger home ranges in this species support the role of *K. bigibbus* as a mobile herbivorous trophic link (cf. Welsh and Bellwood 2014).

Despite the presence of persistent schools of grey drummer around patch reefs as well as the high degree of home range overlap between long-term residents tagged at the same patch reef, there was no evidence that individuals were consistently detected together when they were detected by receivers away from their home reef. The average monthly coefficient of cohesion was significantly positive, but low, for all pairs of fish tagged at a common reef. The pair of fish with the highest cohesion was the pair that ranged most widely (partly because increased movement makes cohesion easier to detect). Cohesion for this pair increased with the calculation time interval, indicating that although the pair did not forage particularly close together, they tended to move to the same general areas as they used different parts of their home ranges over the study period. The apparent lack of schooling behaviour during movements away from the home reef was unexpected given the high degree of overlap in the home range of conspecifics tagged at the same patch reefs and infrequent but near simultaneous detections of groups of up to four fish at receivers 10 km away from home reefs. Thus, although some individuals appear to form persistent schools around their home reefs, the timing of movement away from the home reef appears to be affected by individual behaviour and not group behaviour. Although the timing of movements away from the home reef varied among individuals, the distance and direction of movement away from home reefs was largely similar, resulting in the use of different habitats at the same time (when away from home reefs) but the same habitat use over time.

Ecological implications of movement

The two patch reefs where *K. bigibbus* were tagged have been identified previously as areas of high *K. bigibbus* density, and have a high density of other browsing herbivorous fish (Downie *et al.* 2013). Circular halos around these patch reefs were visible from aerial images and were due to very low algal biomass compared with areas more than 120 m away. These halos were attributed to intensive grazing by herbivorous fish that resulted in a strong density gradient of algae on the pavement away from the home reef (as per Downie *et al.* 2013). Downie *et al.* (2013) used remote cameras and a 24-h tethered algae experiment to investigate grazing rates at 0, 30, 60, 90 and 120 m away from these patch reefs and demonstrated that grazing, in terms of both numbers of bites and reduction of tethered algae, was highest within 60 m but negligible at 90–120 m, with no bites taken from tethered algae more than 90 m away (where the biomass of macroalgae communities began to dominate substrate cover). Using data from individuals tagged at these same patch reefs, we have demonstrated that *K. bigibbus* tagged on the same patch reefs forage over considerably larger distances than original grazing experiments and visual observations suggested, with fish regularly detected up to 3 km away from patch reefs. These data highlight the importance of large mobile herbivores in maintaining coral–algal balance adjacent to their home reef and up to several kilometres away. The use of acoustic telemetry to investigate the range and scale of movements of herbivorous fish are providing a valuable insight into the ecological functionality of coral reefs (Welsh and Bellwood 2012*b*, 2014) and highlight the complexity of movement patterns of roving herbivorous fish.

Intraspecific differences in behaviour

Fish tagged at adjacent patch reefs were detected on different parts of the array. Fish tagged at MBBOM2 primarily used the area to the east of their home reef, whereas fish tagged at MBBOM1 primarily foraged to the west of their home reef. Even in the absence of detailed movement data, variation in individual movement and behavioural differences not related to sex, size or age class have long been acknowledged from a wide range of taxa (Bolnick *et al.* 2003). Heterogeneity in cores area used by generalist predatory fish species not attributed to ontogenetic shifts has been demonstrated in the sea bream *Diplodus sargus*, with this species exhibiting differing diurnal patterns depending on the habitat individuals occupy (Koeck *et al.* 2013; Di Lorenzo *et al.* 2016). Evidence of groups of individuals occupying different areas has also been demonstrated in tropical Lutjanids (Hammerschlag-Peyer and Layman 2010), temperate Sparids (Egli and Babcock 2004) and freshwater Esocidae (Kobler *et al.* 2009).

The schooling behaviour and use of distinct areas by groups of *K. bigibbus* tagged less than 400 m apart is one of the more extreme cases of heterogeneity in habitat use in the fish movement literature. The similarity in habitat available to the two groups of fish suggests that individual and schooling behaviour around their home reef, rather than habitat, were responsible for these differences. That groups of schooling fish in close proximity to one another exhibit such little overlap in core and total home range has important ecological ramifications with regard to coral reef resilience because the two groups are responsible for the large-scale removal of algae in largely non-overlapping areas, with one group foraging to the west of their home reef and the other to the east. Although both groups showed positive selection of algal pavement and patch reefs, differences between the groups with regard to reef pass and coral- and pavement-dominated reef slope suggest the two schools exert their functional roles in differing habitats.

Area-specific differences in rates of algal removal by herbivorous fish as a result of schooling behaviour can have important functional implications (Welsh and Bellwood 2012*b*; Michael *et al.* 2013). For example, *K. bigibbus* within schools of conspecifics took more bites than single fish, resulting in significantly higher feeding intensity (Michael *et al.* 2013). Similarly, *Scarus rivulatus* in schools of fish took twice as many bites as single fish (Welsh and Bellwood 2012*b*). Despite similar benefits in forming schools (Robertson *et al.* 1976; Lukoschek and McCormick 2000), the schooling behaviour of *S. rivulatus* was different to that observed in *K. bigibbus* in the present study. Individual *S. rivulatus* had limited fidelity to the schools they were tagged in, with individuals from one school mixing with individuals from another school as long the home range of the schools overlapped. Individual *S. rivulatus* were also equally likely to be solitary (Welsh and Bellwood 2012*b*). In *K. bigibbus*, limited home range overlap occurred despite the home range of groups of individuals being significantly larger than the distance between the two home reefs. Furthermore, individuals within schools were detected together at their home reefs for up to 3 years, suggesting that schools can persist for multiple years with a stable home range. Schooling behaviour in *K. bigibbus* appears to increase the importance of this species functional role in algal removal by facilitating increased browsing rates, as well as increasing the spatial extent of browsing, with different schools feeding in different areas despite the proximity of their home reefs. Although we did not investigate the diet of fish, comparisons of gut content from fish captured at adjacent patch reefs are required to determine the degree to which differences in habitat use result in dietary differences that would lead to further intraspecific heterogeneity in herbivore functionality on coral reefs.

Schooling behaviour can disproportionally affect a species functional role when populations are overharvested, with rate of foraging potentially exhibiting a non-linear rather than linear decline (Welsh and Bellwood 2012*b*). Furthermore, given the restricted movement patterns of individuals from adjacent patch reefs, it is uncertain whether a reduced browser biomass would be compensated for by individuals from adjacent patch reefs. The ecological importance of large roving herbivores that exhibit an increasing array of complex behaviours that we are only beginning to understand highlights the need to encompass large areas within marine protected areas to ensure that not only is the range of habitats that individuals occupy protected, but also that the range of behaviours that individuals within groups of fish exhibit is adequately protected to ensure the maintenance of functional processes. Although Kyphosid species are not targeted by fisheries in Australia, elsewhere they are a valuable resource (Sakai 2003). The removal of animals from specific habitats or home reefs is therefore likely to have a disproportionate effect on local reef resilience given the apparent school-specific home range exhibited by *K. bigibbus*.

Although the overall frequency of movements of resident *K. bigibbus* away from their home reef was relatively small, a seasonal pattern was observed, with fish more likely to move further away from their home reef in winter than in summer. This was also reflected in home-range estimates with core area in autumn and winter larger than in spring and summer. The increased frequency of long-distance movement may be related to availability of preferred food, with the biomass of some important species being significantly lower in the cooler months (Fulton *et al.* 2014). Fulton *et al.* (2014) demonstrated that the biomass of canopy-forming algae within the Ningaloo lagoon showed strong seasonal fluctuations that were attributed to temperature. Total biomass of algae in summer was nearly twice that in winter. Summer biomass was dominated by *Sargassum* spp., whereas understorey species *Dictyopteris*, *Lobophora* and *Dictyota* reached peak biomass in winter (Fulton *et al.* 2014).

Diet of *K. bigibbus* in south-west Japan (Yatsuya *et al.* 2015) included many of the genera that were abundant at the patch reefs where fish were tagged (Downie *et al.* 2013), with Yatsuya *et al.* (2015) demonstrating marked seasonal changes in the diet of *K. bigibbus* that predominantly mirrored the abundance of macroalgae at their study site. The low density of algal biomass adjacent to the patch reefs where fish were tagged, combined with the high density of fish and the ability of Kyphosids to remove large quantities of algae in short time periods (Cvitanovic and Bellwood 2009; Downie *et al.* 2013; Michael *et al.* 2013), presumably results in fish having to move away from the shelter of these home reefs in order to obtain enough food. However, despite the existence of areas of high macroalgal density to the east-north-east of home reefs, fish were not detected in this area. The presence of structurally complex habitat has been linked with grazing intensity (McCook 1997), with the risk to predation increasing away from structure. Observations of schools of *K. bigibbus* adjacent to structurally complex habitat in the lagoon and on the reef slope, together with home range centres of resident fish around patch reefs, support this. In the present study we have demonstrated that the potential grazing footprint of a species is likely to be affected by the availability of shelter and the spacing of home reefs, variability in the movement patterns of individuals and in the schooling behaviour of groups of fish at particular patch reefs.

Given the close association with the patch reef where individuals were tagged, it was expected that fish may return to these patch reefs at night and forage more widely during the day; however, although this pattern was observed in most individuals, it was not consistent across all animals. The lack of a consistent difference between day and night core and total KUD areas, as well considerable overlap in day and night KUDs, suggest that daily nocturnal sheltering at the home reef did not occur in all individuals and did not result in large differences in the size of day and night home range measures. However, for all individuals where differences in area were apparent, daytime KUD area was larger than night-time area and detections at the home reef were highest at night. Similarly, estimates of daily dispersal away from the home reef showed that animals were more likely to be detected up to 1000 m away from their home reef during the day, with the majority of night detections at or close to the home reef. Several studies on herbivorous fish have demonstrated individual variation in the degree of nocturnal movements (Meyer and Holland 2005; Welsh and Bellwood 2014; Stocks *et al.* 2015) and an overall pattern of increased diurnal movement. It is unknown whether detection of fish away from their home reef during the night represents nocturnal foraging or was due to individuals sheltering in the numerous caves and crevices along the reef slope following diurnal foraging in these areas. Large schools of grey drummer were repeatedly observed in structurally complex areas on the reef slope during UVC transects, suggesting that schools of *K. bigibbus* also have home range centres on the reef slope. The detection frequency of moored acoustic tags has been shown to be reduced at night (Payne *et al.* 2010), suggesting that the ability to interpret diurnal behaviour could be compromised by both animal behaviour (sheltering at night) and background noise (reducing tag detection range at night). However, given that home range measures (as opposed to activity patterns investigated by Payne *et al.* 2010) were not markedly affected by the total number of detections, it is unlikely that changes in diurnal detectability would affect the home range measures used in the present study. Furthermore, using moored acoustic tags in a coral reef environment, Welsh and Bellwood (2012*a*) found no diurnal pattern in detection frequency.

Conclusion

The present study contributes to the increasing body of literature on the variability and complexity of relationships between herbivorous fish and algal consumption on coral reefs. The coral–algal balance and ability of coral reefs to recover from algal dominance has been attributed to browsing by herbivorous fish (McCook 1997; Hughes *et al.* 2007; Burkepile and Hay 2010). Grazing rates and subsequent algal biomass have been shown to vary over a range of spatial and temporal scales, with these differences attributed to the availability of shelter for grazing fish (McCook 1997; Vergés *et al.* 2011; Downie *et al.* 2013), small-scale variability in the species responsible for macroalgal removal (Cvitanovic and Bellwood 2009), species-specific food preferences and grazing intensity (Bellwood and Choat 1990; Choat 1991; Pillans *et al.* 2004), feeding behaviour of individuals and schools of fish (Michael *et al.* 2013) and differences in the movement patterns of species (Marshell *et al.* 2011; Welsh and Bellwood 2014; present study). Herein we provide evidence of different habitat use and movement patterns of groups of the same species tagged only a few hundred metres apart, adding further evidence that variability in intraspecific foraging behaviour and movement can have implications on the foraging footprint of a single species, effectively increasing the species foraging area. The overall contribution to herbivory, and therefore maintenance of functional process, is increased by schooling through increased feeding rates, as well as expanded spatial extent of non-overlapping home range in schools of fish.

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References

Attwood, C. G., and Bennett, B. A. (1994). Variation in dispersal of galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1247–1257. doi:10.1139/F94-124

Bellwood, D. R., and Choat, J. H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* **28**, 189–214. doi:10.1007/BF00751035

Bellwood, D. R., Hughes, T. P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature* **429**, 827–833. doi:10.1038/NATURE02691

Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**, 1–28. doi:10.1086/343878

Burkepile, D. E., and Hay, M. E. (2010). Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS One* **5**, e8963. doi:10.1371/JOURNAL.PONE.0008963

Calenge, C. (2011). 'Home Range Estimation in R: the adehabitatHR Package.' (Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France.)

Choat, J. H. (1991). The biology of herbivorous fishes on coral reefs. In 'The Ecology of Fishes on Coral Reefs'. (Ed. P. F. Sale.) pp. 120–155. (Academic Press: San Diego, CA, USA.)

Choat, J. H., Clements, K. D., and Robbins, W. D. (2002). The trophic status of herbivorous fishes on coral reefs – I: dietary analyses. *Marine Biology* **140**, 613–623. doi:10.1007/S00227-001-0715-3

Cvitanovic, C., and Bellwood, D. R. (2009). Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs* **28**, 127–133. doi:10.1007/S00338-008-0433-0

Di Lorenzo, M., Fernandez, T. V., Badalamenti, F., Guidetti, P., Starr, R. M., Giacalone, V. M., Di Franco, A., and D'Anna, G. (2016). Diel activity and variability in habitat use of white sea bream in a temperate marine protected area. *Marine Environmental Research* **116**, 1–9. doi:10.1016/J.MARENVRES.2016.02.007

Downie, R. A., Babcock, R. C., Thomson, D. P., and Vanderklift, M. A. (2013). Density of herbivorous fish and intensity of herbivory are influenced by proximity to coral reefs. *Marine Ecology Progress Series* **482**, 217–225. doi:10.3354/MEPS10250

Egli, D. P., and Babcock, R. C. (2004). Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus aura*tus) in a temperate no-take marine reserve. *ICES Journal of Marine Science* **61**, 1137–1143. doi:10.1016/J.ICESJMS.2004.07.004

Eristhee, N., and Oxenford, H. A. (2001). Home range size and use of space by Bermuda chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufrie're Marine Management Area, St Lucia, West Indies. *Journal of Fish Biology* **59**, 129–151.

Ferguson, A. M., Harvey, E. S., Taylor, M. D., and Knott, N. A. (2013). A herbivore knows its patch: luderick, *Girella tricuspidata*, exhibit strong site fidelity on shallow subtidal reefs in a temperate marine park. *PLoS One* **8**(5), e65838. doi:10.1371/JOURNAL.PONE.0065838

Fieberg, J., and Kochanny, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *The Journal of Wildlife Management* **69**, 1346–1359. doi:10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Fulton, C. J., Depczynski, M., Holmes, T., Noble, M. M., Radford, B., Wernberg, T., and Wilson, S. K. (2014). Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem. *Limnology and Oceanography* **59**, 156–166. doi:10.4319/LO.2014.59.1.0156

Garcia, J., Rousseau, Y., Legrand, H., Saragoni, G., and Lenfant, P. (2014). Movement patterns of fish in a Martinique MPA: implications for marine reserve design. *Marine Ecology Progress Series* **513**, 171–185. doi:10.3354/MEPS10940

Garcia, J., Mourier, J., and Lenfant, P. (2015). Spatial behaviour of two coral reef fishes within a Caribbean marine protected area. *Marine Environmental Research* **109**, 41–51. doi:10.1016/J.MARENVRES.2015.06.004

Gitzen, R. A., Millspaugh, J. J., and Kernohan, B. J. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *The Journal of Wildlife Management* **70**, 1334–1344. doi:10.2193/0022-541X(2006)70[1334:BSFFAO]2.0.CO;2

Gray, C. A., Haddy, J. A., Fearman, J., Barnes, L. M., Macbeth, W. G., and Kendall, B. W. (2012). Reproduction, growth and connectivity among populations of *Girella tricuspidata* (Pisces: Girellidae). *Aquatic Biology* **16**, 53–68. doi:10.3354/AB00428

Hammerschlag-Peyer, C. M., and Layman, C. A. (2010). Intrapopulation variation in habitat use by two abundant coastal fish species. *Marine Ecology Progress Series* **415**, 211–220. doi:10.3354/MEPS08714

Hoey, A. S., and Bellwood, D. R. (2008). Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* **27**, 37–47. doi:10.1007/S00338-007-0287-X

Hoey, A. S., and Bellwood, D. R. (2010). Among-habitat variation in herbivory on *Sargassum* spp. on a mid-shelf reef in the northern Great Barrier Reef. *Marine Biology* **157**, 189–200. doi:10.1007/S00227-009-1309-8

Horn, M. R. (1989). Biology of marine herbivorous fishes. *Oceanography and Marine Biology – an Annual Review* **27**, 167–272.

Howard, K. G., Claisse, J. T., Clark, T. B., Boyle, K., and Parrish, J. D. (2013). Home range and movement patterns of the redlip parrotfish (*Scarus rubroviolaceus*) in Hawaii. *Marine Biology* **160**, 1583–1595. doi:10.1007/S00227-013-2211-Y

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwsky, N., Pratchett, M. S., Steneck, R. S., and Willis, R. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* **17**, 360–365. doi:10.1016/J.CUB.2006.12.049

Ivlev, V. S. (1961). 'Experimental Ecology of the Feeding of Fishes.' (Yale University Press: New Haven, CT, USA.)

Iwama, G. K., McGeer, J. C., and Pawluk, M. P. (1989). The effects of five fish anaesthetics on acid–base balance, haematocrit, blood gases, cortisol, and adrenaline in rainbow trout. *Canadian Journal of Zoology* **67**, 2065–2073. doi:10.1139/Z89-294

Kenward, R. E., Marcstrom, V., and Karlbom, M. (1993). Post-nestling behaviour in goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. *Animal Behaviour* **46**, 371–378. doi:10.1006/ANBE.1993.1199

Kernohan, B. J., Gitzen, R. A., and Millspaugh, J. J. (2001). Analysis of animal space use and movements. In 'Radio Tracking and Animal Populations'. (Eds J. J. Millspaugh and J. M. Marzluff.) pp. 126–166. (Academic Press: San Diego, CA, USA.)

Kobler, A., Klefoth, T., Mehner, T., and Arlinghaus, R. (2009). Coexistence of behavioural types in an aquatic top predator: a response to resource limitation. *Oecologia* **161**, 837–847. doi:10.1007/S00442-009-1415-9

Koeck, B., Aló, J., Caro, A., Neveu, R., Crec'hriou, R., Saragoni, G., and Lenfant, P. (2013). Contrasting fish behavior in artificial seascapes with implications for resources conservation. *PLoS One* **8**(7), e69303. doi:10.1371/JOURNAL.PONE.0069303

Lukoschek, V., and McCormick, M. I. (2000) A review of multi-species foraging associations in fishes and their ecological significance. In 'Proceedings of the 9th International Coral Reef Symposium', 23–27 October 2000, South Kuta, Bali, Indonesia. (Eds M. K. Moosa, S. Soemodihardjo, A. Soegiarto, K. Romimohtarto, A. Nontji, Soekarno, and Suharsono.) pp. 23–27. (Ministry of Environment, Indonesian Institute of Sciences and International Society for Reef Studies: Bali, Indonesia.)

MacDonald, B. D., Lewison, R. L., Madrak, S. V., Seminoff, J. A., and Eguchi, T. (2012). Home ranges of East Pacific green turtles *Chelonia mydas* in a highly urbanized temperate foraging ground. *Marine Ecology Progress Series* **461**, 211–221. doi:10.3354/MEPS09820

Makowski, C. A., Seminoff, J. A., Salmon, M. A., and English, G. (2006). Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Marine Biology* **148**, 1167–1179. doi:10.1007/S00227-005-0150-Y

Marshell, A., Mills, J., McIlwain, J. L., and Rhodes, K. L. (2011). Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. *Coral Reefs* **30**, 631–642. doi:10.1007/S00338-011-0770-2

McCook, L. J. (1997). Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. *Marine Biology* **129**, 713–722. doi:10.1007/S002270050214

McCook, L. J., Jompa, J., and Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* **19**, 400–417. doi:10.1007/S003380000129

Meyer, C. G., and Holland, K. N. (2005). Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes* **73**, 201–210. doi:10.1007/S10641-005-0559-7

Meyer, C. G., Papastamatiou, Y. P., and Clark, T. B. (2010). Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. *Marine Biology* **157**, 1499–1511. doi:10.1007/S00227-010-1424-6

Michael, P. J., Hyndes, G. A., Vanderklift, M. A., and Verges, A. (2013). Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Marine Ecology Progress Series* **482**, 227–240. doi:10.3354/MEPS10262

Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., Holmes, K. E., Mendes, J. M., Broad, K., Sanchirico, J. N., Buch, K., Box, S., Stoffle, R. W., and Gill, A. B. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**, 98–101. doi:10.1126/SCIENCE.1121129

Parsons, D. M., Morrison, M. A., McKenzie, J. R., Hartill, B. W., Bian, R., and Francis, R. I. C. C. (2011). A fisheries perspective of behavioural variability: differences in movement behaviour and extraction rate of an exploited sparid, snapper (*Pagrus auratus*). *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 632–642. doi:10.1139/F2011-005

Payne, N. L., Gillanders, B. M., Webber, D. M., and Semmens, J. M. (2010). Interpreting diel activity patterns from acoustic telemetry: the need for controls. *Marine Ecology Progress Series* **419**, 295–301. doi:10.3354/MEPS08864

Pillans, R. D., Franklin, C. E., and Tibbetts, I. R. (2004). Food choice in *Siganus fuscescens*: influence of macrophyte nutrient content and availability. *Journal of Fish Biology* **64**, 297–309. doi:10.1111/J.0022-1112.2004.00261.X

Pillans, R. D., Bearham, D., Boomer, A., Downie, R. A., Patterson, T. A., Thomson, D. P., and Babcock, R. C. (2014). Multi year observations reveal variability in residence of a tropical demersal fish, *Lethrinus nebulosus*: implications for spatial management. *PLoS One* **9**(9), e105507. doi:10.1371/JOURNAL.PONE.0105507

Robertson, D. R., Sweatman, H. P. A., Fletcher, E. A., and Cleland, M. G. (1976). Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* **57**, 1208–1220. doi:10.2307/1935045

Sakai, K. (2003). Kyphosidae. In 'FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 5. Bony Fishes Part 3 (Menidae to Pomacentridae)'. (Eds K. E. Carpenter and V. H. Niem.) pp. 3290–3295. (FAO: Rome, Italy.)

Silverman, B. W. (1986). 'Density Estimation for Statistics and Data Analysis.' (Chapman and Hall: London, UK.)

Stocks, J., Gray, C., and Taylor, M. (2015). Out in the wash: spatial ecology of a temperate marine shallow rocky-reef species derived using acoustic telemetry. *Marine and Freshwater Research* **66**, 559–571. doi:10.1071/MF14182

Van Winkle, W. (1975). Comparison of several probabilistic home-range models. *The Journal of Wildlife Management* **39**, 118–123. doi:10.2307/3800474

Vergés, A., Vanderklift, M. A., Doropoulos, C., and Hyndes, G. A. (2011). Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. *PLoS One* **6**(2), e17115. doi:10.1371/JOURNAL.PONE.0017115

Welsh, J. Q., and Bellwood, D. R. (2012*a*). How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. *Coral Reefs* **31**, 991–1003. doi:10.1007/S00338-012-0922-Z

Welsh, J. Q., and Bellwood, D. R. (2012*b*). Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs* **31**, 55–65. doi:10.1007/S00338-011-0813-8

Welsh, J. Q., and Bellwood, D. R. (2014). Herbivorous fishes, ecosystem function and mobile links on coral reefs. *Coral Reefs* **33**, 303–311. doi:10.1007/S00338-014-1124-7

White, G. C., and Garrott, G. A. (1990). 'Analysis of Wildlife Radio-tracking Data.' (Academic Press: San Diego, CA, USA.)

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168. doi:10.2307/1938423

Yatsuya, K., Kiyomoto, S., and Yoshimura, T. (2015). Seasonal changes in dietary composition of the herbivorous fish *Kyphosus bigibbus* in southwestern Japan. *Fisheries Science* **81**, 1025–1033. doi:10.1007/S12562-015-0919-Y

Zeh, D. R., Heupel, M. R., Limpus, C. J., Hamann, M., Fuentes, M. M. P. B., Babcock, R. C., Pillans, R. D., Townsend, K. A., and Marsh, H. (2015). Is acoustic tracking appropriate for air-breathing marine animals? Dugongs as a case study. *Journal of Experimental Marine Biology and Ecology* **464**, 1–10. doi:10.1016/J.JEMBE.2014.11.013

13.3 Report appendix 3. Communications

PMCP (WHOLE OF PARTNERSHIP)

Articles

A media release about the project and the partnership was given on the 13th February, 2014 and a link to the press release created on the CSIRO website (https://www.csiro.au/en/News/News-releases/2014/Pilbara-marine-health-check-good-and-bad-news). This resulted in 5 print articles, ~40 online articles (regional, national and international syndicated coverage), 11 radio mentions/interviews, and 3 TV mentions/interviews; all together reaching an audience of almost 1.5 million people. Highlights included live interviews on ABC News 24, Channel 7 News Perth and radio interviews/features on Triple J, 2GB and ABC Sydney.

At the same time, a CSIRO Blog was published about the commencement of the PMCP (https://blog.csiro.au/going-undercover-with-a-marine-biologist/).

The Oceans Institute ran a one-page piece on the PMCP symposium in the 2014 Annual Report (http://www.oceans.uwa.edu.au/__data/assets/pdf_file/0008/2763359/122237_OCEINS-web-spreads.pdf) read by over 1000 stakeholders.

Symposia and presentations

During the course of the PMCP project, two symposia were run in Western Australia, Perth. Both were an overwhelming success with ~100 attendees at each event, with representatives from over 30 institutions. The aim of the symposium in 2014 was to showcase the initial work done in the PMCP project (alongside other research done in the Pilbara) and to foster open discussions on future work and direction. In 2016, another symposium was run to present the findings of four years of research conducted in the Pilbara region – again primarily by the PMCP team, but also other agencies. Presentations from the 2016 Symposium can be found at https://research.csiro.au/pmcp/pmcp-publications/2016-pmcp-symposium-outputs/.

Following the 2016 Symposium, a PMCP working group brought together interested stakeholders from DBCA, Fisheries and the PMCP to discuss results and science needs of management.

Numerous lead researchers from the PMCP team participated in a series (3) of “Lunch n Learn” sessions held in the DBCA offices at Kensington, where these key researchers shared their scientific findings from this partnership. Presentations and audio recordings of the seminars can be found at https://research.csiro.au/pmcp/pmcp-publications/.

Capability development

The PMCP played an important role in generating collaborations, diversifying and developing skills across a large number of marine scientists in WA, nationally and internationally. In total, the number of authors involved in PMCP publications totals 122 across 22 institutions.

ENVIRONMENTAL DRIVERS

Articles

A *Coastlines* (WA Department of Planning and Infrastructure) article titled 'Mapping our Pilbara seabed biodiversity' was published in April 2016. The item can be found on page 7 here: http://www.planning.wa.gov.au/dop_pub_pdf/Coastlines_Autumn_Edition_2016.pdf

Presentations

At the 3rd DBCA Lunch and Learn series of talks, Professor Ryan Lowe (UWA) and Dr Fabio Boschetti (CSIRO) presented a talk titled "Understanding factors causing environmental change in the Pilbara region". The presentation can be viewed at https://www.youtube.com/watch?v=0bFaaDFdnco&feature=youtu.be.

CORAL REEF HEALTH

Articles

The following CSIRO Blogs were published:

- https://blog.csiro.au/the-thorny-issue-threatening-the-coral-reefs-of-pilbara/ (November 2014)
- https://blog.csiro.au/monitoring-mandu-10-years/ (March 2016)
- https://blog.csiro.au/spawning-in-the-wind-full-moon-triggers-currents-of-coral-sperm-and-eggs/ (March 2016) with resulting media
    - 29 March 2016 11:00, pre-recorded interview with Angus Sargeant ABC Pilbara
    - 29 March 2016 13:00, phone conversation with Tarek Dale (Policy Advisor to Rachel Siewert – Greens Senator for WA)
    - 30 March 2016 07:20, live interview with ABC North-West
    - Online newspaper publications (China.org.cn; Xinhuanet.com; Businessinsider.com.au)

In February 2015, Channel 9's evening news presented a feature article on PMCP surveys of COTS outbreaks in the Montebello and Barrow Islands (https://www.youtube.com/watch?v=KuToGv8jd38). This lead to significant interest from media in relation to COTS survey and COTS outbreak with several interviews with radio (ABC RN, News Radio, State and regional radio in WA, ABC TV).

The article "WA's coral reefs are in trouble: we mustn't ignore them" was published in The Conversation in January 2016, with resulting media:

- 27 Jan 2016 17:22, Radio National, Canberra (PM)
- 27 Jan 2016 18:26, 666 ABC Canberra, Canberra (PM)
- 27 Jan 2016 19:18, ABC News Radio, Melbourne (Evenings)
- 27 Jan 2016 19:12, ABC Online

Presentations

At the 13th International Coral Reef Society in June 2016, in Hawaii, a presentation was given on

“High densities and selective feeding of COTS threatens post-bleaching recovery of coral reefs in north-western Australia” by Mick Haywood. A PDF of the presentation can be found at https://research.csiro.au/pmcp/wp-content/uploads/sites/65/2016/03/2016_June_ICRS_MHaywood_MontesCOTS.pdf.

At the 2nd DBCA Lunch and Learn series of talks, Dr Russ Babcock (CSIRO) presented a talk titled “Dynamics of Coral Communities” and Professor Malcolm McCulloch (UWA) presented a talk titled “Corals Past and Future”. The presentations can be viewed at https://www.youtube.com/watch?v=a560KL4jqJI&feature=youtu.be.

FISH AND SHARKS

Social media

Weekly postings and communications have been uploaded to the following social media pages:

- Facebook (https://www.facebook.com/marineecologygroupUWA) posts have followed the progress of the project and generated >1100 likes and >1090 followers.
- Science communication outreach through Youtube (https://www.youtube.com/channel/UCZJl1AUIa-O6WgTSgViNeew)
- Science communication outreach through Instagram: MEG_fish_lab

Presentations

- presentations (3) at the Australian Society for Fish Biology conference, Sydney 2015,
- presentations (4) at the Australian Society for Fish Biology conference, Albany 2017,
- a presentation at the 13th International Coral Reef Society in June 2016, in Hawaii, titled “Evidence of three level trophic cascades within reef fish assemblages from body-size distributions”,
- a presentation at the 1st DBCA Lunch and Learn series of talks, titled “Uncovering the nature of fish – habitat relationships in the Pilbara”, presented by Dr Di Mclean (UWA) and Dr Tim Langlois (UWA). The presentation can be viewed at https://www.youtube.com/watch?v=awgBwf6xfwo&feature=youtu.be.

Research student education opportunities

The following students have worked within the Fish and Shark component of the PMCP project:

- one PhD student,
- six Masters students,
- four Honours students.

Global fish archive

One of the project’s most important outputs has been the creation of web-based tool for archive and synthesising historical and modern ecological data sets and Open Data access to the data collected during the project. This tool, globalarchive.org has been developed with initial funding from the current project, the UWA Emerging Leaders Fund and the NectarCloud.

Over the last year, this tool has been enthusiastically taken up by national data institutions and has received additional support from Australian Ocean Data Network and the Integrated Marine Observing System. This tool has also been adopted by the National Environmental Science

Programme network for Baited Remote Underwater Video (BRUV), including all the major holders of BRUV data in Australia. There is now an opportunity for additional funding to develop the globalarchive.org tool as part of a national Marine Research Data Cloud funding opportunity via IMOS and Australian National Data Services, Research Data Services and Nectar. This tool is now being taken up nationally for State of the Environment reporting.

13.4 Report appendix 4. Theme summary documents

MAPPING SEABED DIVERSITY

Pilbara Marine Conservation Partnership

Environmental Pressures - Mapping our seabed biodiversity

The Pilbara shelf is an important area, for both its exceptional biodiversity, and its economic development significance. Natural resource conservation is a primary goal for the region which supports extensive human activities like offshore gas and petroleum production as well as commercial and recreational fishing. Planning, assessment and management of the Pilbara's marine environment requires a thorough understanding of the distribution of habitats and biodiversity. It has been highlighted that managers need more information about marine habitats and biodiversity distribution patterns and risks on the Pilbara shelf to ensure human activities are conducted sustainably. A team of Pilbara Marine Conservation Partnership researchers have delivered vital seabed biodiversity maps to help achieve this outcome.

Background

The Pilbara shelf has been a centre of activity over the last decade with large scale developments occurring both on the shelf and along the coastline. Development in the Pilbara's marine environment has, at times, occurred at a rate faster than our capacity to fill key knowledge gaps. Most of the current knowledge of the region has also come from historical offshore fisheries surveys. The lack of detailed understanding of the dynamics within this marine area have made environmental assessments challenging for both industry and the responsible regulators.

To help close this gap the Pilbara Marine Conservation Partnership (PMCP) has been undertaking research on a range of topics in the Pilbara.

Figure 1: Photograph illustrating an example of the abundance and diversity of sponges observed in the Pilbara study area (CSIRO).

The Approach

Between 2012 and 2015, the Pilbara Seabed Biodiversity Mapping & Characterisation Project mapped marine habitats and their associated biodiversity across the length and breadth of the west Pilbara shelf. The regional seabed biodiversity study area spanned the region between northern Ningaloo to the Dampier Archipelago, encompassing Barrow Island and the area west of the Montebello Islands, to depths of approximately 50 metres. The key objective of the study was to provide a region-wide characterisation of biodiversity and habitat patterns in the west Pilbara.

Comprehensive information on biodiversity of the seabed gathered during the Pilbara Seabed Biodiversity Mapping & Characterisation Project was collected by visiting 125 sites, representing a wide range of environments on the Pilbara shelf. Data were collected and processed from over 63 kilometres of towed video, 1469 benthic sled samples and 382 demersal fish trawl samples. Taxonomists and other staff from the WA Museum identified 1326 species or taxa.

All this information was used to identify key environmental variables important for structuring seabed distributions, and the development of predictive models of bio-physical relationships between seabed species, their assemblages and the physical environment.

Pilbara Marine Conservation Partnership

Environmental Pressures - Mapping our seabed biodiversity

What did we uncover?

From the information and data collected during the surveys and environmental data sets already in existence (e.g. bathymetry; sediment properties; seabed current stress; NASA Ocean colour; human use data layers) predictive models were developed to quantify the bio-physical relationships between seabed species, their assemblages and the physical environment.

Ten unique biogeographic areas were identified, including details on their composition in terms of habitats, species and characteristic environmental attributes (e.g. depth; salinity; slope).

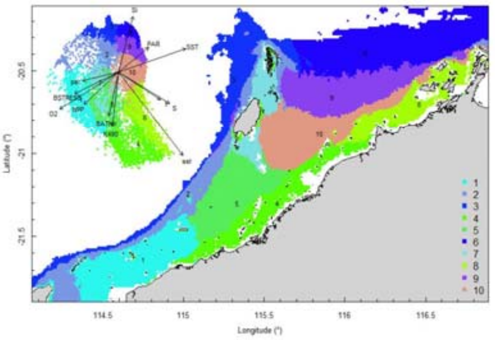

Figure 2: Final seabed characterisation of the west Pilbara region (5-50 m water depth). Ten assemblage types were defined based on analyses of new and existing biological survey data with multiple environmental layers. The biplot indicates the principal variables associated with the assemblages.

Maps were also produced of the predicted distribution and abundance of 180 seabed species throughout the Pilbara study region.

These new data and its analyses have documented the important relationships between sampled species distributions and environmental gradients and have been used to predict patterns of seabed assemblages and species distributions at a regional scale.

Other outputs from the project include thousands of valuable biodiversity specimens accessioned into the WA Museum, and the identification of several new species.

Who is this information useful to?

The project has demonstrated substantial biodiversity on the seabed in the Pilbara region, and has filled in data gaps for the majority of the ~18,700 km² study area, much of which had no pre-existing data.

The information provided by the project will help support the sustainable management of the Pilbara region by providing a range of maps that can be utilised in quantitative environmental assessments, to support spatial planning and management applications across the west Pilbara including conservation and assessments of current uses. The maps can also assist program design for monitoring of biodiversity attributes with respect to various human uses, mapping biodiversity values and quantifying their levels of protection in sanctuary or special purpose zones, and exposure to areas of use.

The characterisation maps also have the potential to provide information for evaluating future development proposals — thus providing lasting benefits.

Lead contact details

Roland Pitcher, CSIRO: roland.pitcher@csiro.au

Jane Fromont, WA Museum: jane.fromont@museum.wa.gov.au

The Pilbara Marine Conservation Partnership (PMCP), has been a five year program (2012-2017) supported by the Gorgon Barrow Island Net Conservation Benefits Fund, an initiative of the Western Australian Government to provide funding for conservation work at the leading edge of scientific knowledge.

To find out more visit: https://research.csiro.au/pmcp/

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CONNECTIVITY

Pilbara Marine Conservation Partnership

Environmental Pressures - Connectivity

The Pilbara region in Western Australia features extensive and globally-significant fringing coral reef ecosystems with high levels of endemism given the number of species only found in this area. It is thought that some reefs may contribute disproportionally more to recruitment stock than other locations, meaning these "source" reefs are especially important to ensuring the resilience of the wider-reef ecosystem. The reverse can also be true with some reefs receiving a disproportionally high supply of larvae, meaning these "sinks" could potentially be more robust to disturbances. Having an understanding of these complex patterns and processes is important to inform management of marine resources. Using a combination of sophisticated 3D modelling of ocean currents and data on the behaviour and distribution of corals and fish, the PMCP research team has mapped out the "connectedness" of coral reef species in the Pilbara region.

Background

A huge diversity of habitats including coral reefs, seagrass meadows and sponge gardens are found in the Pilbara. Many of these habitats have patchy distributions, with organisms needing to travel long distances to reach the ones they favour.

Ordinarily, this dispersal activity occurs in the first month of life when larvae swim or float in the water column as microscopic plankton. This phase of life connects the fates of distant populations and has the potential to profoundly affect their resilience to human or natural perturbations. Yet, dispersal is extremely difficult to measure in marine environments because larvae are tiny and the ocean is vast.

Little is known about how well connected the major habitats in the Pilbara are. This region features extensive and globally-significant fringing coral reef ecosystems with over a thousand discrete reefs and islands recorded. It encompasses several Marine Protected Areas (MPAs) and supports important fisheries and major oil and gas developments.

How interdependent are individual reef communities in the Pilbara? Do the strong coastal currents mean they are well-connected by frequent dispersal, and so resilient to disturbance? Or, are some parts isolated and therefore, more vulnerable, requiring different management strategies?

The PMCP connectivity project addressed these questions and sought to understand the biophysical drivers of connectivity in the Pilbara.

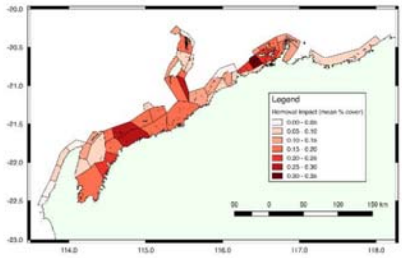

Figure 1 Impact analysis. The change in coral cover in all remaining zones, as a result of a perturbation which destroys the coral supporting habitat in a zone. Red zones have a higher regional impact.

The Approach

The PMCP researchers at CSIRO used 3D modelling of ocean currents coupled with behaviour and distribution data of representative corals and fish, to predict the connectedness of populations in the Pilbara and to evaluate how this is likely to vary across the region, through space and time. The team also used network analysis that coupled connectivity models with population dynamics, to evaluate the likely inter-dependencies in recruitment among reefs generally and between MPAs and unprotected areas, including estimating the significance of different reefs to overall system resilience (Figure 1).

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Pilbara Marine Conservation Partnership

Environmental Pressures - Connectivity

What did we uncover?

The Coral Larvae Dispersal model predicted that some reefs are consistently important in both exporting and receiving larvae, so are key to sustaining the network of reefs in the region. For example, reefs off Onslow, south of Barrow Island (Figure 1) were predicted to be important for maintaining regional resilience. These results have important implications for marine conservation and development planning in the west Pilbara.

A run of the Coral Larvae Dispersal Model can be viewed at the CSIRO PMCP website. See 'Connectivity' for more details.

The models also predict year-to-year variation in how far and in which direction coral and fish larvae will be transported by currents. For example, many corals spawn during a narrow time window in autumn. In some years, such as 2008, this coincided with a dominant south-westward trend in currents, but in other years such as 2004 it coincided with a dominant north-eastward trend.

In contrast, fish like the spangled emperor *(Lethrinus nebulosus*), spawn over a long period from late spring (November) to early autumn (March), and larvae spend more than a month in the plankton before settling on or near reefs. The models predict that fish larvae spawned near the Montebello/Barrow Island marine conservation reserves in September are likely to recruit nearby, but by March most larvae are expected to be transported as far as Ningaloo Reef due to the onset of the Holloway Current (Figure 2).

Fish larvae, unlike those of corals, are strong swimmers and can swim towards favoured habitats. Can this counteract the strong currents experienced on the Pilbara? Models showed that yes, swimming does make a big difference. It means that on average fish settle on or near reefs closer to where they are spawned than would be expected purely according to currents. This matches what has been seen in field studies elsewhere.

It's important to recognise that these results are based on computer simulations that must make several simplifying assumptions because knowledge of the biology of fish and coral larvae is limited. The PMCP team have undertaken a field program measuring actual recruitment and have used those results to test model predictions.

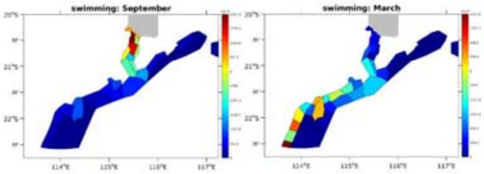

Figure 2: A comparison of the fates of spangled emperor larvae spawned near Montebello Island early and late in the season. Colours indicate the number of larvae predicted to settle after 32 days.

Who is this information useful to?

This information should assist agencies tasked with managing marine biodiversity and fisheries resources, including the planning of marine parks, and designing strategies for sustainable harvest.

Lead contact details

Dr Ming Feng, CSIRO: Ming.feng@csiro.au
Dr Russ Babcock, CSIRO: Russ.babcock@csiro.au
Dirk Slawinski, CSIRO: Dirk.slawinski@csiro.au
Fabio Boschetti, CSIRO: Fabio.boschetti@csiro.au
Dr Oliver Berry, CSIRO: Oliver.berry@csiro.au

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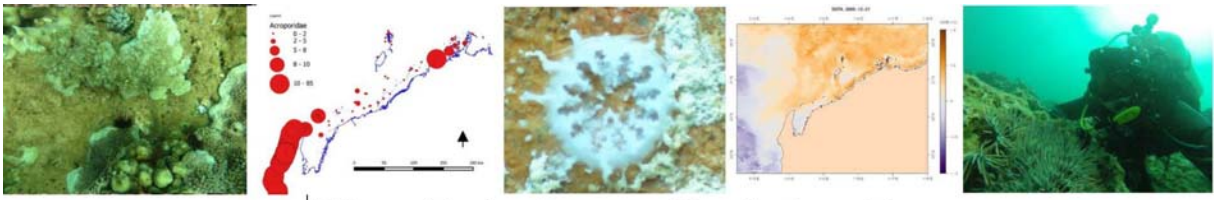
CORAL REEF HEALTH



Pilbara Marine Conservation Partnership

Coral Reef Health – Coral Community Dynamics

The Pilbara shelf in Western Australia supports a wide range of marine life including coral reef systems which contribute to the area's productive fisheries. Operating in close proximity to these important natural assets are some of Australia's largest offshore gas and petroleum production activities and the state's largest bulk export port. Planning, assessment and management in the Pilbara's marine environment requires a robust level of understanding about the distribution of coral reefs and their ability to withstand and recover from impacts, both natural events like cyclones and more localised effects such as port developments. The Pilbara Marine Conservation Partnership (PMCP) have worked closely with researchers from Western Australia's statutory agencies to deliver a broad scale understanding of coral reefs in the Pilbara in order to help deliver better conservation outcomes both now and into the future.

Background

The coastal bioregions of the west Pilbara (in Western Australia) comprise globally-significant fringing coral reef ecosystems, characterised by species from both Indonesian and Pacific origins. The region is also adjacent to the world's largest fringing coral reef system, Ningaloo Reef, which was declared a World Heritage Area in 2011.

These ecosystems are unique, because of their location adjacent to an arid coast that receives very little terrestrial runoff, thereby facilitating high coral growth; exceptional for a continental margin.

In recognition of the conservation value of the area a number of marine parks and marine management areas have been declared and are managed by Parks and Wildlife (Western Australia). A base level of understanding about the distribution of coral reefs and their ability to withstand and recover from impacts is required to ensure conservation and economic development aspirations can be balanced.

The Approach

Between 2013 and 2017, the Pilbara Marine Conservation Partnership (PMCP), a partnership between CSIRO and the University of Western Australa, collected data from reefs throughout the west Pilbara region and Ningaloo (Figure 1), to provide an assessment of the condition of the region's reefs and to strengthen the understanding of the processes that affect them. The information gathered on the diversity of reef types and habitats encountered and the challenges faced by reefs in the region will be used to complement existing management and assessment programs to provide ongoing advice in the region. Key objectives for the research included:

- Establishing a monitoring program which was compatiable with other monitoring work occurring in the region;
- Investigating abundances and diversity of coral reef benthos and describing their current condition across regional gradients; and
- Understanding regional patterns and temporal variability in assemblages.

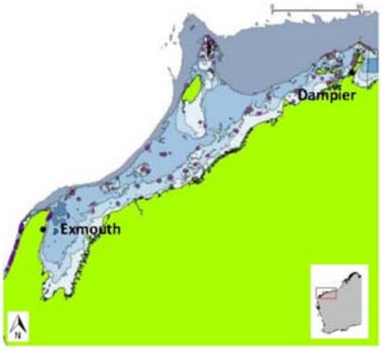
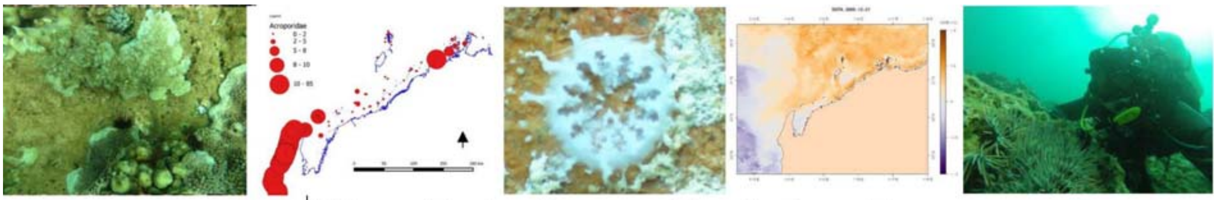


Figure 1: Locations of fifty-five reefs and more than 100 sites sampled by the PMCP team.



Pilbara Marine Conservation Partnership

Coral Reef Health – Coral Community Dynamics

What did we uncover?

Marine heat wave effects

Surveys of reefs from the Dampier Archipelago and Montebello Islands to the Muiron Islands and Northwest Cape in the south, showed the impacts of two separate coral bleaching events which occurred in 2011 and 2013 respectively. In such events, corals lose their colour and are often killed by the unusually high water temperatures which force them to expel their zoozanthellae.

As a result of these heat waves, corals such as branching *Acropora* (the most abundant corals that builds reefs in the region) were decimated in the central west Pilbara (Figure 2). Even mortality of hardy, centuries-old *Porites* bommies was observed in some locations (Figure 3a). The scale of the impact has been documented by PMCP researchers, with little or no recovery observed in the affected reefs monitored post 2013.

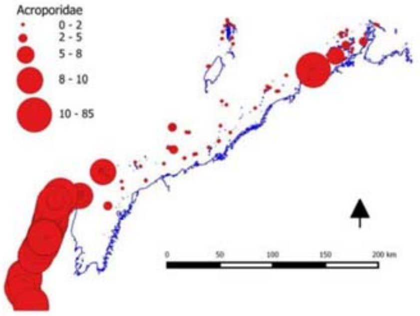


Figure 2: Relative cover of live *Acropora* corals post bleaching in 2013, showing lack of live coral in the central region affected by bleaching.

While cyclone activity in the region has been unusually low since the bleachings, outbreaks of the crown-of-thorns starfish (*Acanthaster*; Figure 3b) have added to the effects of bleaching and slowed or reversed recovery in some areas around the Barrow and Montebello islands.

It is important to document the rate of recovery of these reefs. By doing this can we understand their ability to recover from impacts associated with weather and climatic extremes that are predicted to become even more frequent and severe in the future. Data collected on recovery is also linking into connectivity modelling being undertaken to predict the flow of coral larvae around and between reefs to better understand reef recovery via larvae supply.

Figure 3: (a) A partially bleached massive *Porites* colony (b) *Acanthaster* (crown-of-thorns starfish) feeding on a *Symphyllia* coral.

Who is this information useful to?

The work completed has shown not only the diversity of reef types and habitats encountered but also provided insights into the challenges faced by reefs in the region. It is hoped that information provided directly to marine park managers will translate into actions that help maintain high levels of environmental management effectiveness in the region.

The information will be useful to Marine Parks and Fisheries managers, as well as to environmental regulatory bodies and environmental consultants.

Lead contact details

Russ Babcock, CSIRO: russ.babcock@csiro.au
Mick Haywood, CSIRO: mick.haywood@csiro.au
Damian Thomson, CSIRO: damian.thomspon@csiro.au

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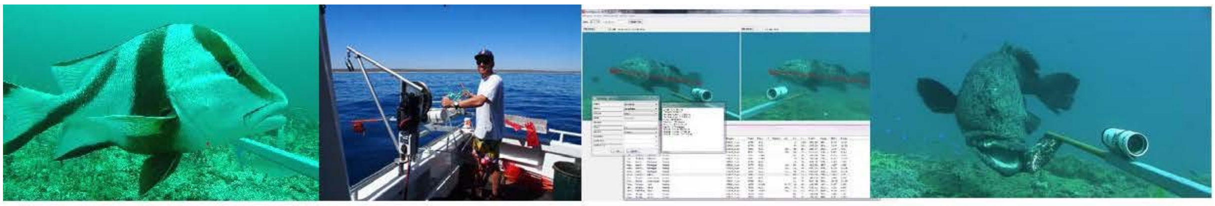
FISH AND SHARKS



Pilbara Marine Conservation Partnership

Fish and Sharks – Uncovering Fish-Habitat Relationships

The Pilbara region in Western Australia is known for its rich marine biodiversity, recreational and commercial fishing and its contribution to the Australian economy. The region is home to an array of fish and shark communities, which are described as highly diverse and play an important ecological role in the regions marine environment. Given the need to balance the goals of natural resource conservation alongside developments such as offshore gas and petroleum production, a baseline understanding of habitats, fish diversity and distribution is needed. To help achieve this outcome, the Pilbara Marine Conservation Partnership have worked closely with the state's statutory agencies to deliver a broad scale understanding of the patterns of fish and shark abundance distribution in relation to habitat, and developed novel methods for future work.

Background

The Pilbara region (in Australia's north-west) hosts a highly diverse fish assemblages which are also noted for their and economic importance to both commercial and/or recreational fishers.

Fish assemblages are known to be particularly vulnerable to fishing pressure, climate change and activities that affect habitat quality. Those responsible for the management of natural resources are challenged with finding a balance between the economic benefits of extractive industries such as fisheries and oil and gas development with the maintenance of biodiversity and ecosystem services.

To help inform these decisions, researchers from The University of Western Australia (UWA) and CSIRO, through the Pilbara Marine Conservation Partnership (PMCP) have undertaken the first regional-scale assessment of the conditions of, and threats to, finfish and shark biodiversity assets.

The Approach

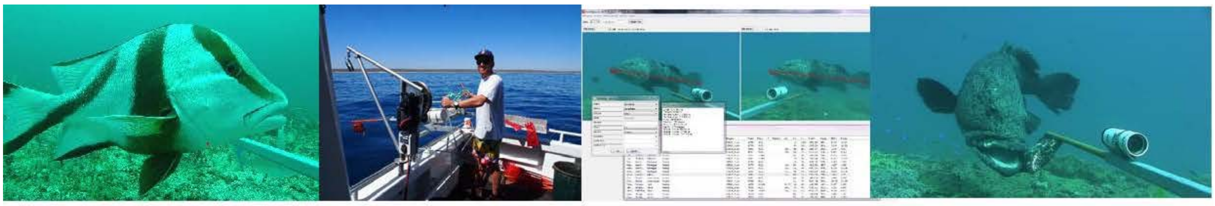
The key objectives of the fish and shark research included gathering a baseline and quantifying the condition of fish and shark assemblages across the Pilbara; and investigating human-induced changes by assessing and comparing composition, abundance, size-structure and biomass of fishes across gradients in fishing pressure (including inside and outside closed fishing areas).

To achieve these objectives the team surveyed ~340 km of coastline between Coral Bay and Dampier (2013 to 2016), deploying almost 2000 Stereo Baited Remote Underwater Video systems (BRUVs) and conducting over 1200 Diver Operated stereo-video (DOVs) transects.

Data on size, distribution and abundance for over 550 fish and shark species were collected and their relationship with a range of nearshore habitat, environmental and geographical variables assessed.

As part of the research, the team has also developed new light-weight and cost effective techniques for the rapid assessment of fish-habitat associations.

Figure 1: BRUVS showing Bass, cod and sea snake.



Pilbara Marine Conservation Partnership

Fish and Sharks – Uncovering Fish-Habitat Relationships

What did we uncover?

The research team investigated fish and habitat associations by analysing fish assemblages of four dominant habitat types (Fig 2). The results show that islands in the southern part of the Pilbara, including North and South Muiron, Serrurier, Bessieres, Thevenard and Airlie Islands possessed species-rich assemblages with high abundances of fish, including important species targeted by fishers and protected species. These islands have structurally complex reef systems with a high coverage of hard corals, macroalgae and soft corals.

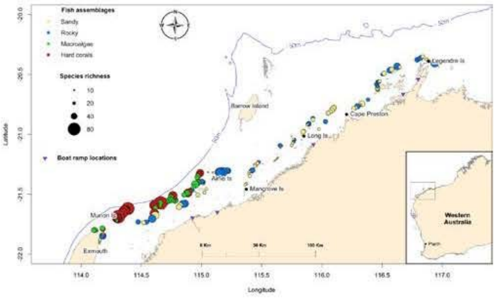


Figure 2: Spatial distribution of species richness as sampled by stereo-BRUV and the associations of particular fish assemblage types with particular types of dominant benthos as indicated by multivariate regression trees. Courtesy of Laura Pittino.

Data collected near Dampier Archipelago on the short-lived commercially important target species the blue spotted emperor (*Lethrinus punctulatus*) revealed strong associations with depth, with small juveniles showing a strong preference for shallow macroalgal beds. Individuals were found to shift from shallow to deep water as they grow to avoid predators. This observation highlights the importance of shallow water habitats for maintaining stock levels and the need for these areas to be considered in decisions which are aimed at enhancing sustainable fisheries management practices in the region.

As part of this work, a novel, cost-effective, standardised method for rapidly quantifying habitat cover and relief was derived for data collected using forward-facing stereo BRUVS. The technique developed uses CATAMI (the Australian standard for habitat classification) and has been made freely available on Github.

Figure 3: Stereo-BRUVs set-up (left) and Stereo-DOVs transect being completed (right).

Who is this information useful to?

Substantial datasets from this work are now available (online at GlobalArchive) for reporting on the condition of fish and shark assemblages across fishing pressure and environmental gradients. Understanding where juvenile fish and shark are associated with benthic habitat is critical for conservation planning, characterising habitat and sustainable management of the fisheries in the Pilbara. The data from this research also form the much needed baseline for researchers to study impacts, and are invaluable to industry for impact assessment and oil spill planning and response purposes.

The powerful analytical approach developed as part of this research for gathering knowledge is now available for broader application in biogeography studies.

Lead contact details

Tim Langlois, UWA: Timothy.langlois@uwa.edu.au
Dianne McLean, UWA: Dianne.mclean@uwa.edu.au

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To find out more visit: https://research.csiro.au/pmcp/

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