

# Mesophotic depths as refuge areas for fishery-targeted species on coral reefs

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**Abstract** Coral reefs are subjected to unprecedented levels of disturbance with population growth and climate change combining to reduce standing coral cover and stocks of reef fishes. Most of the damage is concentrated in shallow waters (<30 m deep) where humans can comfortably operate and where physical disturbances are most disruptive to marine organisms. Yet coral reefs can extend to depths exceeding 100 m, potentially offering refuge from the threats facing shallower reefs. We deployed baited remote underwater stereo-video systems (stereo-BRUVs) at depths of 10–90 m around the southern Mariana Islands to investigate whether fish species targeted by fishing in the shallows may be accruing benefits from being at depth. We show that biomass, abundance and species richness of fishery-targeted species increased from shallow reef areas to a depth of 60 m, whereas at greater depths, a lack of live coral habitat corresponded to lower numbers of fish. The

majority of targeted species were found to have distributions that ranged from shallow depths (10 m) to depths of at least 70 m, emphasising that habitat, not depth, is the limiting factor in their vertical distribution. While the gradient of abundance and biomass versus depth was steepest for predatory species, the first species usually targeted by fishing, we also found that fishery-targeted herbivores prevailed in similar biomass and species richness to 60 m. Compared to shallow marine protected areas, there was clearly greater biomass of fishery-targeted species accrued in mesophotic depths. Particularly some species typically harvested by depth-limited fishing methods (e.g., spearfishing), such as the endangered humphead wrasse *Cheilinus undulatus*, were found in greater abundance on deeper reefs. We conclude that mesophotic depths provide essential fish habitat and refuge for fishery-targeted species, representing crucial zones for fishery management and research into the resilience of disturbed coral reef ecosystems.

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## Introduction

Coral reefs provide resources for millions of people but are under severe threat from local and broad-scale impacts including coral bleaching, storm damage, coastal development, sedimentation and fishing pressure (Hoegh-Guldberg et al. 2007; Newton et al. 2007; Bridge et al. 2013). Fishing, in particular, is recognised as the most widespread, exploitative activity in the marine environment, driven by its importance as a provider of protein to a large part of the human global population (Jennings and Kaiser 1998; Pauly

et al. 2005). Fishing impacts are especially relevant on coral reefs, where an estimated 6 million fishers depend on coral reefs worldwide, evidently supporting the socio-economic well-being of numerous coastal communities (Teh et al. 2013). Unfortunately, coral reef fishery catches have declined around the world in recent decades (Newton et al. 2007; Cuetos-Bueno and Houk 2015), prompting calls for improved management of this valuable resource (Houk et al. 2012).

Threats to coral reefs are ever increasing yet typically concentrated on the shallowest depths where fishing pressure is most focused and where disturbances such as storms and coral bleaching are most influential (Bongaerts et al. 2010; Bridge et al. 2013; Graham et al. 2015). Once-productive habitats near shore and closer to population centres have deteriorated in many locations, prompting fishers to access new fishing grounds or adopt more efficient fishing practices. For example, since the middle of last century, industrial fishing fleets have responded to diminishing global catches by targeting fishes in deeper waters to maintain high catch rates (Pauly et al. 2005; Morato et al. 2006). On tropical reefs, such a shift in fishing practices to deeper depths has been observed for sea cucumber fisheries (Friedman et al. 2011) and SCUBA has been used for spearfishing to access deeper waters and target high value but vulnerable coral reef fish that have declined in shallow depths (Lindfield et al. 2014). Targeting fish in increasingly deeper water has been termed “fishing down the deep”, and it was recognised a decade ago that rather than exploiting the last refuges for commercial fish species, deep-water habitats should be new candidates for conservation (Morato et al. 2006).

Coral reefs that lie below conventional SCUBA diving depths ( $> \sim 35$  m) are commonly referred to as mesophotic coral ecosystems (MCEs) that represent the extent of the lower distributional limit of zooxanthellate, reef-building corals (Kahng et al. 2014). MCEs are closely linked to shallow reef areas, usually forming a contiguous or semi-contiguous belt of habitat along a depth gradient. While previous work has demonstrated that some fish and other reef organisms have depth ranges that traverse the shallow and mesophotic zones (Brokovich et al. 2008; Slattery et al. 2011; Fitzpatrick et al. 2012; Kahng et al. 2014), the majority of coral reef research has focused on shallow waters ( $< 30$  m) due to technical and logistical constraints on working at mesophotic depths (Kahng et al. 2014). Despite the limitations in studying MCEs, recent studies have revealed that these depths may provide critical refuge habitats; at least one species of fish has been found to be genetically connected between shallow and mesophotic zones (Tenggardjaja et al. 2014), and corals found on deeper reefs can contribute substantially to larval

production compared to shallow reefs (Holstein et al. 2015). It is therefore likely that deep-water reefs may also serve as refuges for coral reef fishes subjected to fishing pressure.

Our study aimed to address the question, “Do MCEs sustain populations of reef fish species that are targeted by fishing within the shallower reef zones?” The waters surrounding the southern Mariana Islands are exceptionally clear, allowing light penetration to great depths, and subsequently allow the development of extensive MCEs, with hard coral recorded to a depth of 150 m (Blyth-Skyrme et al. 2013). The shallow reefs of the region are subject to intense fishing pressure as people still commonly linefish, spearfish, net and glean to augment their protein intake as they have for millennia (Amesbury and Hunter-Anderson 2003; Houk et al. 2012; Cuetos-Bueno and Houk 2015). To address the study question, we quantified the structure of mesophotic fish communities using baited remote underwater stereo-video systems (stereo-BRUVs) in a depth-stratified design.

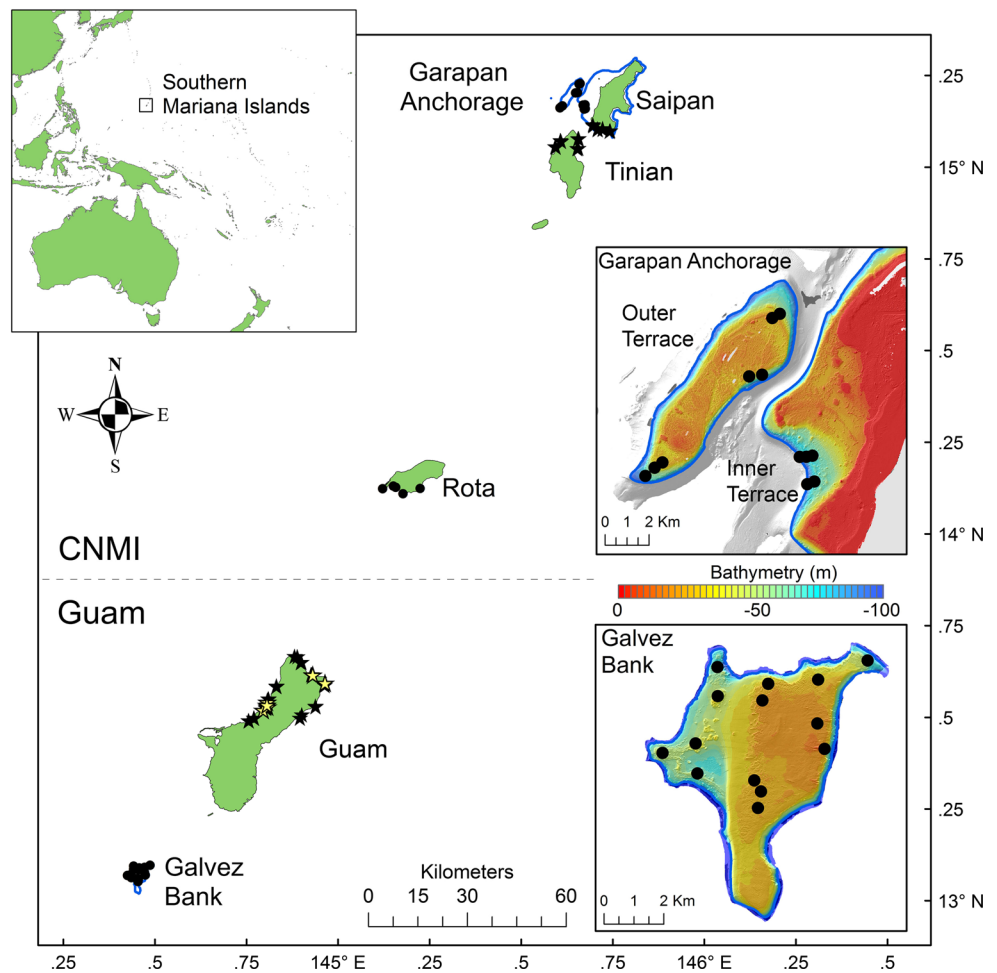
## Methods

### Study area

The southern Mariana Islands (Fig. 1) include the coral reef islands and submerged banks of Guam and the Commonwealth of the Northern Mariana Islands (CNMI). These islands are home to over 200,000 people and have received among the highest levels of fishing pressure in the region, resulting in reduced fish stock abundances and diminished ecological function (Houk et al. 2012; Cuetos-Bueno and Houk 2015).

Sampling locations were chosen to represent a range of depths, wave exposures and levels of fishing pressure found in the southern Mariana Islands. Accordingly, some sites were located in marine protected areas and at sheltered and exposed locations of inshore and offshore reefs (Fig. 1; Table 1). MCEs were sampled at the offshore locations of Galvez Bank, Garapan Anchorage and the inshore coastal waters of Rota. Galvez Bank is a submerged reef located 22 km south-west of Guam (Fig. 1). The shallowest depth is 20 m, but the majority of the bank is within 30–40 m depth with consolidated reef that extends to depths of at least 70 m. Garapan Anchorage is situated off the west coast of Saipan and is closer to shore, but covers a similar depth range of approximately 20–100 m (Fig. 1). Garapan Anchorage consists of an inner terrace and an outer terrace (also known as double reef) and forms the largest shallow insular shelf (58 km<sup>2</sup>) in the entire Mariana Archipelago

**Fig. 1** Study locations in the southern Mariana Islands. Mesophotic sites are indicated as *black circles*, inshore euphotic depths (<35 m) are indicated as *stars*, with MPA sites in Guam coloured *yellow*. The 100 m *contour line* is shown in *blue* for Garapan Anchorage and Galvez Bank



**Table 1** Summary details of the number of sites and stereo-BRUV replicates surveyed at each location

Location	MPA status	Shore/exposure	Sites	Stereo-BRUVs	Min. depth (m)	Max. depth (m)
Galvez Bank	Fished	Offshore exposed	14	54	31	68
Garapan inner terrace	Fished	Offshore sheltered	5	21	60	91
Garapan outer terrace	Fished	Offshore sheltered	7	33	33	68
Rota	Fished	Inshore exposed	2	10	38	65
	Fished	Inshore sheltered	3	11	40	62
Guam North	Fished	Inshore exposed	8	40	10	32
	MPA	Inshore exposed	4	20	10	32
Guam West	Fished	Inshore sheltered	8	40	10	33
	MPA	Inshore sheltered	6	30	10	32
Saipan South	Fished	Inshore sheltered	8	40	9	31
Tinian	Fished	Inshore exposed	8	40	10	32

(Blyth-Skyrme et al. 2013). Previous surveys using towed video camera sleds at Garapan Anchorage identified extensive areas of MCEs on both the inner and

outer terraces, with the greatest hard coral cover in the 60–80 m depth range, associated with a large stand of *Euphyllia* stony coral (Blyth-Skyrme et al. 2013).

## Sampling methods

Fish communities were sampled using baited remote underwater stereo-video systems (stereo-BRUVs). These systems are a practical and cost-effective technique for surveying reef fish across a range of depths and habitats (Langlois et al. 2010). The stereo-BRUVs consisted of two Sony CX-7 high-definition video cameras in purpose-built underwater housings that were mounted on a base bar, 0.7 m apart and inwardly converged at 8°. Detailed information on the design and photogrammetric specifics of these systems is presented in Harvey et al. (2010). Each system was baited with 1 kg of chopped and crushed Pacific saury (*Cololabis saira*), which was placed in a plastic-coated wire basket and suspended 1.2 m in front of the two cameras. The systems were left to film on the seafloor for 60 min during daylight hours before they were retrieved.

MCEs of Galvez Bank, Garapan Anchorage and Rota were sampled in February and March 2010 with a fleet of eight stereo-BRUVs during a research cruise on the NOAA vessel *Oscar Elton Sette*. Sampling positions were haphazardly chosen at least 250 m apart with GPS coordinates selected from multibeam bathymetry data (PIBHMC 2010) with a focus on consolidated and preferably high-complexity reef. These deployments were grouped into sites (3–5 replicates) that were spatially clustered together within a similar depth range (Table 1). The coastal waters of Guam, Tinian and Saipan were sampled at depths of 10 and 30 m (as presented in Lindfield et al. 2014). Sampling was attempted in deeper water (30–100 m) at these locations, but the benthic substrate was found to be predominantly sand so we did not continue sampling. A total of 42 sites (5 replicates per site) were sampled around these coastal waters between 1 July and 29 October 2010. Overall, the 73 sites sampled represent data from 339 stereo-BRUVs (Table 1).

## Data processing

Stereo-BRUVs video footage was analysed using specialised software, EventMeasure-Stereo ([www.seagis.com.au](http://www.seagis.com.au)). The maximum number of any one species seen at once during a 60-min recording (MaxN) was used as the measure of relative abundance, with fish measured for fork length (mm FL) at the time of MaxN. To ensure accuracy of the length measurements (see Harvey et al. 2010) while accurately identifying and counting as many fish as possible, we used the following guidelines: small-bodied individuals up to 100 mm length were only counted within 4 m of the cameras; fish to 500 mm were counted to 8 m distance; and larger fish were counted to a maximum distance up to 10 m from the cameras. For individual fish that

could not be measured (e.g., obscured from one of the camera views), we used the average length for that species from that site to calculate biomass.

Historical catch data from Guam were used to classify coral reef fish species targeted by fishing. Fishery-targeted species were selected by reviewing data collected from creel surveys conducted by the Guam Department of Aquatic and Wildlife Resources (DAWR) and the Western Pacific Fisheries Information Network. We selected the top one hundred fish species that contributed to the total biomass of landings from inshore and offshore creel surveys (excluding the landings of deep-water bottom fish caught below the depths of this study). We excluded four small species that are not regarded as fishery targets, but were ranked in this list as they are commonly encountered and sometimes retained by fishers (*Melichthys vidua*, *Balistapus undulatus*, *Odonus niger* and *Cephalopholis urodeta*). In addition, we also included some larger-bodied species that were similar in appearance to other fish species in the list and expected to be retained by fishers, including the majority of species from families Carangidae, Epinephelidae, Lutjanidae, Lethrinidae, the Scarinae tribe of Labridae and the *Naso* genus of Acanthuridae.

Fishery-targeted species recorded on the stereo-BRUVs were measured for length and converted to biomass (g) using the relationship  $\text{weight (g)} = a \times \text{length (mm FL)}^b$ . The  $a$  and  $b$  values required for calculating length–weight relationships were derived from power regressions using accurate fish lengths and weights provided by Guam DAWR. When adequate sample sizes did not allow the formulation of locally derived  $a$  and  $b$  values, we used data from other sources (Froese and Pauly 2013). Each fish species was grouped into one of five trophic groups: (1) primary consumers (including herbivores and detritivores); (2) secondary consumers (including invertivores, corallivores, and omnivores); (3) planktivores (primarily consuming zooplankton); (4) piscivores (including species with fish as the dominant diet item) excluding sharks; and (5) sharks. Trophic classifications followed Sandin and Williams (2010) except for *Lethrinus rubrioperculatus*, which has been recently classified as a piscivore in this region (Trianni and Tenorio 2012). Fish species analysed in this study are listed in Electronic Supplementary Material (ESM) Table S1, along with trophic groupings, length–weight relationship values and the maximum and minimum depth ranges recorded.

Environmental variables were measured for each replicate stereo-BRUVs deployment. Habitat metrics of structural complexity, reef slope and the benthic cover of five habitat types [live coral, macroalgae, turf algae, crustose coralline algae (CCA) and unconsolidated sediment] were visually estimated from the imagery of the video cameras. Estimates of structural complexity followed those used by

Wilson et al. (2007), where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex with numerous fissures and caves, 5 = exceptionally complex with numerous caves and overhangs. Reef slope was also estimated on a 6-point scale from flat to vertical wall. Benthic cover for the five habitat types was graded, where 0 = trace (0 %), 1 = sparse (1–10 %), 2 = low (10–25 %), 3 = medium (25–50 %), 4 = dense (50–75 %), 5 = very dense (>75 %). We extracted values for the distances to deep water (100 m contour), land and the nearest boat ramp using ArcGIS. Maximum depth (m) was recorded using digital depth gauges attached to the stereo-BRUVs.

Individual stereo-BRUVs deployments were clustered into depth groups (e.g., the 30 m depth group ranged from 25.0 to 34.9 m). To show differences between the inshore and offshore locations, the 30 m depth groups sampled at Galvez Bank and Garapan Anchorage were separated from the 30 m sites at the inshore waters of Guam, Tinian and Saipan. Rota was the only inshore location where mesophotic depths (>35 m) were sampled but these data were presented together due to a low number of replications and the similarity of the fish community variables to the offshore locations. To visualise the depth ranges for the main species from each trophic group along with their relative abundance, a heatmap plot was made by averaging the relative abundance counts (MaxN) for each species over all replicates at each depth group and then ranking the abundance values on a standard scale. Graphical plots were created with the ggplot2 package (Wickham 2009) in the R language and environment (R Core Team 2014).

### Statistical analyses

To investigate which explanatory variables contributed to the observed differences in the reef fish assemblage biomass, we used two complementary multivariate methods: multivariate regression trees (MRTs) and distance-based redundancy analysis (De'ath 2002). Explanatory variables for each site (averaged from replicates) were as follows: depth (9–91 m), marine protected area status (fished or MPA), jurisdiction (Guam or CNMI), shore and exposure (inshore/offshore and exposed/sheltered), distance to land, travelling distance to the nearest boat ramp, distance to deep water (100 m contour), the seven habitat metrics and the spatial covariables of latitude and longitude.

MRTs are a powerful and robust method used to analyse complex ecological data including imbalanced designs with both numeric and categorical explanatory variables (De'ath 2002). This method determines clusters that are comparable in species dissimilarity, with each cluster defined by a set of environmental variables (Borcard et al. 2011). MRT analysis was first done to identify the main explanatory

variables and any interactions that may be contributing to the structure of the assemblage. To reduce the importance of large values, but still give low weights to rare species, the fish data were Hellinger-transformed prior to analysis by dividing the biomass of each species by the site total and square root transforming the result (Borcard et al. 2011). We ran the model 100 times to select the optimal tree size for predictive accuracy and chose the tree size that minimised the cross-validated relative error (following Borcard et al. 2011). The results of the MRTs are graphically displayed with threshold values for each split displayed at each tree “node”. Analyses were done using the R package *mvpart* (De'ath 2014).

Indicator values for the MRT were calculated from the Dufrene and Legendre Index (DLI; Dufrene and Legendre 1997) using the function *indval* in the R package *labdsv* (Roberts 2013). This index is maximal when all individuals of a species are found at the particular tree node and when that species is represented at all of those sites (Dufrene and Legendre 1997). The statistical significance of the indicator values (i.e., the probability of obtaining by chance an indicator value as high as that observed) is assessed by means of a permutation test (Borcard et al. 2011). A maximum of ten species that are significant indicators ( $p < 0.05$ ) were displayed on the MRT and ordered by decreasing DLI values.

To identify other explanatory variables that may be important for structuring the assemblage over environmental gradients, we used the distance-based linear modelling (DISTLM) procedure in the PERMANOVA + add-on package for PRIMER v6 (Anderson et al. 2008). Between-sample dissimilarity for this multiple regression analysis was constructed with a Bray–Curtis dissimilarity matrix and square root-transformed biomass data. Model selection was based on the modified Akaike's information criterion (AICc), and the *best* procedure was used to identify the simplest models with the greatest explanatory power. Distance-based redundancy (db-RDA) routine was then used to perform a constrained ordination on the fitted values from the *best* model (Anderson et al. 2008). To visualise the ordination, total biomass values for each site were scaled as bubbles and the fish species that were correlated (Pearson values >0.4) with the assemblage variation were displayed as vectors indicating the strength and direction of the relationships.

## Results

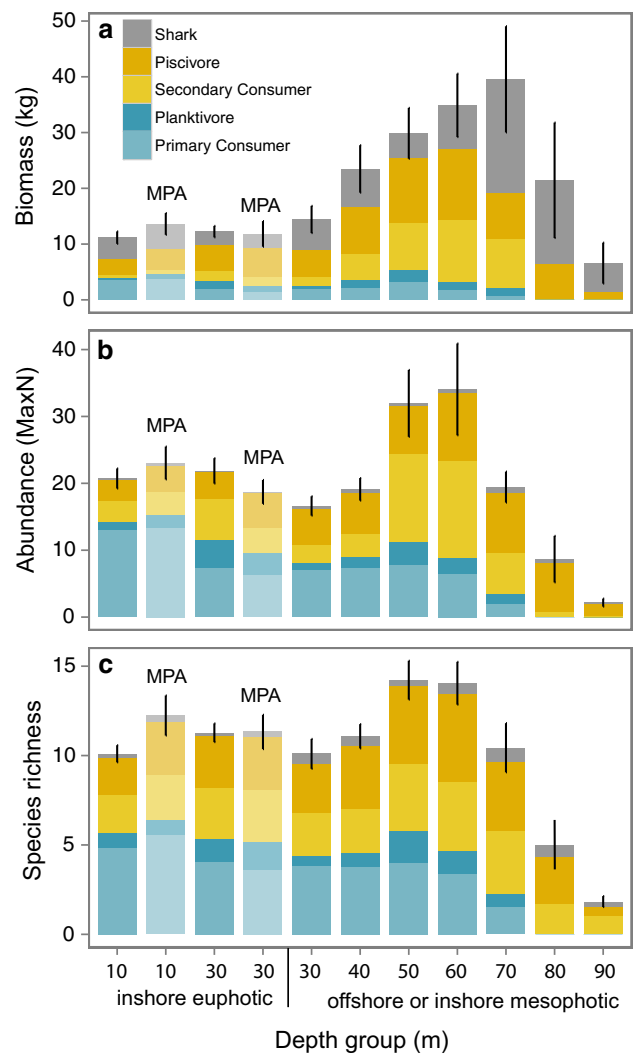
### Diversity and depth distributions

Overall, 7332 individual fish of 100 species and 17 families were counted (ESM Table S1). The majority (75 %) were

observed with depth distributions traversing the shallow ( $\leq 35$  m) and mesophotic zones ( $>35$  m). Only 17 fishery-targeted species were not observed at mesophotic depths, whereas eight species were observed only from mesophotic depths. Of the 32 species of primary consumers that are targeted by fishing, the majority (76 %) had depth ranges extending to mesophotic depths with eight species only recorded at depths  $<35$  m, and three species (*Acanthurus lineatus*, *A. triostegus* and *Naso brachycentron*) only recorded in depths less than 15 m.

Consolidated reef and live coral was observed to a maximum depth of 73 m at Galvez Bank (ESM Fig. S1c). At greater depths, the benthos was dominated by unconsolidated sediment including rubble, sand and foraminifera to the maximum depth sampled of 94 m at the inner bank of Garapan Anchorage (ESM Fig. S1d). Average values of the visually estimated habitat metrics are presented in Table 2; structural complexity was greatest at the inshore euphotic depths and also at the 50 m depth group. At depths greater than 70 m, structural complexity was low, which corresponds to a lack of live coral and high proportions of unconsolidated sediment (Table 2). When habitat variables were analysed with a principal components analysis, replicates from the deeper sites (80–90 m) and one site from 70 m were clearly separated from the majority of shallower replicates due to an increased proportion of unconsolidated sediment and lower structural complexity (ESM Fig. S2). Importantly, the other sites (at depths of 10–70 m) showed no clear pattern with the measured habitat variables among depth groups, indicating similar broad habitat characteristics across the depth range from 10 to 70 m.

Fish community variables of biomass, abundance and species richness peaked at depths of 50–60 m (Fig. 2). These values declined at greater depths, which correspond to the increased proportion of unconsolidated sediment at depths of 70–90 m (Table 2; ESM Fig. S2). At the inshore euphotic depth groups of 10 and 30 m, the comparison of the surveyed MPAs in Guam to all fished locations revealed only a slight (1.1–1.2 times) increase in biomass, abundance and species richness at 10 m depth. Average



**Fig. 2** Mean values ( $\pm$ SE) of **a** relative biomass (kg), **b** relative abundance (MaxN) and **c** species richness of fish communities by depth group and trophic classification. MPA sites are labelled and semi-transparent

biomass of fishery-targeted species increased steadily with increasing depth to a maximum of 70 m, where values were over three times greater than in shallow inshore waters at depths of 10–30 m. Greater biomass in deeper

**Table 2** Average values of the visually estimated habitat metrics recorded from the stereo-BRUVs by depth group. Relative scales range from 0 (lowest) to 5 (greatest)

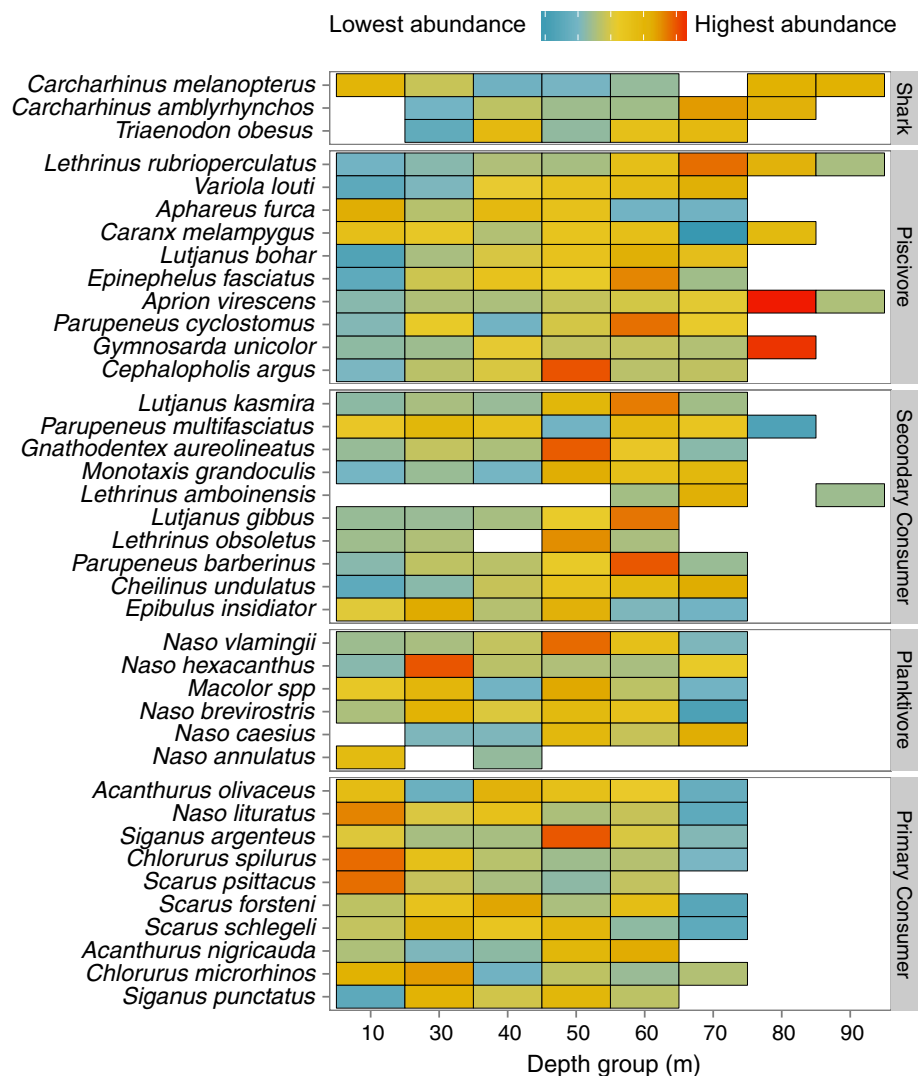
Depth group	Inshore euphotic		Offshore or inshore mesophotic						
	10 m	30 m	30 m	40 m	50 m	60 m	70 m	80 m	90 m
Structural complexity	2.3	2.7	1.2	1.8	2.1	2.3	1.9	0.3	0.2
Reef slope	0.8	1.4	0.4	0.6	1.0	0.8	0.6	0.0	0.0
Live coral	1.7	1.3	1.4	1.6	0.8	1.7	1.9	0.0	0.0
Macroalgae	1.6	2.3	2.7	2.3	2.3	2.0	1.9	2.3	2.2
Turf algae	3.0	2.3	2.0	2.0	2.1	2.0	1.8	2.0	1.3
CCA	1.4	1.8	1.6	1.7	1.7	1.5	1.3	0.7	0.2
Unconsolidated sediment	0.1	0.4	0.5	0.4	1.2	0.9	0.9	3.0	3.7

water was attributed to a greater proportion of higher trophic levels, piscivores (including sharks) and secondary consumers. The relative abundance of fishery-targeted species was greatest in the 50–60 m depth groups and was driven by greater numbers of secondary consumers (Fig. 2b). The increase in relative abundance between the inshore euphotic depths and peak abundances in mesophotic depths was only by a factor of ~1.7, which indicates that the observed threefold increase in biomass was due to the size (length) of fish being greater in mesophotic depths. The abundance of primary consumers was greatest at 10 m depth (mean MaxN = 13) and then relatively consistent at depths of 30–60 m with an average of 6–8 fish per replicate, whereas species richness for this trophic group was relatively consistent over 10–60 m. Species richness of fishery-targeted species peaked at 50–60 m, averaging 14 species per stereo-BRUVs deployment, due

to greater diversity of piscivores and secondary consumers (Fig. 2c).

The depth distribution and relative abundance of the ten most abundant fishery-targeted species for each trophic group (Fig. 3; ESM Table S2) show that the majority of these species were present from 10 m depth to at least 70 m. Some species were found in greater proportions in deeper water (indicated by the warmer colours in Fig. 3), such as the piscivores *Lethrinus rubrioperculatus*, *Variola louti* and *Lutjanus bohar*. The humphead wrasse *Cheilinus undulatus* steadily increased in abundance to 70 m, whereas other species such as the primary consumers *Naso lituratus* and *Chlorurus spilurus* declined in abundance with increasing depth. Most of these primary consumers were still found to depths of 70 m and some were found in greatest relative abundance in mesophotic depths (e.g., the rabbitfish *Siganus argenteus* and the surgeonfish *Acanthurus nigricauda*).

**Fig. 3** Heatmap plot showing the depth distribution of the ten most abundant fishery-targeted species in each trophic group. The relative abundance counts (MaxN) were averaged for each species over all replicates in each depth group; then, abundance values were ranked on a standardised scale. Cooler colours (*blue*) are the lowest relative abundance, and warmer colours (*red*) are the highest relative abundance



### Assemblage structure of fishery-targeted species

Depth was the only explanatory variable that best predicted identifiable assemblage groups of fishery-targeted species (Fig. 4). The optimal multivariate regression tree (based on predictive accuracy) explained 19 % of the variation in the assemblage structure, identifying two distinct assemblage groups. The relatively low percentage variance explained is not unusual for studies such as this, which contain large numbers of species occurring with low abundance (Cappo et al. 2007). The primary split in the tree occurred at a depth of 33.5 m, which generally separated the assemblages between euphotic and mesophotic reefs, with the deeper waters sampled at Rota, Garapan Anchorage and Galvez Bank on the left side of the tree. The next most important split was at a depth of 20 m, separating the shallow (10 m) inshore reefs from the 30 m depth group. Indicator species (Dufrêne and Legendre index; DLI) were listed to characterise the assemblage structure at each level of the tree (Fig. 4). The top two indicator species for the mesophotic depths were the shark *Triaeonodon obesus* and the grouper *V. louti*. Indicator species for the shallowest depth group (10 m) included the parrotfish *Scarus psittacus* and wrasse *C. trilobatus*, and depths of 20–33 m were characterised by the parrotfish *S. schlegeli* and the grouper *Epinephelus fasciatus*.

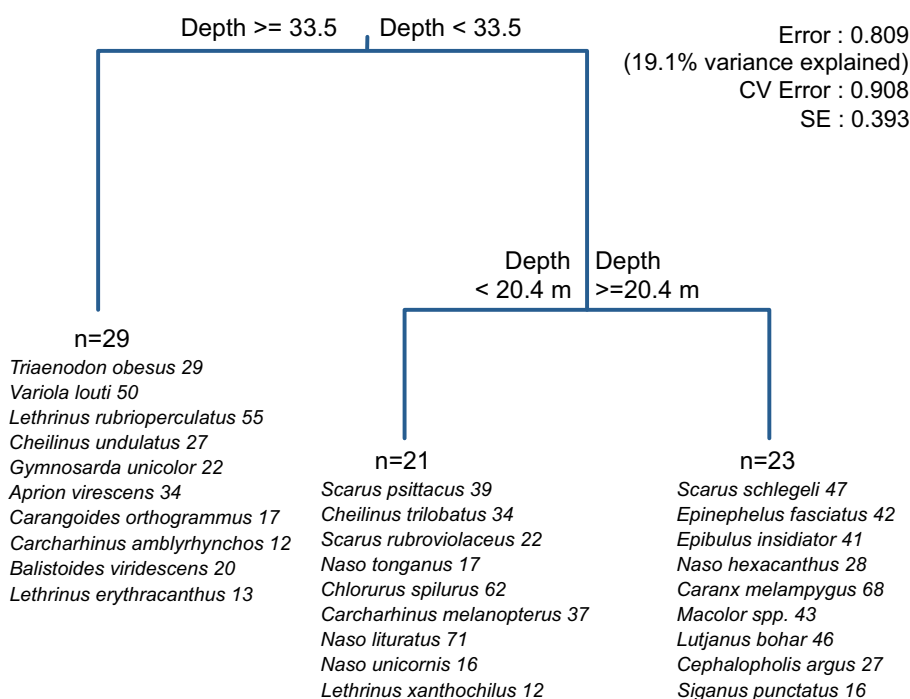
Further examination of the relationships between targeted fish assemblage biomass and environmental variables using DISTLM revealed that 38.9 % of the variation could be attributed to a combination of the seven environmental

variables. Depth again contributed to the highest percentage variance explained, accounting for 14 % of the variability in assemblage structure, followed by distance to land (11 %). As indicated by the size of the bubbles in the db-RDA plot, there was a trend of increasing biomass in the direction of increasing depth (Fig. 5a). Species correlated with increasing depth were the grouper *V. louti* and wrasse *C. undulatus*, whereas in conjunction with distance to land, the emperor *Lethrinus rubrioperculatus* and shark *T. obesus* were more frequently observed (Fig. 5b). Fish that were particularly associated with higher structural complexity and reef slope included the snapper *Lutjanus bohar* and unicornfish *N. hexacanthus*.

### Discussion

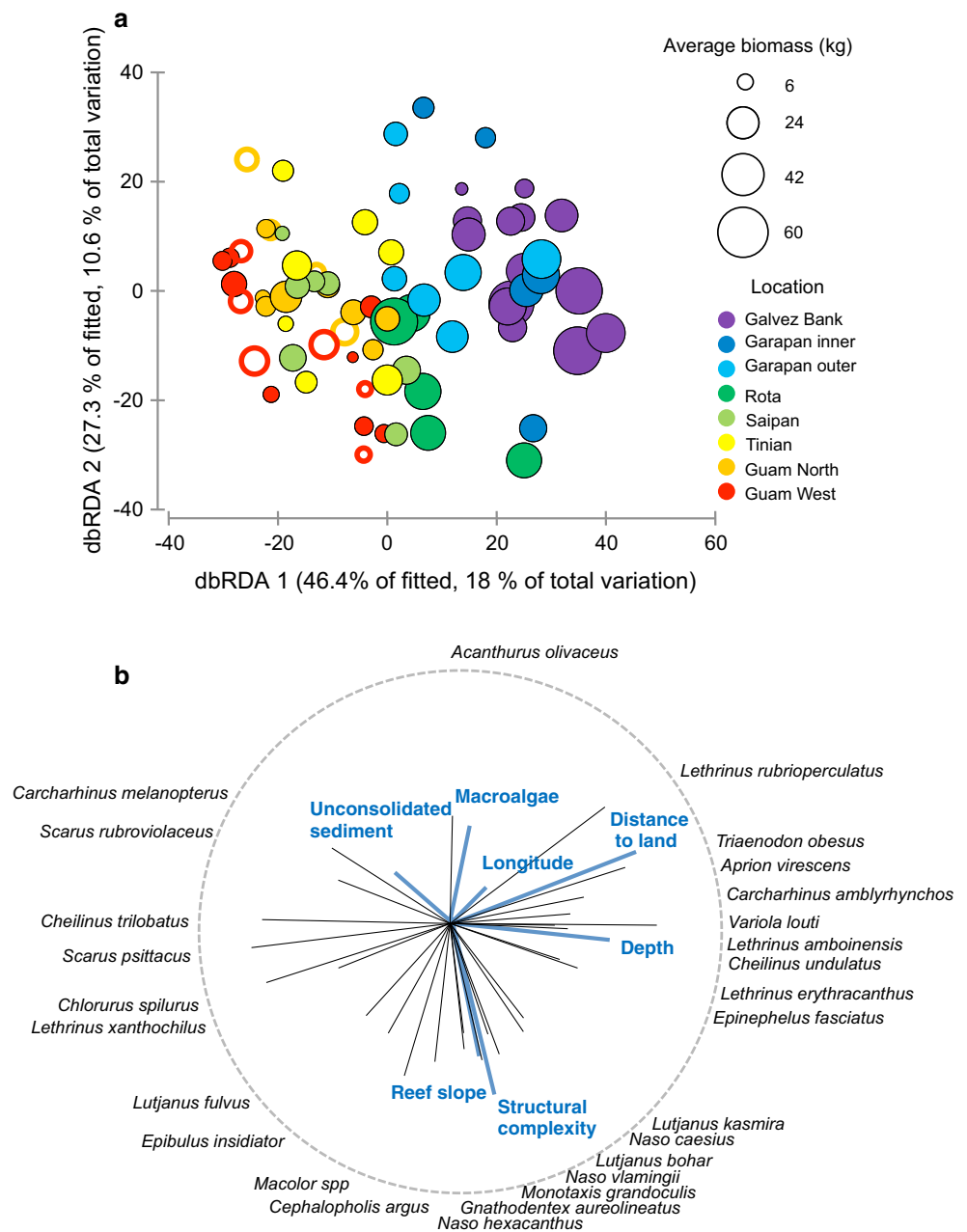
Increasing depth had a greater positive influence on the biomass and assemblage structure of coral reef fishes than the other explanatory variables measured. Considering coral reef fisheries are predominantly focused on the shallowest depths, the results highlight the role of deeper coral reefs in providing important refuge from fishing pressure. Where consolidated reef dominated the benthic habitat, total fish biomass increased threefold from 10 to 70 m depth, with most of the biomass consisting of piscivorous species. As fishing activities typically target large-bodied piscivores, the relative biomass of this trophic group can provide a useful indicator of fishing pressure (Jennings and Polunin 1996; Weijerman et al. 2013).

**Fig. 4** Multivariate regression tree analysis defining relative biomass of fishery-targeted species in terms of explanatory variables. The number of sites that correspond to the combination of explanatory variables is shown at the terminal leaves. The top ten significant ( $p < 0.05$ ) indicator species for each leaf are listed in order of decreasing Dufrêne and Legendre Index values along with the number of sites where each species was recorded





**Fig. 5** Distance-based redundancy analysis (db-RDA) on the assemblage biomass of fishery-targeted species. **a** The first and second fitted axes relating environmental variables to the fish assemblage are shown with *bubbles* scaled to represent the average relative biomass at each site. Sites are *coloured* for each location with MPA sites shown as *hollow rings*. **b** Vector plot showing the strength and direction of the relationships for species and explanatory variables



Moreover, the storage of biomass at depth has particular resonance given the positive relationship with reproductive capacity (Hixon et al. 2014). Although the most commonly observed piscivores were typically recorded in greatest abundance at mesophotic depths, they still had vertical distributions spanning the depth gradient to the shallow reefs. Hence, we regard MCEs as important habitats for species that are susceptible to fishing pressure on coral reefs.

Because fishing activities predominantly target easily accessible shallow locations, it is likely that fishing pressure has contributed to the lower biomass of targeted

species at inshore euphotic depths (10–30 m). However, the trend of increasing biomass with depth may also be attributed to piscivores being naturally more abundant at mesophotic depths, preying on the abundant small planktivorous species commonly found on deep coral reefs (Thresher and Colin 1986; Kahng et al. 2010; Bejarano et al. 2014). The processes driving the trophic interactions on MCEs are not clear, but it is likely that upwelling and internal waves on deeper reefs support high levels of nutrients and associated plankton growth (Slattery et al. 2011). Nonetheless, the observed biomass trend in the southern Mariana Islands is likely to be more pronounced

compared to lightly fished reefs, as less fishing pressure typically corresponds to greater biomass of fished species on shallow coral reefs (Dulvy et al. 2004; Williams et al. 2015). The comparison of the inshore fished sites to that of two MPAs in Guam revealed little difference when all data were pooled across locations and jurisdictions. However, within a location such as Guam West, the positive effects of MPA refuge were apparent with at least two times greater fish biomass than nearby fished sites at 10 m depth (Lindfield et al. 2014). Similarly, Richards et al. (2012) reported biomass of large-bodied reef fish in the southern Mariana Islands to be approximately half of that observed at the remote and unpopulated northern islands. In the absence of comparable baselines for unfished reefs over large depth gradients, it is difficult to determine the relative impact of fishing on the observed trend of increasing biomass with depth. However, it is clear that greater levels of fish biomass are currently stored on mesophotic coral reefs compared to protected area refuges in Guam.

Deeper reef areas are clearly linked to the shallow inshore waters, with the majority of targeted species found at depths <35 m also occurring on MCEs. However, the degree of connectivity of individual fish between depth strata remains a question of interest if they are to provide a source population to repopulate shallower depths (Slattery et al. 2011). Recent research has shown that for at least one species of damselfish, high levels of genetic connectivity between shallow and mesophotic populations are possible (Tenggardjaja et al. 2014). In addition, studies on the foraging behaviour of two predatory species, the Galapagos shark and giant trevally, revealed that these predators made regular diel movements between MCEs and shallow reefs at an uninhabited Pacific atoll (Papastamatiou et al. 2015). These predatory fish also varied seasonally in their relative use of MCE and shallow water habitats, yet their prey was primarily from shallow reefs. As the fishery-targeted species in this study have relatively large home ranges (Green et al. 2014) and are found over the range of depths where reef was present, it is likely that significant mixing between shallow reefs and MCEs could occur. However, additional tagging or genetic studies may be needed to confirm this.

To be viable reproductive refuges, fish inhabiting MCEs should be sources of reproductive output. Indeed, a population of a depth generalist coral was shown to be more fecund and abundant on deeper reefs, thereby acting as an important source of recruits (Holstein et al. 2015). The same is likely for reef fish. We were able to demonstrate a threefold increase in biomass between 10 and 60 m with the differences in biomass and abundance indicating that fish were larger at mesophotic depths. As there is a strong relationship between fish size and reproductive output (Taylor and McIlwain 2010; Hixon et al. 2014), the larger fish living on deeper reefs are likely a critical source of

recruits. Although “free-spawning” into the water column is a common reproductive strategy, especially in larger-bodied reef fish that aggregate to spawn (Colin 2012), the fate and movement of the resulting fish larvae are difficult to determine. Recent modelling of connectivity between deep and shallow reefs revealed that deeper submerged reefs could export a substantial proportion of larvae per unit area for several coral species on the Great Barrier Reef (Thomas et al. 2015). Although horizontal connectivity (among habitats of the same depth) was shown to be more common than vertical connectivity, approximately half of all recruits originating from deeper reef habitats should settle on shallow reef habitats (<10 m depth) (Thomas et al. 2015). The process of self-recruitment may be crucial for sustaining coral reef fisheries in the southern Mariana Islands, as populations of at least one targeted fish species show relative isolation from the rest of Micronesia (Priest et al. 2012). Hence, the identification of refuge habitats and their influence on supporting fishery resources is of key interest for fishery management.

Marine fisheries refugia have been described as unaltered areas that serve as sources of replenishment for exploited fish stocks to compensate for the effects of overfishing and to enhance fishery yields (Dugan and Davis 1993). Such areas of refuge have been created worldwide through the implementation of MPAs with effectiveness judged by the amount of fish biomass accrued (Edgar et al. 2014). Our results highlight the role of depth as a form of de facto MPA if the fishing methods used to capture targeted species are restricted by depth. Reef fish that rarely take bait, such as herbivorous species, compromise the bulk of coral reef fishery landings in Micronesia (Houk et al. 2012), and these fish are commonly caught using predominantly shallow water (<20 m) fishing methods such as spear guns and gill nets (Cinner et al. 2009; Houk et al. 2012; Lindfield et al. 2014). As we recorded many targeted species on shallow reefs ranging into mesophotic depths, the deeper reef areas can provide some level of protection from depth-limited fishing methods.

The humphead wrasse (*C. undulatus*) is of particular conservation concern as this species is listed as endangered on the IUCN Red List of Threatened Species (Russell 2014). Historical catch data in Guam suggest that SCUBA spearfishing is the main method used to capture this large iconic species (Lindfield et al. 2014). By extending the depth range sampled in our previous study, we found the average abundance of *C. undulatus* steadily increased into mesophotic depths. Previous studies also found increasing depth to be the strongest predictor of this species' distribution in the Mariana Archipelago where it is heavily fished (Richards et al. 2012). We recorded the highest average biomass of *C. undulatus* at the inshore mesophotic depths of Rota where SCUBA spearfishing is banned and

where human population densities are lower than in the other southern Mariana Islands. Humphead wrasse was present in 38 % of replicates at Rota, yet only recorded in 5 % of the stereo-BRUV deployments at the inshore euphotic depths. Mesophotic depths can therefore provide critical refuge to vulnerable coral reef fish species, particularly those species that are not typically harvested by line fishing methods.

It is well known that herbivorous fish decline in abundance with increasing depth (Thresher and Colin 1986; Brokovich et al. 2010; Kahng et al. 2010; Bejarano et al. 2014). However, at least for fishery-targeted herbivores, our results suggest that as long as consolidated reef habitat is available, these fish can still be found in similar relative abundance and species richness at depths greater than 10 m to at least 60 m. But it is important to note that the impact of fishing is also likely to influence the observed depth distribution, as herbivores dominate the fishery catches in the region (Houk et al. 2012; Lindfield et al. 2014). The dominant macroalga we observed at mesophotic depths was calcareous *Halimeda* spp, which is regarded as highly resistant to fish grazing (Lewis 1985). However, hard reef surfaces supported layers of turf algae, a known food source for herbivores (Choat et al. 2004) which may provide an important food source in MCEs. The relationship between herbivorous fish and algae over a wide depth gradient (1–65 m) was investigated in more detail by Brokovich et al. (2010). Their study found herbivorous fish abundance declined rapidly within the first 10 m, and despite large variability in their data set, they also found little difference from 10 to 65 m. These results prompt further questions about processes driving the vertical distribution of herbivorous fish. Although the relative dominance of these functionally important species is known to be greatest in shallow waters (<10 m), their contribution to the ecology of deeper coral reefs should not be overlooked.

Unlike other studies describing patterns of mesophotic reef fish assemblages (Brokovich et al. 2008; Garcia-Sais 2010; Bejarano et al. 2014; Wagner et al. 2014), this study focused on fishery-targeted species. The use of baited stations is beneficial for attracting targeted predatory species without decreasing the abundances of herbivores when compared to unbaited video stations (Harvey et al. 2007). However, it is important to note that the biomass structure of trophic groups presented here from stereo-BRUVs data is not comparable to data collected by other sampling techniques such as diving surveys, as the count is non-instantaneous. The area of attraction of fish to a stereo-BRUV system is highly dependent on species, with predatory fish such as sharks, snappers and emperors expected to approach the system from greater distances and in higher relative abundance than that of small-bodied territorial species.

We show that MCEs can provide critical refuge habitat, especially for fishery-targeted species at higher trophic levels. As defined by the Western Pacific Regional Fishery Management Council's fisheries ecosystem plan for the Mariana Archipelago (WPRFMC 2009), essential fish habitat in the coral reef ecosystem includes the water column and all benthic substrate to a depth of 50 fathoms (91.4 m). Consequently, increased knowledge of fish communities inhabiting MCEs is vital for effective ecosystem-based fisheries management. We suggest MCEs can provide refuge from shallow water fishing methods and could be the last stand for threatened coral reef fish, hence representing key areas for research and management.

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## References

- Amesbury JR, Hunter-Anderson RL (2003) Review of archaeological and historical data concerning reef fishing in the US flag islands of Micronesia: Guam and the Northern Mariana Islands. Western Pacific Regional Fishery Management Council, Honolulu
- Anderson M, Gorley RN, Clarke RK (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. Plymouth Marine Laboratory, Plymouth
- Bejarano I, Appeldoorn RS, Nemeth M (2014) Fishes associated with mesophotic coral ecosystems in La Parguera, Puerto Rico. *Coral Reefs* 33:313–328
- Blyth-Skyrme VJ, Rooney JJ, Parrish FA, Boland RC (2013) Mesophotic coral ecosystems—potential candidates as essential fish habitat and habitat areas of particular concern. Pacific Islands Fishery Science Center, National Marine Fishery Science Center Administrative Report H-13-02, Honolulu
- Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the “deep reef refugia” hypothesis: focus on Caribbean reefs. *Coral Reefs* 29:309–327
- Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Springer, New York
- Bridge TCL, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. *Nat Clim Chang* 3:528–530
- Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S (2008) Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Mar Ecol Prog Ser* 371:253–262
- Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, Genin A, Kark S, Kiflawi M (2010) Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. *Mar Ecol Prog Ser* 399:69–80
- Cappo M, De'ath G, Speare P (2007) Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. *Mar Ecol Prog Ser* 350:209–221

- Choat JH, Robbins W, Clements K (2004) The trophic status of herbivorous fishes on coral reefs: II. Food processing modes and trophodynamics. *Mar Biol* 145:445–454
- Cinner JE, McClanahan TR, Graham NAJ, Pratchett MS, Wilson SK, Raina J (2009) Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. *J Appl Ecol* 46:724–732
- Colin PL (2012) Aggregation spawning: biological aspects of the early life history. In: Sadovy de Mitcheson Y, Colin P (eds) Reef fish spawning aggregations: biology, research and management. Springer, New York, pp 191–224
- Cuetos-Bueno J, Houk P (2015) Re-estimation and synthesis of coral-reef fishery landings in the Commonwealth of the Northern Mariana Islands since the 1950s suggests the decline of a common resource. *Rev Fish Biol Fish* 25:179–194
- De'ath G (2002) Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* 83:1105–1117
- De'ath G (2014) mvpart: multivariate regression trees. R package version 1.6-1. rpart by Terry M Therneau, Beth Atkinson. R port of rpart by Brian Ripley. Some routines from vegan by Jari Oksanen
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Dugan JE, Davis GE (1993) Applications of marine refugia to coastal fisheries management. *Can J Fish Aquat Sci* 50:2029–2042
- Dulvy NK, Polunin NV, Mill AC, Graham NA (2004) Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Can J Fish Aquat Sci* 61:466–475
- Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro MA, Bernard AT, Berkhout J et al (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216–221
- Fitzpatrick BM, Harvey ES, Heyward AJ, Twigg EJ, Colquhoun J (2012) Habitat specialization in tropical continental shelf demersal fish assemblages. *PLoS One* 7:e39634
- Friedman K, Eriksson H, Tardy E, Pakoa K (2011) Management of sea cucumber stocks: patterns of vulnerability and recovery of sea cucumber stocks impacted by fishing. *Fish Fish* 12:75–93
- Froese R, Pauly D (2013) FishBase. <http://www.fishbase.org/>
- Garcia-Sais JR (2010) Reef habitats and associated sessile-benthic and fish assemblages across a euphotic–mesophotic depth gradient in Isla Desecheo, Puerto Rico. *Coral Reefs* 29:277–288
- Graham NA, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97
- Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT (2014) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biol Rev*. doi:10.1111/brv.12155
- Harvey E, Cappo M, Butler J, Hall N, Kendrick G (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, Goetze J, McLaren B, Langlois T, Shortis M (2010) Influence of range, angle of view, image resolution and image compression on underwater stereo-video measurements: high-definition and broadcast-resolution video cameras compared. *Mar Technol Soc J* 44:75–85
- Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J Mar Sci* 71:2171–2185
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Holstein DM, Smith TB, Gyory J, Paris CB (2015) Fertile fathoms: deep reproductive refugia for threatened shallow corals. *Sci Rep* 5:12407
- Houk P, Rhodes K, Cuetos-Bueno J, Lindfield S, Fread V, McIlwain JL (2012) Commercial coral-reef fisheries across Micronesia: a need for improving management. *Coral Reefs* 31:13–26
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol* 34:201–352
- Jennings S, Polunin NVC (1996) Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *J Appl Ecol* 1996:400–412
- Kahng S, Copus J, Wagner D (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Curr Opin Environ Sustain* 7:72–81
- Kahng S, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29:255–275
- 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. *Aquat Biol* 9:155–168
- Lewis SM (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* 65:370–375
- Lindfield SJ, McIlwain JL, Harvey ES (2014) Depth refuge and the impacts of SCUBA spearfishing on coral reef fishes. *PLoS One* 9:e92628
- Morato T, Watson R, Pitcher TJ, Pauly D (2006) Fishing down the deep. *Fish Fish* 7:24–34
- Newton K, Côté IM, Pilling GM, Jennings S, Dulvy NK (2007) Current and future sustainability of island coral reef fisheries. *Curr Biol* 17:655–658
- Papastamatiou YP, Meyer CG, Kosaki RK, Wallsgrove NJ, Popp BN (2015) Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. *Mar Ecol Prog Ser* 521:155–170
- Pauly D, Watson R, Alder J (2005) Global trends in world fisheries: impacts on marine ecosystems and food security. *Philos Trans R Soc Lond B Biol Sci* 360:5–12
- PIBhMC (2010) Commonwealth of Northern Mariana Islands (CNMI) and Guam. Pacific Islands Benthic Habitat Mapping Center. [http://www.soest.hawaii.edu/pibhmc/pibhmc\\_cnmi.htm](http://www.soest.hawaii.edu/pibhmc/pibhmc_cnmi.htm)
- Priest MA, Halford AR, McIlwain JL (2012) Evidence of stable genetic structure across a remote island archipelago through self-recruitment in a widely dispersed coral reef fish. *Ecol Evol* 2:3195–3213
- R Core Team (2014) R: a language and environment for statistical computing. Version 3.1.0. R Foundation for Statistical Computing, Vienna
- Richards BL, Williams ID, Vetter OJ, Williams GJ (2012) Environmental factors affecting large-bodied coral reef fish assemblages in the Mariana Archipelago. *PLoS One* 7:e31374
- Roberts DW (2013) labdsv: ordination and multivariate analysis for ecology. R package version 1.6-1
- Russell M (2014) *Cheilinus undulatus*. [www.iucnredlist.org](http://www.iucnredlist.org)
- Sandin SA, Williams I (2010) Trophic classifications of reef fishes from the tropical US Pacific (version 1.0). Scripps Institution of Oceanography Technical Report, Scripps Institution of Oceanography, UC San Diego, La Jolla, CA
- Slattery M, Lesser MP, Brazeau D, Stokes MD, Leichter JJ (2011) Connectivity and stability of mesophotic coral reefs. *J Exp Mar Bio Ecol* 408:32–41
- Taylor B, McIlwain J (2010) Beyond abundance and biomass: effects of marine protected areas on the demography of a highly exploited reef fish. *Mar Ecol Prog Ser* 411:243–258
- Teh LSL, Teh LCL, Sumaila UR (2013) A global estimate of the number of coral reef fishers. *PLoS One* 8:e65397

- Tenggardjaja KA, Bowen BW, Bernardi G (2014) Vertical and horizontal genetic connectivity in *Chromis verater*, an endemic damselfish found on shallow and mesophotic reefs in the Hawaiian Archipelago and adjacent Johnston Atoll. *PLoS One* 9:e115493
- Thomas CJ, Bridge TCL, Figueiredo J, Deleersnijder E, Hanert E (2015) Connectivity between submerged and near-sea-surface coral reefs: can submerged reef populations act as refuges? *Divers Distrib* 21:1254–1266
- Thresher RE, Colin PL (1986) Trophic structure, diversity and abundance of fishes of the deep reef (30–300 m) at Enewetak, Marshall Islands. *Bull Mar Sci* 38:253–272
- Trianni MS, Tenorio MC (2012) Gross diet composition and trophic level estimation of the spotcheek emperor, *Lethrinus rubrioperculatus* (Actinopterygii: Perciformes: Lethrinidae), in the Commonwealth of the Northern Mariana Islands, Micronesia. *Acta Ichthyologica Et Piscatoria* 42:89–99
- Wagner D, Kosaki RK, Spalding HL, Whitton RK, Pyle RL, Sherwood AR, Tsuda RT, Calcinaï B (2014) Mesophotic surveys of the flora and fauna at Johnston Atoll, Central Pacific Ocean. *Mar Biodivers Rec* 7:1–10
- Weijerman M, Fulton EA, Parrish FA (2013) Comparison of coral reef ecosystems along a fishing pressure gradient. *PLoS One* 8:e63797
- Wickham H (2009) *ggplot2: elegant graphics for data analysis*. Springer, New York
- Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015) Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One* 10:e0120516
- Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Mar Biol* 151:1069–1076
- WPRFMC (2009) Fishery ecosystem plan for the Mariana Archipelago. Western Pacific Regional Fishery Management Council, Honolulu