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Identifying zooplankton community changes between shallow and upper-mesophotic reefs on the Mesoamerican Barrier Reef, Caribbean

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Abstract

Mesophotic coral ecosystems (MCEs, reefs 30-150m) are understudied, yet the limited research conducted has been biased towards large sessile taxa, such as scleractinian corals and sponges, or mobile taxa such as fish. Here we investigate zooplankton communities on shallow reefs and MCEs around Utila, on the southern Mesoamerican Barrier Reef using planktonic light traps. Zooplankton samples were sorted into broad taxonomic groups. Our results indicate similar taxonomic zooplankton richness and overall biomass between shallow reefs and MCEs, but that abundance of larger bodied (>2 mm) zooplanktonic groups, including decapod crab zoea, mysid shrimps and peracarid crustaceans was higher on MCEs than shallow reefs. Our findings highlight the important of considering zooplankton when identifying broader reef community shifts across the shallow reef to MCE depth gradient.

Introduction

Tropical coral ecosystems are some of the most diverse ecosystems on the planet (Sala and Knowlton 2006), with light-dependent reefs extending from the surface down to approximately 150 m depth (Hinderstein et al. 2010). Yet most coral reef research is heavily biased towards the shallows (<30 m) (Menza et al. 2008) because of the difficulties associated with accessing deeper reefs. Mesophotic coral ecosystems (MCEs), reefs from 30 m to 150 m, are increasingly recognized as containing important components of reef diversity, both as refuge habitats for shallow reefs but also as unique ecological assemblages that need protection in their own right (Bongaerts et al. 2010; Bridge et al. 2013; Andradi-Brown et al. 2016a). Most of the limited work on MCEs has focused on large sessile taxa, such as scleractinian corals and sponges, or large mobile taxa such as fish (Kahng et al. 2010; Kahng et al. 2014). It has, however, been estimated that 168,000 invertebrate species have been described on coral reefs (Ruppert et al. 2003; Stella et al. 2011), far greater than the approximately 5,000 fish species and 700 scleractinian coral
species currently recognized (Veron 2000; Bellwood et al. 2012). Most biodiversity on reefs is therefore comprised of small mobile invertebrates, many of which are cryptic and found associated with other sessile reef fauna or in the zooplankton (Fautin et al. 2010; Plaisance et al. 2011).

Zooplankton is comprised of a diverse range of organisms, with different components normally classified into coarse groups based on size, for example mesozooplankton range from 0.2 – 20 mm and macrozooplankton from 2 – 20 cm (Johnson and Allen 2012). In the Caribbean zooplankton recorded adjacent to coral reefs has generally been found to be dominated by copepods, with amphipods, isopods, polychaetes, shrimp larvae and crab larvae all present but at lower abundances (Heidelberg et al. 2004; Heidelberg et al. 2010). Previous studies have suggested major factors affecting zooplankton abundance on reefs include active zooplankton avoidance behavior of reef habitats and differing exploitation patterns by predators (Motro et al. 2005; Yahel et al. 2005; Heidelberg et al. 2010). Many zooplankton can exhibit active swimming behavior to avoid predation or areas with higher risk of predation (Haury et al. 1980; Ohman 1988). Approximately 20% of reef invertebrates are crustaceans, making them one of the largest and most speciose groups on coral reefs (Kramer et al. 2014) and so an important component of reef fish diets (Randall 1967). Planktivorous fish predation pressure is thought to lead to depleted plankton abundance over reefs, though because planktivorous fish tend to feed <1.5 m over the reef, this effect is limited to close to the reef surface (Motro et al. 2005).

On Caribbean MCEs zooplankton is particularly important as a food source, with zooplanktivorous and mobile-invertebrate feeding widely observed as the dominant fish trophic groups (Garcia-Sais 2010; Bejarano et al. 2014; Andradi-Brown et al. 2016b) and studies suggesting approximately 60% of MCE reef fish feed on zooplankton and mobile-invertebrates on the Mesoamerican Barrier Reef, Caribbean (Andradi-Brown et al. 2016b). Shallow-reef corals also feed on zooplankton, providing an important additional energy source to that provided by their symbionts (Ferrier-Pagès et al. 2003). On MCEs however, because of low light availability, corals are believed to increase heterotrophic feeding, likely making them more dependent on zooplankton than their shallow counterparts (Lesser et al. 2010). In addition,
invertebrate groups such as decapods have important functional roles in maintaining fish health. For example, cleaning fish of parasites, e.g. cleaner shrimp (Becker and Grutter 2004), and defending coral colonies from predators and clearing excess sediment thus preventing smothering of coral polyps, e.g. Trapezia crabs (McKeon and Moore 2014).

Despite the important roles zooplankton are likely to have on MCEs, few studies have documented MCE zooplankton communities and how they differ from those on shallow reefs. Here we investigate the mesozooplankton and macrozooplankton community on shallow reefs and upper-MCEs on the Mesoamerican Barrier Reef, Caribbean, to identify differences in abundance, biomass and community structure across the depth gradient.

**Methods**

Surveys were conducted on the south shore of Utila, Bay Islands, Honduras. Utila is located off the north shore of Honduras, with its reefs forming the southern extent of the Mesoamerican Barrier Reef. Off the south shore of Utila, shallow reefs form a spur and groove system, with a reef slope down to approximately 35 m, where the seabed flattens and a patch reef MCE is formed. From these MCE patch reefs, the south shore seabed continues to gently slope to approximately 70 - 80 m before rising to the Honduran mainland. Three replicate light trap deployments were conducted at 15 m (shallow) and 40 m (MCE) at three sites: Coral View, Black Coral Wall and Little Bight (Figure 1, see Supplemental Table S1 for GPS locations) during July - September 2015. Light traps were built following Jones (2006). Traps were modified from these specifications to use twelve 12 V light-emitting diodes (LEDs) powered by a 12 V, 4,800 mAh rechargeable lithium ion battery as the light source in each trap. LEDs were white light emitting with each LED having a luminous intensity of 12,000 – 14,000 mcd and wavelength of 5,000 – 6,500 nm. Light traps were deployed by divers 0.5 m above the reef at each depth during the afternoon. They were activated with a digital timer set to illuminate the trap 30 minutes before sunset and remain lit until sunrise the following morning. Divers recovered the light...
traps at 7:30 am the morning following deployment. Sites and depths were surveyed
over multiple nights, with no more than two traps deployed at a site in a single night.
All light traps were placed a minimum of 20 m distance from previous light trap
deployments. Research permits for this work were issued to Operation Wallacea by
the Instituto de Conservación Forestal (ICF), Honduras. As the focus of the work was
on invertebrates, and no higher vertebrates were involved, ethical review was not
required.

Figure 1. The three survey sites on the south shore of Utila, Bay Islands, Honduras.
Sites were: (1) Little Bight, (2) Black Coral Wall and (3) Coral View. See Supplemental
Table S1 for full GPS location data. Inset – The location of Utila is indicated with a
black circle relative to the western Caribbean and Gulf of Mexico.

Samples were sorted following groupings used in Johnson and Allen (2012)
into broad taxonomic and developmental groups readily identifiable in the field with
the use of a dissecting microscope. These groups were: (i) arrow worms, (ii) barnacle
larvae, (iii) cladocerans, (iv) copepods, (v) decapod crab zoea, (vi) decapod shrimp
zoea, (vii) decapod crab megalopae, (viii) lobster phyllosoma, (ix) mantis shrimp larvae, (x) mysid shrimps, (xi) peracarid crustaceans, (xii) oligochaetes, (xiii) polychaetes, (xiv) mites, (xv) urochordates and (xvi) fish larvae. All sampled individuals >2 mm were counted to give abundance, and all individuals regardless of size were sorted and dry weighed to record biomass.

Nonmetric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) were used to visualize and test for differences in abundance and biomass between the two depths based on Bray-Curtis dissimilarities on a fourth root transformed matrix (Anderson et al. 2008), while differences in richness were tested using a Euclidean PERMANOVA. Transformed data were used to reduce the influence of the most abundant taxonomic groups when assessing community differences in the PERMANOVA (Anderson et al. 2008). When processing samples, one 15 m Black Coral Wall light trap collected no taxonomic groups with sufficient biomass to register on our field scales (weight <0.01g), this necessitated its removal from multivariate analysis of biomass data. All PERMANOVAs were run for 99999 permutations and run using the ‘adonis’ function in vegan (Oksanen et al. 2013) in R (R Core Team 2013). Constrained analysis of principal coordinates (CAP) was conducted for the abundance data using the ‘capscale’ function in vegan (Oksanen et al. 2013). All taxonomic groups with a Pearson correlation coefficient |>|0.5| with either of the first two CAP axes were identified as potential drivers of community difference with depth. The abundance of these taxonomic groups was then individually tested using a Euclidian PERMANOVA to identify whether they changed with depth.

Results

Overall we found similar richness of taxa groups on shallow and mesophotic reefs (Figure 2A), with much variation in the overall abundance and biomass at both depths (Figure 2B-C). We used an NMDS to visualise differences in the community sampled by the light traps at shallow and mesophotic depths. Abundance data appeared to show a difference in the community between shallow and mesophotic
reefs (Figure 3A), while biomass-weighted data showed no clear patterns (Figure 3B). We tested these patterns in a PERMANOVA (Table 1), finding differences in the recorded light trap community taxonomic richness, abundance, and biomass between survey sites. Abundance of taxonomic groups also changed between the two depths, but no pattern with depth was found for taxonomic richness or biomass.

Figure 2. (A) Number of different taxonomic groups recorded, (B) mean abundance per light trap, and (C) total biomass across all taxa groups comparing reefs at 15 m and 40 m. Bars show mean ± 1 standard error.

Figure 3. Nonmetric multidimensional scaling plot for (A) abundance and (B) biomass of the invertebrate and fish larvae. Colours indicate different depths, while shapes
indicate different survey sites. Sites were: BCW – Black Coral Wall, LB – Little Bight and CV – Coral View.

Table 1. PERMANOVA results testing for differences in the recorded light trap community between sites and depth for abundance and biomass data.

| Survey Site | DF  | pseudo-F | P    | Abundance | pseudo-F | P     | Biomass | pseudo-F | P     |
|-------------|-----|----------|------|-----------|----------|-------|---------|----------|-------|
|             | 2   | 3.97     | 0.04 | 5.58      | <0.0001  | 2.33  | 0.01    |          |       |
| Depth       | 1   | 0.76     | 0.41 | 2.71      | 0.03     | 1.42  | 0.24    |          |       |
| Residual    | 13  |          |      |           |          |       |         |          |       |
| Total       | 16  |          |      |           |          |       |         |          |       |

We conducted Euclidian PERMANOVAs on abundance results correlating with the CAP axis to identify taxonomic groups varying with depth (Table 2). We identified decapod crab zoea, mysid shrimps, peracarid crustaceans and oligochaete abundance as increasing on MCEs compared to shallow reefs, with no oligochaetes recorded on shallow reefs. We did not detect any zooplanktivorous groups at greater abundance on shallow reefs than MCEs, nor any changes in fish larvae abundance between shallow reefs and MCEs.

Table 2. Euclidian PERMANOVA results for abundance of taxonomic groups that correlate |>0.5| with the first or second CAP analysis.

| Taxonomic Group | Shallow (15 m) | Mesophotic (40 m) | Pseudo-F | P   |
|-----------------|---------------|-------------------|----------|-----|
|                 | Mean | SE  | Mean     | SE   |     |       |
| First axis      |      |     |          |      |     |       |
| Decapod crab megalopae | 25.00 | 18.92 | 15.78   | 14.13 | 0.47 | 0.24  |
| Decapod crab zoea | 17.89 | 17.39 | 69.11   | 56.53 | 2.31 | <0.01 |
### Discussion

While MCEs are of increased interest because of their potential role as refuges for threatened shallow-reef taxa (Bongaerts et al. 2010), almost all existing research has focused on large sessile benthic taxa such as hard corals, macroalgae and sponges or large mobile organisms such as fishes (Kahng et al. 2010; Kahng et al. 2014). Few studies have considered changes in small mobile invertebrates making up reef cryptofauna and zooplankton. We found significant differences in zooplankton richness, abundance and biomass between study sites and, interestingly, higher abundances on MCEs than on shallow reefs while biomass did not change. Previous work has suggested zooplankton, in particular larger planktonic individuals such as mysids, isopods and decapod larvae are particularly important prey items for planktivorous fish (Hobson and Chess 1978). Unlike in many locations (see Kahng et al. 2010; Kahng et al. 2014), a previous study on Utila at our study sites found no difference in relative planktivorous reef fish biomass between shallow reefs and MCEs, and a decline in actual biomass of planktivorous reef fish with increased depth (Andradi-Brown et al. 2016b). This pattern is surprising as we identified greater abundance of zooplankton >2 mm size and no change in biomass of zooplankton across the depth gradient, suggesting similar or potentially greater

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| Decapod shrimp zoea | 52.00 | 19.66 | 38.22 | 26.72 | 0.27 | 0.53 |
| Mysid shrimps | 84.11 | 63.12 | 637.44 | 600.61 | 1.52 | 0.04 |
| Peracarid crustaceans | 68.22 | 44.79 | 216.11 | 93.51 | 5.04 | <0.01 |
| Urochordates | 29.11 | 29.11 | 83.89 | 74.11 | 1.32 | 0.15 |
| Second axis |  |  |  |  |  |  |
| Cladocerans | 4.33 | 4.33 | 0.33 | 0.33 | 2.44 | 0.10 |
| Oligochaetes | 0.00 | 0.00 | 93.67 | 93.67 | 2.28 | <0.01 |
food resources for planktivorous fish on MCEs. In addition, planktivorous reef fish exhibit high visual system plastic adaptive ability, and show few differences in feeding ability caused by changes in light levels across depth gradients, suggesting they should be able to feed efficiently at MCE depths included in this study (Brokovich et al. 2010). However, the previous planktivorous fish study from Utila was conducted during daylight hours (Andradi-Brown et al. 2016b), while light traps in this study were deployed overnight. Therefore, as zooplankton are known to have diurnal movement patterns (Angel 1985), the abundance of zooplankton we recorded here may not be available to the planktivorous fish during daylight hours.

MCEs on the south shore of Utila exist as a gently sloping patch reef system on the continental shelf that remains within mesophotic depths before rising to become the mainland of Honduras. Therefore, unlike other MCEs adjacent to deep-sea habitats, at the sites we surveyed there is unlikely to be a large diurnal migration of zooplankton from deeper water at night.

Our finding of greater abundance of some zooplanktivorus groups on MCEs, and no change in zooplankton biomass between shallow reefs and MCEs contrast with previously identified zooplankton depth patterns. In Jamaica, Ohlhorst (1985) studied zooplankton across a 6 – 24 m depth gradient using traps placed over the reef, finding that both the abundance of zooplankton and the volume of zooplankton per trap declined with depth. When looking at specific taxonomic groups, we identified greater abundance of mysid shrimps and peracarid crustaceans on MCEs (40 m) than shallow reefs (15 m). Whereas, no difference was identified in mysid shrimp or peracarid crustacean abundance between 15 m and 24 m in Jamaica (Ohlhorst 1985). In Hawaiian reef cryptofauna, brachyuran crab abundance has been reported to decline across a 12 – 90 m depth gradient (Hurley et al. 2016). However much of this pattern was caused by one crab genus, which when excluded led to crab abundance increasing with depth. While these Hawaiian brachyuran crabs had settled on the reef, we identified increased abundance of decapod crab zoea on MCEs on Utila, though no difference in decapod crab megalopae with depth. In addition, we found similar abundances of fish larvae between shallow reefs and MCEs. However, fish larval recruitment is known to be seasonal, and previous studies have identified abundance differences in fish larval recruits across 10 – 40 m
in the Caribbean (Luckhurst and Luckhurst 1977). These fish recruitment patterns are highly species specific, with fish recruits more abundance for some species at 40 m than 10 m, while the reverse is true for other species (Luckhurst and Luckhurst 1977).

In this study we found no change in taxa richness between shallow reefs and MCEs, though we only classified invertebrates into broad taxonomic groups, lacking the resolution needed to detect fine scale richness patterns. In Jamaica, Ohlhorst (1985) reported an increase in taxonomic richness across depths from 6 – 24 m, but using higher resolution taxonomic groupings. In contrast, in Hawaii Hurley et al. (2016) reported the greatest brachyuran crab reef cryptofauna diversity on shallow reefs, with 40% of species at 12 m and declining richness with depth to 90 m.

Differences in richness patterns with depth between these studies are likely caused by different reef habitats, taxonomic resolution, biogeographic regions, and sampling techniques. Patterns in species richness across the shallow to mesophotic gradient has been a major focus of research (Kahng et al. 2010; Kahng et al. 2014), potentially being used to inform conservation management and in defining MCE ecology (Laverick et al. 2016).

This study provides a first glimpse of the patterns in zooplankton communities associated with MCEs in the Caribbean. Further research is necessary to determine fine-scale patterns across the depth gradient in zooplankton communities to help identify depth transition zones between communities and areas with unique biodiversity assemblages.

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