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ORIGINAL ARTICLE

Near-reef zooplankton differs across depths in a subtropical seascape

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Our knowledge of zooplankton in proximity to benthic marine habitats is hampered by challenges sampling near complex substrates. To address this, we deployed light traps near the benthos of four depth-specific coral reef ecosystems to measure nocturnal zooplankton abundance and assemblage composition. Replicate light traps at shallow shelf (SS10, <10 m) and deep shelf (DS30, 20–30 m) habitats in the Florida Keys and at mesophotic depths at the Dry Tortugas (DT60, 40–60 m) and Pulley Ridge (PR70, 60–70 m) on the west Florida shelf revealed zooplankton assemblages that differed in both magnitude and composition. SS10 and DS30 were dominated by meroplankton, in contrast to the deeper sites where holoplankton were most abundant. Meroplankton and demersal plankton were significantly more abundant at SS10 and DS30 than at DT60 or PR70. Zooplankton assemblage composition overlapped between SS10 and DS30 depths, but shifted beyond those depths such that PR70 zooplankton assemblages were entirely distinct. DT60 assemblages were intermediate and included taxa with both shallow and deep affinities. Reflecting proximity to adult spawning populations and potentially different zooplankton prey with depth, such depth-related differences in zooplankton assemblages likely impact food availability for benthic organisms with consequences to community composition, habitat quality and population connectivity.

KEYWORDS: zooplankton; coral reef; mesophotic coral ecosystems; meroplankton; holoplankton

INTRODUCTION

Zooplankton studies often focus on pelagic environments, yet zooplankton near benthic marine habitats, particularly those with rich demersal communities, are important constituents of those ecosystems (e.g. Hamner *et al.*, 2007). From an energetic and food web perspective, zooplankton serve a critical role in benthic-pelagic coupling as prey for planktivores and benthic suspension feeders, and as both prey and predators of pelagic larval forms (Marcus and Boero, 1998). This dual role of both predator and prey affects food availability for benthic life stages of marine organisms, and the survival and distribution of pelagic larvae that are key to population replenishment and ecological connectivity among local benthic marine populations (Cowen and Sponaugle, 2009). Despite the pivotal trophic role of zooplankton in these ecosystems, sampling is rarely conducted primarily due to the limited and complex spatial scales associated with proximity to the benthos. Towing plankton nets from surface vessels is challenging near complex benthic habitats and settlement traps do not effectively capture all zooplankton taxa. Hand collection of zooplankton by divers can provide insight into major taxonomic differences (Heidelberg *et al.*, 2004, 2010), but these are necessarily time limited and likewise challenging to conduct at depth. Passive sampling methods, such as the Channel Midwater Neuston Net and the Reef Edge Net, provide promising results to quantify zooplankton in these ecosystems; however, these gears may not adequately sample larger zooplankton capable of gear avoidance (Santos *et al.*, 2017). Thus, our knowledge of habitat-related differences in zooplankton composition near benthic habitats lags our knowledge of the ecology of benthic marine ecosystems.

Tropical and subtropical coral reef systems are known to be oligotrophic yet simultaneously support a diverse zooplankton community. Oceanic and reef-sourced zooplankton are critical to food webs, as they serve as prey to benthic suspension feeders such as corals as well as mobile reef-associated planktivorous fishes (Holzman and Genin, 2003; Yahel *et al.*, 2005; Le Bourg *et al.*, 2018). Stable isotope analysis and environmental DNA techniques have advanced our understanding of nutrient subsidies and the flow of energy across these shallow, nutrient poor ecosystems (Nakajima *et al.*, 2017; Le Bourg *et al.*, 2018), and much effort is focused on how meroplankton, that spend a portion of their life in the pelagic realm, survive as part of the zooplankton to successfully replenish reef populations (Cowen and Sponaugle, 2009). Beyond replenishing benthic populations, the movement of oceanic zooplankton into nearshore reef ecosystems maintains benthic ecosystems by bringing deep sea nutrients and prey into shallow water habitats. Zooplankton can also be conduits

of disease (Certner *et al.*, 2017), and evidence is accumulating that changing ocean conditions, particularly ocean acidification, is having a detrimental effect on near-reef zooplankton (Carrillo-Baltodano and Morales-Ramirez, 2016; Smith *et al.*, 2016). Changes in zooplankton community composition and the arrival of zooplankton to reefs can significantly affect metapopulation functioning and trophic interactions through density-dependent spatial coupling between zooplankton prey, planktivorous fish and piscivorous fish (White and Samhoury, 2011).

Even though much research continues to be focused on the functioning of shallow coral reef ecosystems, recent efforts have expanded into deeper waters to investigate the ecological relationships between shallow coral reefs and mesophotic coral ecosystems (MCEs; ~30–150 m depth; Srinivasan, 2003; Lesser *et al.*, 2009; Hinderstein *et al.*, 2010; Hurley *et al.*, 2016; Andradi-Brown *et al.*, 2017; Loya *et al.*, 2019). MCEs may serve as refuges for shallow water species impacted by physical and anthropogenic stressors, and as a source of larvae to help replenish impacted shallow water populations (Bongaerts *et al.*, 2010; Holstein *et al.*, 2015; Lindfield *et al.*, 2016; Lesser *et al.*, 2018). For a planktivorous fish at mesophotic depths, access to a different zooplankton prey may contribute to higher per capita reproductive output than for fishes on shallow reefs (Goldstein *et al.*, 2016b, 2017). In addition to affecting growth and condition of adults, different zooplankton prey abundance and composition are also known to influence larval growth rates of several subtropical fish species (Sponaugle *et al.*, 2009; Shulzitski *et al.*, 2015). Despite the importance of zooplankton to multiple ecological components of subtropical reef ecosystems, we have little knowledge of differences in zooplankton assemblages across broad depth strata.

To compare near-reef zooplankton composition across a subtropical seascape, we used a common sampling gear, light traps, deployed 5–6 m off the benthos at reef sites ranging from <10-m depth to >60 m on the Florida shelf. We hypothesized that the abundance and composition of zooplankton would vary significantly across this broad depth stratum. Near-reef zooplankton community composition provides information about vertical variability in population replenishment of a range of benthic organisms, benthic-pelagic coupling and food webs in coral reef ecosystems.

METHODS

Replicate light traps were used to sample nocturnal near-reef zooplankton at four depths: shallow (SS10; <10 m) and deep shelf (DS30; 20–30 m) reefs at two sites, American Shoal and Looe Key, in the Lower Florida Keys;

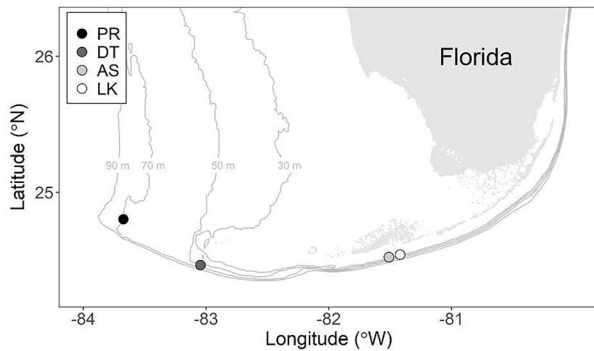


Fig. 1. Florida and the Florida Keys, USA, bathymetry lines and study sites. Shallow Shelf (*SS10*) and Deep Shelf (*DS30*) reef sites included samples from American Shoal (AS) and Looe Key (LK) reefs. Mesophotic reef sites (*DT60* and *PR70*) included samples from Dry Tortugas (DT) and Pulley Ridge (PR), respectively.

and MCEs at Dry Tortugas (DT60; ~53 m) and Pulley Ridge (PR70; ~67 m) on the southwestern shelf (Fig. 1). Although light traps only work at night and select for phototactic organisms, they are suitable for a variety of zooplankton taxa and for relative measures of abundance. Light traps consisted of a ~1-m tall 505- μ m mesh Nitex cylinder surrounding a white LED light. Traps were deployed overnight and three funnel-shaped openings in the cylinder enabled phototactic nocturnal zooplankton to enter the traps and become trapped inside until trap retrieval the following morning. Based on the original design in Sponaugle and Cowen (Sponaugle and Cowen 1996), these light traps have been used in multiple subtropical locations, primarily targeting meroplankton such as the pelagic early life stages of crabs (Reyns and Sponaugle, 1999) and fishes (D'Alessandro *et al.*, 2007), but also collecting a diversity of other zooplankton taxa. Previously, we deployed these traps ~1 m below the surface seaward of nearshore reefs to intercept larvae settling to shallow reef habitats. For the purposes of the present study, traps were deployed ~5–6 m off of the benthos across all collection sites (Fig. 1).

In the Florida Keys, four replicate traps were deployed and retrieved at each site and depth from a small boat; replicate traps at PR70 and DT60 were deployed from a larger research vessel during dedicated collaborative research cruises. Mesophotic light traps were deployed in two series of three: two cables extended from the benthos to the surface and a single trap was positioned at each of three depths (Fig. 2). Given depth limitations, mesophotic traps were designed to release automatically and rise to the surface to facilitate retrieval. To be comparable with the near-reef traps deployed at shallow and deep depths in the Florida Keys, and for purposes of the present study, we focused on only the two deepest, near-reef traps at PR70 and DT60.

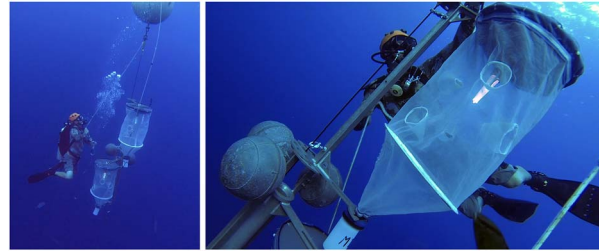


Fig. 2. Deployment of light traps at mesophotic sites. Each mooring ($n=2$) consisted of a cable extending from the benthos to the surface that supported an array of three light traps positioned at each of three depths. To be comparable with the shelf reef sites, we used only the collections from the deepest two traps. Photos credit: Brian Cousin, Harbor Branch Oceanographic Institute, Florida Atlantic University.

The above deployment constraints hindered simultaneous sampling across all sites, but we narrowed the range of sampling nights we analyzed to compare samples during periods of similar lunar cycles. This helped to standardize collections across years since many biological activities such as migration, spawning and settlement are associated with lunar phases (Gliwicz, 1986; D'Alessandro *et al.*, 2007). In particular, many reef organisms (meroplankton) settle to the reef at night during the dark half of the lunar cycle—third quarter to new moon period (e.g. Reyns and Sponaugle, 1999; D'Alessandro *et al.*, 2007)—so our data analysis focused on a total of 19 nights of sampling between the third quarter to new moon in the month of August over 3 years: 2012, 2013 and 2014 (Table I). During 2012, SS10, DS30 and MCE (PR70) were sampled; in 2013, SS10, DS30 and MCE (DT60) were sampled; and in 2014, MCEs (PR70 and DT60) were sampled. In total, shallow and deep shelf reefs were sampled for seven nights, and MCE for 12 nights (seven nights at PR70 and five nights at DT60; Table I).

Upon retrieval, the contents of each trap were preserved in 95% ethanol and the sample brought back to the laboratory. All larval fishes were sorted from the samples and larval fish abundances are reported in a separate manuscript encompassing other fish life stages. Remaining zooplankton samples were split using a Folsom Plankton Splitter or a box splitter and zooplankton in a subsample were identified to the lowest taxonomic level and life history stage (e.g. decapod zoea and megalopae). Although some rare taxa were likely collected in the traps only passively and somewhat randomly, they are included here to provide an overall measure of richness. Each subsample was multiplied by the split to estimate the absolute abundance of each taxa in the total sample. For analysis, we also grouped taxa by life history (holoplankton, meroplankton or demersal plankton) following Heidelberg *et al.* (2004). A few taxa included members of both holo- and

Table I: Month, year, calendar day, lunar day (1–30, with new moon as 1) and associated lunar phase that replicate light traps were deployed at each of three sites: Shallow shelf (SS10) and deep shelf (DS30) in the Florida Keys, Dry Tortugas (DT60) and Pulley Ridge (PR70)

Month/Year	Deployment day	Lunar day	Lunar phase	Total traps per site			
				SS10	DS30	DT60	PR70
August, 2012	10	23	Q	3	4		
	12	25	Q	4	3		
	13	26	Q	4	3		
	14	27	N	4	4		
	17	1	N				2
	19	3	N				2
August, 2013	20	4	N				2
	1	25	Q	4	4		
	3	27	N	4	4		
	5	29	N	4	4		
	24	19	Q			2	
August, 2014	25	20	Q			2	
	15	20	Q				2
	16	21	Q				2
	17	22	Q				2
	18	23	Q				2
	23	28	N			2	
	24	29	N			2	
26	2	N			2		
Total Nights Sampled				7	7	5	7

The sum of the number of nights sampled at each site is noted in the final row. SS10 and DS30 were averaged across two Keys locations, American Shoal and Looe Key. N = new moon (± 3 days); Q = third quarter moon (± 3 days). Numbers indicate number of traps sampled at each site, each night.

meroplankton (Table II) so for analysis we divided those taxa between each category (i.e. half to each). To provide an overall estimate of how zooplankton composition and abundance varied among strata, we averaged across shallow reef, deep reef and mesophotic sites. Where necessary, abundance data were log-transformed to meet assumptions of normality and then compared among strata using analysis of variance (ANOVA). Where ANOVA indicated significance, data pairs were compared using Tukey’s honestly significant difference (HSD) test. All data analyses were conducted using the software package R (R Core Team, 2019; version 3.6.1).

Zooplankton taxonomic diversity was plotted against the cumulative number of traps deployed at each depth strata over the three sampling period to generate rarefaction curves. The slopes of such curves reflect the relative diversity sampled at each depth strata—steeper slopes indicating higher variability among sampling nights; asymptotes indicating that sampling adequately characterized diversity.

To compare zooplankton communities across locations, we conducted a non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity index (Clarke and Ainsworth, 1993) analysis using the R package vegan (Oksanen *et al.*, 2020). For the analysis, abundances of each taxon were averaged among replicates within strata.

Gelatinous organisms were excluded from the NMDS, and early (zoea) and later (megalopae) stages were grouped into a broader larval decapod category, resulting in a total of 23 taxa in the analysis. Prior to analysis, mean abundances of taxa among replicates were square-root transformed to minimize the influence of highly abundant taxa. Species scores were plotted as weighted averages for taxa that were present during at least 2.5% of the collections and 90% data ellipses were included for each depth stratum to visually distinguish differences.

In situ currents were not measured at each trap, yet ocean currents can influence zooplankton distributions as well as collections. To compare currents among depth strata, we obtained data from Hybrid Coordinate Ocean Model (HYCOM) model global re-analysis with 1/12° resolution (<https://www.hycom.org/data/server/gofs-3pt1/reanalysis>). Velocity components (u and v) were extracted from HYCOM at light trap deployment locations (within specific boundary boxes; Fig 1; Supplementary Table S1) from the start to the end dates of each annual series of light trap deployments at each respective stratum (Table I). Current speeds were calculated using the square root of squared u and v velocity components at the surface of the water column for SS stations, and at the bottom of the water column for DS, DT and PR stations.

Table II: Invertebrate zooplankton identified in the light traps and their ecological classification based on (Heidelberg et al. 2004): holoplankton (H), meroplankton (M), demersal plankton (D)

Invertebrate group	Classification	Total ($\times 10^3$)	Mean per trap ($\times 10^3$)
Larval decapoda	M	7 000	100
Hyperiid	H	4 000	50
Mysida	D	700	10
Calanoida	H	600	8
Stomatopoda	M	500	7
Shrimp	MD	300	4
Cumacea	D	300	4
Chaetognatha	H	300	4
Isopoda	D	200	2
Polychaeta	HMD	60	0.8
Gammaridea	D	25	0.3
Ostracoda	D	21	0.3
Other decapoda	HMD	15	0.2
Phyllosoma	M	5	0.06
Tanaidacea	D	4	0.05
Euphausiacea	H	3	0.04
Gastropoda	H	2	0.03
Gelatinous	H	0.9	0.01
Poecilostomatoida	H	0.5	0.007
Harpacticoida	HD	0.02	0.0002

Taxa are arranged in order of abundance. Some groups have representative species in more than one category. The taxonomic group *larval decapoda* consisted of crab zoea and megalopae. *Lucifer* spp., larvae of non-crab decapods, slipper lobster, juvenile crab and unidentified decapods were identified as *other decapoda*. The taxon *gastropoda* included pteropods, heteropods and gymnosomes; and *gelatinous* included salps, doliolids, siphonophores, pyrosomes and hydromedusae. All copepods, euphausiacea, shrimp and chaetognath classifications were based on habitat description in Brusca and Brusca (1990). Total number of individuals collected over the sampling period and mean abundance per trap were rounded for simplicity (number $\times 10^3$).

RESULTS

We identified a total of 29 taxonomic groups. Zooplankton were more than four times as abundant at SS10 and DS30 reef sites than at mesophotic depths, both at PR70 and DT60 (Fig 3; Supplementary Table S2). Additionally, the most dominant group in SS10 and DS30 reef samples was the meroplankton (61 and 58%, respectively); whereas mesophotic samples were dominated by holoplankton (PR70 = 94%; DT60 = 75%). The abundance of all three categories (holoplankton, meroplankton and demersal plankton) differed significantly among depths (ANOVA on log transformed data: all $P_s < 0.0001$). Meroplankton and demersal plankton were significantly more abundant in SS10 and DS30 depths than at both mesophotic depths (Tukey HSD: all $P_s < 0.001$). Abundances of holoplankton were highly variable among SS10 replicates, resulting in the only significant differences occurring between DS30 and both DT60 and SS10 (Tukey HSD: all $P_s < 0.001$). Despite these differences in abundance, overall nightly richness hovered at ~ 12 groups per trap at all depths, with only DT60 exhibiting significantly higher richness than DS30 and PR70 (ANOVA: $P = 0.01$; Tukey HSD: $P = 0.008$ and 0.02 , respectively; Supplementary Fig. S1). However, consideration of all of the samples in rarefaction curves indicates that the two deeper sites—DT60 and PR70—achieved higher taxonomic richness more rapidly

(Fig 4), largely due to a higher proportion of rarer taxa (which were mostly holoplankton). The slope of the rarefaction curve was steepest for PR70, reflecting a greater variability in zooplankton taxa among nights than at other depth strata. The fact that the PR70 rarefaction curve did not reach an asymptote suggests that richness would likely have continued to increase with additional sampling. In contrast, despite a steep slope (high nightly richness), the DT60 rarefaction curve slowed to an asymptote, indicating that most of its taxonomic richness was captured by our sampling and that overall strata richness was lower than at PR70.

On a taxonomic level, several patterns emerged from the samples: The most abundant taxa were larval decapods, followed by hyperiid amphipods, mysid shrimp and stomatopods (Fig 5). Chaetognaths were the sixth most abundant zooplankton at DS30, but were less common at the other sites. Cumaceans were fairly abundant at the SS10 and DS30 sites, but were almost absent at mesophotic depths. Polychaete worms exhibited the same pattern, although at overall lower abundances. In contrast, euphausiids were abundant at PR70, but were never present at SS10 or DS30. The only gastropods collected at the shelf sites were pteropods (more abundant at DS30) but at mesophotic depths, in addition to pteropods, traps collected heteropods and gymnosomes. Occasionally at mesophotic depths, appendicularia,

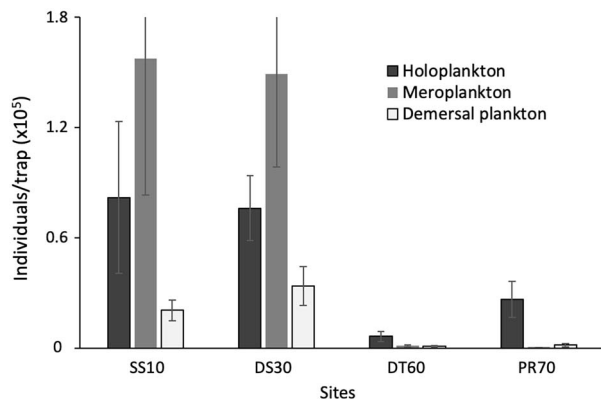


Fig. 3. Mean abundance of invertebrate zooplankton collected in replicate light traps deployed during the dark half of the lunar cycle across four depth strata (numbers next to the site abbreviation indicate maximum depth of trap deployment): Shallow Shelf (SS10), and Deep Shelf (DS30) in the Florida Keys, Dry Tortugas (DT60) and Pulley Ridge (PR70). SS10 and DS30 were averaged across two Florida Keys locations, American Shoal and Looe Key. Taxa classified into one of three ecological categories based on Heidelberg *et al.* (2004). Error bars represent standard error.

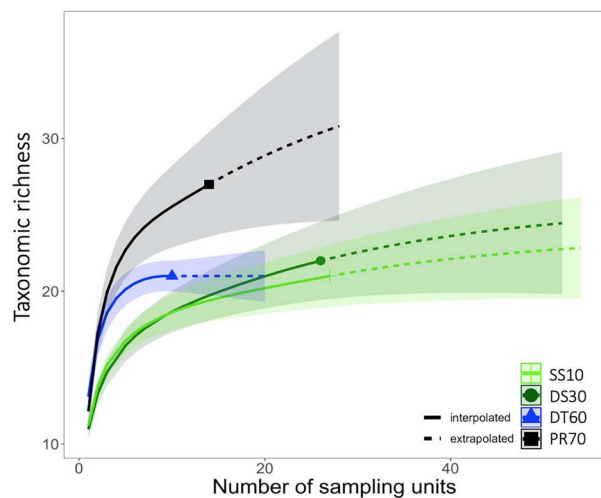


Fig. 4. Rarefaction curves of zooplankton taxa collected from replicate light traps deployed at four depth strata (numbers next to the site abbreviation indicate maximum depth of trap deployment): Shallow Shelf (SS10), and Deep Shelf (DS30) in the Florida Keys, Dry Tortugas (DT60), and Pulley Ridge (PR70) over 3 years. Taxonomic richness plotted against cumulative number of traps deployed at each strata.

brachiolaria and poecilostomatoid copepods were present, but they were never collected in SS10 or DS30 samples. Although gelatinous zooplankton are not generally well preserved in ethanol samples, we note that they were present in 62.5% of MCE samples, but in only 7.5% of SS10 and DS30 samples.

NMDS analysis of the zooplankton community collected across the four habitats demonstrated that while

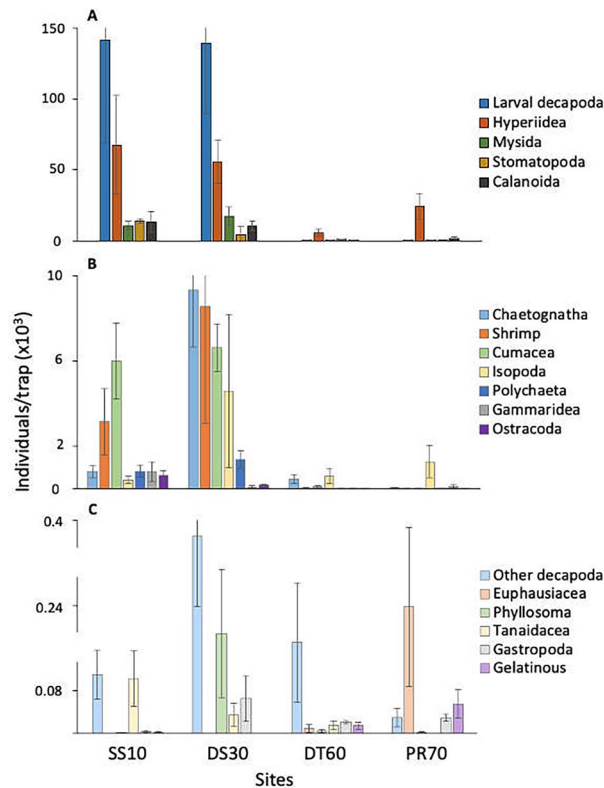


Fig. 5. Mean abundance of invertebrate zooplankton collected in replicate light traps deployed during the dark half of the lunar cycle across four depth strata (numbers next to the site abbreviation indicate maximum depth of trap deployment): Shallow Shelf (SS10), and Deep Shelf (DS30) in the Florida Keys, Dry Tortugas (DT60), and Pulley Ridge (PR70), where numbers were (A) > 10 000 individuals/trap, (B) > 500 individuals/trap and (C) > 50 individuals/trap. SS and DS were averaged across two Florida Keys locations, American Shoal and Looe Key. Note different y-axis scales. Other groups of invertebrates identified (e.g. copepods other than calanoids; brachiolaria; appendicularia; cephalopoda) were not illustrated in figures due to low abundance. Taxa plotted in descending order of abundance. Error bars represent standard error.

there was overlap among sites, the taxonomic zooplankton community differed among depth strata, transitioning from SS10 to DT60 to PR70, with intermediate depth DS30 appearing as a somewhat less variable subset of SS10 (Fig. 6; stress value of 0.06 with 2D, non-metric fit $r^2 = 0.996$ and linear fit $r^2 = 0.986$). Differences between deeper sites (DT60 and PR70) can primarily be attributed to higher abundance of isopods and some holoplankton taxa such as poecilostomatoids and pteropods (Fig. 6).

Despite limitations of the resolution of the HYCOM model at the scale of our sampling sites, there was evidence of variability in current direction and speed among depth strata and years with generally faster currents at SS10 and PR70 (Supplementary Fig. S2). Current direction varied to the greatest degree within and among years at PR70. Based on the model, north–south flow at DS30

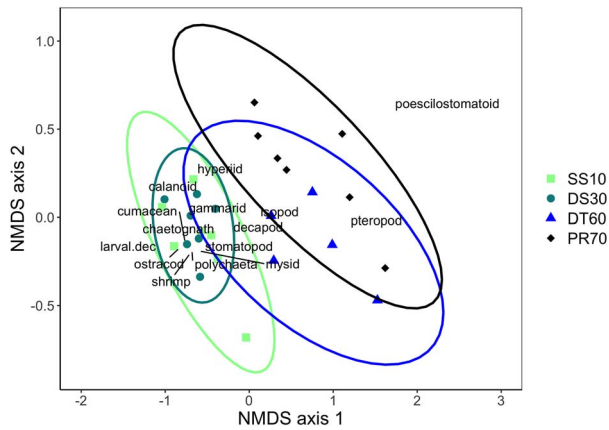


Fig. 6. NMDS of zooplankton communities collected in replicate light traps deployed during the dark half of the lunar cycle across four depth strata (numbers next to the site abbreviation indicate maximum depth of trap deployment): Florida Keys Shallow Shelf (SS10) and Deep Shelf (DS30) reefs and two mesophotic coral ecosystems, Pulley Ridge (PR60) and Dry Tortugas (DT70). 90% data ellipses are included for each strata to help delineate differences among strata. Taxa names correspond to weighted averages (in NMDS space) of the taxa that were present at least 2.5% percent of the time. Additional taxa were included in the analysis, but names could not be included due to space limitations.

and DT60 was minimal near the benthos. Currents were highly variable within strata during each sampling period and differences in zooplankton abundance, such as high abundance at SS10 and DS30 (Fig. 3), did not have a consistent relationship with current speed or direction.

DISCUSSION

Depth-related differences in zooplankton abundance and composition

Our light trap samples demonstrated that nocturnal zooplankton communities from the four depth strata differed significantly in both magnitude and composition, consistent with our hypothesis. Larger zooplankton abundances at the shallowest sites (SS10 and DS30 reefs) likely reflect proximity to abundant shallow-water benthic adult populations as well as higher nutrient availability and productivity. Populations of benthic marine organisms that produce pelagic larvae (meroplankton) are more abundant at shallower reef sites relative to mesophotic depths (Kahng *et al.*, 2010; Garcia-Sais, 2010; Bejarano *et al.*, 2014; Goldstein *et al.*, 2016a; Reed *et al.*, 2017), thus recently spawned young should be more abundant near these adult populations. Late-stage meroplankton returning to settle to benthic adult populations will also be concentrated in areas close to these shallow water sites. A shorter water column may further concentrate

meroplankton in these areas. Recruitment of juvenile fishes to benthic populations is typically higher at shallow shelf sites (D'Alessandro *et al.*, 2007) compared to mesophotic depths (Goldstein *et al.*, 2016a), and the same pattern is likely true for decapods and other shallow water invertebrates. Near-reef zooplankton may also be more abundant at shallow sites due to higher levels of sunlight and nutrients [from terrestrial runoff, nearshore upwelling (Szmant and Forrester, 1996; Leichter *et al.*, 1998, Hitchcock *et al.*, 2005) and fish excretion (Burkepile *et al.*, 2013)], supporting higher levels of nearshore primary productivity. Such higher primary production would support higher levels of secondary production of zooplankton.

The composition of the light trap collections is consistent with these concepts: zooplankton at both SS10 and DS30 sites were dominated by meroplankton. The dominance of meroplankton at our shallowest reef sites is similar to findings of a recent study of mesozooplankton on Brazilian coral reefs (Santos *et al.*, 2019). Even though the proportion of meroplankton at any site has the potential to be highly variable owing to periodic reproductive patterns of different taxa, the proportion of meroplankton at PR70 and DT60 was significantly lower than holoplankton, suggesting that zooplankton assemblages at MCEs differ fundamentally from those associated with shallow coral reefs. Indeed, zooplankton assemblages varied among the four depth strata, with more overlap between the two shallowest sites, SS10 and DS30, followed by an apparently transitional assemblage at the intermediate depth site, DT60, and a composition shift to more oceanic zooplankton at the deepest site, PR70. Located geographically closer to the two Florida Keys sites (SS10 and DS30), and at a slightly shallower depth than PR70, DT60 had the highest nightly richness in groups of zooplankton (significantly higher than DS30 and PR70), but rarefaction curves indicated a more intermediate position in overall DT60 richness, with closer similarities to the shallow depth strata. This intermediate composition likely reflects the intermediate depth of DT60 where both shallow water and mesophotic taxa can overlap. Further, the closer proximity of DT60 (relative to PR70) to the Florida Keys track may allow for greater ecological connectivity with Florida Keys' populations (Slattery *et al.*, 2011; Sponaugle *et al.*, 2012; Vaz *et al.*, 2016; Kourafalou *et al.*, 2018).

Unique characteristics of the zooplankton sampled at the two mesophotic sites include a markedly low to absent abundance of cumaceans, a benthic associated invertebrate not often seen in pelagic zooplankton sampling. The deepest site, PR70, notably had the highest abundance of oceanic zooplankton such as euphausiids, gastropods, gelatinous zooplankton and zooplankton

known to associate with gelatinous organisms (hyperiid and poecilostomatoids). Although there are few published data on open ocean zooplankton in the region (Lane *et al.* 2003), and the taxonomic focus of that study was on copepods, this composition at PR70 suggests that, of all the sites, PR70 had the greatest ecological relationship to open ocean zooplankton populations.

Comparative light trap sampling of nocturnal zooplankton

It can be challenging to make direct comparisons among studies due to differences in methodology, sampling design and reef configuration. For example, a recent study also used light traps to examine zooplankton composition across two depths (15 and 40 m) at three sites on the Mesoamerican Barrier Reef off of Honduras, finding that relative zooplankton abundance composition, and taxonomic richness was similar among depths, in marked contrast to our results (Andradi-Brown *et al.*, 2017). Whether this was due to a coarser taxonomic resolution (16 vs 29 taxonomic groups), subtle differences in light trap design (e.g. light levels used to attract zooplankton to traps), time of the lunar cycle during which traps were deployed, sampling of a shallower range, or sites that are closer to shore and each other is unknown. Alternatively, there may be real regional or site-specific differences.

Although light traps sample only nocturnal, phototactic zooplankton, they provide a means of comparably sampling zooplankton assemblages across broad depths. The deployment of light traps at a similar distance above benthic habitats (i.e. 5–6 m) across all depth strata allowed us to compare nocturnal zooplankton assemblages most physically associated with the coral benthos. We further standardized our comparisons by focusing on samples collected during the dark half of the lunar cycle.

Because the number of organisms collected in light traps may be related to the magnitude of currents—i.e. nearby density and exposure of zooplankton to the light (delivery to trap vicinity) and the capacity for phototactic organisms to successfully swim into a trap—we examined current speeds at each depth stratum. We could not control the current in which each trap was deployed (beyond deploying traps at a common depth off the benthos) nor do we have concurrent data on site- and night-specific mean current speeds. Instead, we examined general current patterns for the habitats over the period studied with a combination of HYCOM-based modeling and ADCP current meters at the deepest sites. Overall, current speeds within each depth stratum were highly variable during the time period of light trap deployments and the number of

individuals that were caught in light traps was not predictably related to current speeds. ADCP records at PR70 and DT60 during the study period indicate that near bottom currents tended (67% of the time) to be southward but were variable in speed, ranging from 0 cm s⁻¹ to >50 cm s⁻¹ (Kourafalou *et al.*, 2018). Near-bottom currents, generally reduced relative to surface currents, were weaker (<10 cm s⁻¹) in August 2012 and 2014, and stronger (>40 cm s⁻¹) in August of 2013 (Kourafalou *et al.*, 2018). Although no comparable ADCP current data are available for the shallower shelf sites, previously published current meter data from the 30-m isobath near these sites in 1990–1991 indicate similarly variable currents up to 40 cm s⁻¹ (Lee *et al.*, 1995). Thus, high variability of currents at each site and among collections suggests that consistent trends in zooplankton abundance and composition are likely associated with differences among strata rather than sampling gear complications and catchability.

Movement of zooplankton among depth strata

The present study was not designed to measure movement among depth strata thus it is impossible to determine the degree to which sampled zooplankton were resident. For zooplankton higher in the water column in the Florida Straits, transient mesoscale and submesoscale eddies enhance primary productivity, concentrate plankton and transport larval fishes (Hitchcock *et al.*, 2005; Sponaugle *et al.*, 2005; D’Alessandro *et al.*, 2007; Shulzitski *et al.*, 2016). For deeper plankton, internal tidal bores regularly move deep nutrient- and zooplankton-rich water up onto shallower reefs (Leichter *et al.*, 1998). Although numerous physical oceanographic mechanisms can transport zooplankton (Hamner *et al.*, 2007; Alldredge and King, 2009), because benthic currents are typically slower than surface currents, it is likely that benthic zooplankton experience higher levels of residency than surface oriented plankton.

Ecological effects of depth-related patterns of zooplankton abundance and composition

Near-reef zooplankton are a central link in the food web of these subtropical benthic marine ecosystems. They are critical prey for suspension feeders, such as hermatypic corals, and zooplanktivorous organisms such as fishes (Kiflawi and Genin, 1997; Yahel *et al.*, 2005; Wyatt *et al.* 2012; Goldstein *et al.*, 2017; Williams *et al.*, 2018). A large portion of the zooplankton community at shallower depths was comprised of meroplankton, suggesting that zooplankton prey for benthic organisms in shallower habitats may be dictated by reproductive cycles to a

greater degree than in deeper habitats. Pulsed zooplankton abundances in shallower reef habitats may impact food availability for planktivores (Goldstein *et al.*, 2017) and provide a less consistent food source than deeper reef environments dominated by holoplankton. Demersal zooplankton, known to emerge from the benthic reef habitat into the water column at night (Yahel *et al.*, 2005; Brito-Lolaia *et al.*, 2020), were primarily diel vertically migrating mysids in our sampling region. Hyperiid, calanoid copepods and chaetognaths, the most abundant representatives of holoplankton in our study, are known to drive increased nighttime biomass of zooplankton over coral reefs due to advection during their diel vertical migrations (Yahel *et al.*, 2005; Nakajima *et al.*, 2008). Therefore, the bulk of zooplankton abundance sampled may not be readily or consistently available to corals feeding close to the benthos at night (Sebens *et al.*, 1998) or planktivorous fishes that feed during daylight hours (Lesser *et al.*, 2018).

Fundamental differences in the availability, abundance and taxonomic composition of zooplankton likely affect the biomass of higher trophic levels that can exist in these habitats. But subtle differences in the nutritional content of these zooplankton taxa may support benthic predators more than differences in volume would predict. For example, PR70 had the highest abundance of euphausiids, gelatinous zooplankton and appendicularians. The latter were found in the gut contents of adult zoo-planktivorous bicolor damselfish (*Stegastes partitus*) feeding at PR70 and may contribute to the higher condition of these fish at mesophotic depths (Goldstein *et al.*, 2017). In oligotrophic environments, nutrient recycling through the microbial loop may enhance retention of nutrients near reefs. The detritus-/microbial loop-based feeding of appendicularians may provide an important recycled source of nutrients for mesophotic populations. Relative to their shallow water counterparts, planktivorous bicolor damselfish at PR70 live longer, attain larger sizes and are able to invest heavily in reproduction (Goldstein *et al.*, 2016b, 2017).

There is some evidence that water quality and zooplankton abundance and composition may be changing in nearshore waters in the Caribbean (Jacobson and Edmunds, 2010; Lapointe *et al.*, 2019). Increasing water temperatures associated with global climate change and rising coastal eutrophication may increase local primary production and the frequency and intensity of phytoplankton blooms (Shangguan *et al.*, 2017; Paerl *et al.*, 2020), but how this is ultimately translated into secondary production of zooplankton, particularly at depth, is unclear. Consistent patterns of zooplankton abundance and taxonomic composition across depth strata suggest that shifts in assemblages associated with global climate change could have major impacts on the

replenishment of benthic organisms and food quality for near-reef planktivores.

CONCLUSION

Differences in patterns of abundance and composition of near reef nocturnal zooplankton have implications for the replenishment of benthic marine organisms and food webs. Shallow reef environments in the Florida Straits had zooplankton assemblages that differed significantly in abundance and composition from assemblages on mesophotic reefs. By definition, meroplankton-dominated shallow and deep shelf reefs play a critical role in the replenishment of many diverse benthic marine organisms. In contrast, the dominance of oceanic holoplankton on mesophotic reefs serves as a valuable, consistent food source for populations of organisms at depth. Transitional sites, such as DT60, that exhibit intermediate overall richness and taxa overlap in zooplankton between shelf habitats and the deepest mesophotic reef (PR70) are likely ecologically valuable sites for connectivity between shallow nearshore reef populations and potential mesophotic ecological refuges (Sponaugle and Cowen, 2019). Focusing protection and management on such transitional sites may be increasingly important to mediate climate change related damage to coral reef ecosystems (Griffiths *et al.*, 2017).

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

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DATA ARCHIVING

Zooplankton data are deposited at the National Centers for Environmental Information <https://doi.org/10.25921/stmm-5783>.

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