

# Trophic designation and live coral cover predict changes in reef-fish community structure along a shallow to mesophotic gradient in Hawaii

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**Abstract** Reef-fish community structure and habitat associations are well documented for shallow coral reefs (<20 m) but are largely unknown in deeper extensions of reefs (mesophotic reefs; >30 m). We documented the community structure of fishes and seafloor habitat composition through visual observations at depth intervals from 3 to 50 m in West Hawaii. Community structure changed gradually with depth, with more than 78% of fish species observed at mesophotic depths also found in shallow reef habitats. Depth explained 17% of the variation in reef-fish community structure; live coral cover explained 10% and prevalence of sand accounted for 7% of the fitted variation indicating that depth-related factors and coral habitat play a predominant role in structuring these communities. Differences in community structure also appear to be linked closely with feeding behavior. Trophic designation accounted for 31% of the fitted variation, with changes in herbivore abundance accounting for 10% of the variation. These findings suggest that changes in reef-fish community composition from shallow to mesophotic environments are largely influenced by trophic position, coral habitat and indirect effects of depth itself.

**Keywords** Fish assemblages · Community structure · Depth refuge · Mesophotic coral ecosystems · Oceanic islands

## Introduction

Factors structuring reef-fish communities have been researched extensively in the past 50 yr, largely following the advent and widespread use of SCUBA diving (Sale 1991; Pyle 2000; Hixon 2011). Much of the spatial variation in reef-fish community composition has been linked to habitat availability and complexity (Hixon and Beets 1993; Munday 2000; Almany 2004; Gratwicke and Speight 2005; Brokovich et al. 2006). In addition to habitat parameters, depth and associated abiotic gradients are also known to play substantial roles in the community composition and abundance of reef fishes at shallow depths (<20 m; McGehee 1994; Friedlander and Parrish 1998; Arreola-Robles and Elorduy-Garay 2002; Donaldson 2002; Brokovich et al. 2006). Due to the limitations of conventional SCUBA gear, most knowledge of reef fishes and their habitats has been limited to depths of 20 m or less, yet coral reefs commonly extend to depths in excess of 80 m (Maragos and Jokiel 1986; Kahng and Maragos 2006; Menza et al. 2007; Reaka et al. 2008; Kahng et al. 2010).

The few ecological studies conducted on mesophotic reefs (30–150 m) support the premise of deep reefs providing substantial habitat for fishes (Brokovich et al. 2007, 2008; Lesser et al. 2009; Bejarano et al. 2014). Studies of mesophotic communities in the Caribbean and Red Sea reveal that coral cover is consistent to at least 50–60 m depth (Goreau and Goreau 1973; Fricke and Schumacher 1983; Liddell and Ohlhorst 1988; Liddell et al. 1997; Bak et al. 2005; Brokovich et al. 2008). Recent work in the Au'au Channel in Hawaii has

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revealed a unique and extensive mesophotic coral bed, providing structure for immense mesophotic fish communities (Kahng et al. 2010). These findings suggest that the extent of coral reefs is much greater than previously thought and that mesophotic ecosystems may provide significant habitat and possible refuge for shallow coral reef fishes (Bridge et al. 2013; Baker et al. 2016).

Mechanisms underlying changes in coral reef communities from shallow to mesophotic depths are not well understood (Slattery et al. 2011; van Oppen et al. 2011; Kahng et al. 2014). Corals, fish and other organisms have been found from shallow to upper mesophotic zones (30–50 m); in the Caribbean, nearly 80% of coral species occur to depths greater than 30 m, while over 40% of coral species extend to 30+ m in the Indo-Pacific (Bridge et al. 2013). Few studies have focused on the ecology of fishes of mesophotic coral ecosystems (MCE; >30 m). These studies predominantly describe species composition and species–habitat relationships using observational techniques, and relate changes in community structure largely to depth and changes in coral abundance or morphology (Colin 1974; Thresher and Colin 1986; Pyle 2000; Feitoza et al. 2005; Brokovich et al. 2007, 2008, 2010a; Garcia-Sais 2010; Bryan et al. 2013; Bejarano et al. 2014; Schultz et al. 2014; Lindfield et al. 2016). To date, five studies have investigated reef fishes at mesophotic depths in Hawaii: three in the remote northwestern Hawaiian Islands (Parrish and Boland 2004; Kane et al. 2014; Fukunaga et al. 2016); one from Maui in the main Hawaiian Islands (Boland and Parrish 2005); and one encompassing both the northwestern Hawaiian Islands and Au’au Channel in Maui (Pyle et al. 2016). Thus, our understanding of reef-fish abundance and community structure in the Hawaiian Archipelago from shallow to mesophotic depths is extremely limited, and in the majority of islands, completely absent.

In this study, we aimed to test two primary hypotheses: (1) community composition of coral reef fishes changes gradually from shallow to upper mesophotic depths and (2) changes in reef-fish community composition with depth can be predicted by trophic position or habitat variables. Given the absence of quantitative reef-fish data below 20 m in West Hawaii, this study provides the first baseline estimates for reef fishes in shallow mesophotic depths and sheds light on depth-related changes in community structure and function in this underrepresented region.

## Materials and methods

### Study sites

Hawaii Island is geologically the youngest of all the islands in the archipelago with a steep bathymetric gradient and

coral reefs that extend continuously from shore to depths of approximately 50 m. Beyond that depth, large sand flats occur to 70 m depth or more, with reef often re-emerging around 70 m and patchily continuing to depths currently undetermined. Eleven sites were selected along West Hawaii’s coastline in areas where continuous coral reef habitat occurs from shallow waters to at least 30 m (Fig. 1). Due to the steeply sloping bathymetry, the 50 m depths surveyed were often within 100–200 m of the shoreline; thus, physical distance between the shallowest and deepest surveys was between 50 and 200 m from shore.

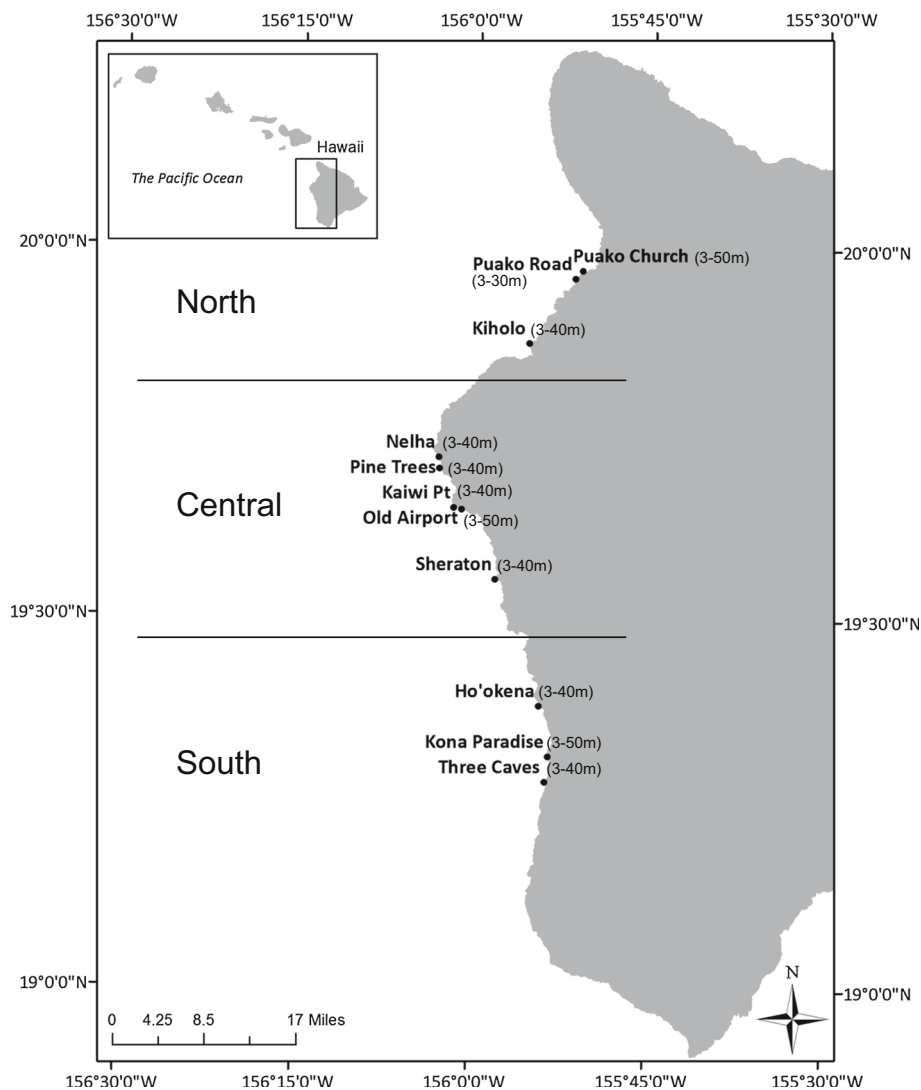
### Sampling design

A stratified sampling design was used to explore changes in reef-fish abundance and community structure with depth. Concordant depth and bathymetric relief among sites was sought to maintain consistency and reduce potential survey bias. Visual surveys of reef fish and benthic substrates were conducted on SCUBA at approximately 10-m depth intervals during July–August in 2013–2015. Due to variability of habitat below 30 m, three sites were sampled to 50 m, seven to 40 m and one to 30 m. In each site, transects were laid parallel to shore at 3, 10 m and then in 10-m depth intervals until the deepest extent of the reef. A minimum of three surveys were conducted at each depth contour at each site. Transects were spaced a minimum of 5 m apart. This resulted in an incomplete survey design with 35 surveys at 3 m, 37 surveys at 10 m, 38 surveys at 20 m, 38 surveys at 30 m, 34 surveys at 40 m and 30 surveys at 50 m (Electronic supplementary material, ESM Table S1). Visual fish surveys were conducted at each depth (3–50 m) using a 25 m × 4 m belt transect (Hill and Wilkinson 2004). Belt length, width and level of replication per depth (minimum  $n = 3$ ) were dictated by technical constraints resulting from the short bottom times allowed from using SCUBA at 50 m depths (Brokovich et al. 2008; Sandin et al. 2008). Within each fish belt transect, all fishes were identified to species (according to Randall 2007) and tallied individually. Benthic survey data were collected at two of the replicate transects within each depth by photographing a 0.25-m<sup>2</sup> quadrat every meter ( $n = 25$  per transect) using an underwater camera equipped with a PVC photoquad framer and dual lighting system.

### Data analysis

Species accumulation curves were used to verify sampling effort (MM model, Primer-E+; ESM Fig. S1). Sites were grouped into three geographic regions (north, central and south) to ensure adequate sampling effort for analyses (Fig. 1; ESM Table S1). To ascertain general trends in

**Fig. 1** Location of study sites in West Hawaii with depth ranges in parentheses



reef-fish diversity and abundance with depth, we calculated the mean species richness (alpha diversity) and abundance of all fishes with depth. Richness (alpha diversity) was analyzed using a generalized linear model (GLM) based on a Gaussian distribution while abundance was analyzed using a GLM based on a Poisson distribution (two factors: depth and region; JMP 12.1.0, SAS Institute Inc.). Post hoc Tukey tests were used to identify significant differences among depths.

Changes in reef-fish community composition were analyzed using principal coordinates (PCO) analyses with PERMANOVA (two factors: depth and region) to identify significant differences among species assemblages and depth using Bray–Curtis similarity matrices on square root-transformed abundance data (Primer version 6.1.13, Primer-E+). Changes in reef-fish community composition were tested against trophic position, benthic composition and physical structure using a distance-based linear model

(DistLM) and redundancy analysis (dbRDA) (Primer version 6.1.13, Primer-E+).

DistLM partitions the variation of multivariate data according to multiple regression models to analyze relationships within a multivariate data cloud (Legendre and Anderson 1999). A dbRDA provided an ordination of fitted values using the multivariate multiple regression of the relationship between reef-fish community structure and the predictor variables (Anderson et al. 2008). Vector overlays on dbRDA ordination diagrams were used to aid in determining the strength and direction of the relationship between variables and redundancy analysis axes. The length of each vector corresponds to the size of the effect the variable had on the construction of dbRDA axes (Anderson et al. 2008). We tested for multicollinearity before DistLM and dbRDA analyses. No two variables had correlations stronger than 0.6 and were therefore considered independent.

Trophic position was examined by binning reef-fish species into six broad trophic guilds. Trophic assignment was classified according to gut content analyses published on Hawaiian fish species in Hobson (1974) and Randall (2007). Species lists and assignments were corroborated with the National Oceanic and Atmospheric Administration's Coral Reef Ecosystem Program. Comparisons of trophic guilds with depth were performed using one-way ANOVAs with post hoc Tukey tests.

Benthic composition and physical structure estimates were examined to investigate changes in the benthos with depth. Benthic photoquadrat samples were analyzed using CoralNet benthic image analysis (Beijbom et al. 2015). Fifty random points were placed within each photograph and the biota or substratum directly underneath each point was identified to the lowest taxonomic classification possible (ESM Table S2; Fenner 2005; Huisman et al. 2007). Taxonomic identifications were pooled to create descriptive habitat categories which included turf algae, macroalgae, sand and live coral cover. These broad categories were selected as live coral cover, turf and macroalgal cover are strongly correlated with reef-fish community composition at shallow depths (Friedlander and Parrish 1998; Arreola-Robles and Elorduy-Garay 2002; Donaldson 2002; Wilson et al. 2010; Hoey et al. 2013; Evans et al. 2014). Live coral cover was further categorized into designations based on general morphology as fishes have been shown to strongly associate with branching and plating coral morphologies. Three categories were included for analysis: branching/plating, encrusting and lobate morphologies. Categories were summed by photoquadrat and averaged ( $n = 25$ ) to obtain one cover estimate per transect to correspond with fish transects. Log-transformed benthic percentage cover data for turf algae, sand and coral were compared across transect depths using one-way ANOVAs with post hoc Tukey tests. Macroalgal data were analyzed using the nonparametric Wilcoxon test and post hoc Wilcoxon planned comparisons as variances were not equal.

We tested whether the underlying physical substrate influenced fish community composition. Each photoquadrat sample was visually assigned a primary (>50% of photograph) structure identification using one of the eight structural categories: basalt—continuous bare lava formations; compressa bed—complex interstitial matrix created by either live or dead *Porites compressa* beds; pavement—flat, hard-bottom structure; pebble/cobble—small (<25 cm) rocks or pebbles; rubble—small fragments of dead coral; carbonate—outer layer of live or dead coral skeletons, predominantly mounding corals; sand/sediment—fine-grain sands or sediments; and boulder—large rocks (>25 cm). Primary benthic structure codes were then summed by

transect ( $n = 25$ ) and averaged to generate percentage cover of structural categories by transect for comparison.

## Results

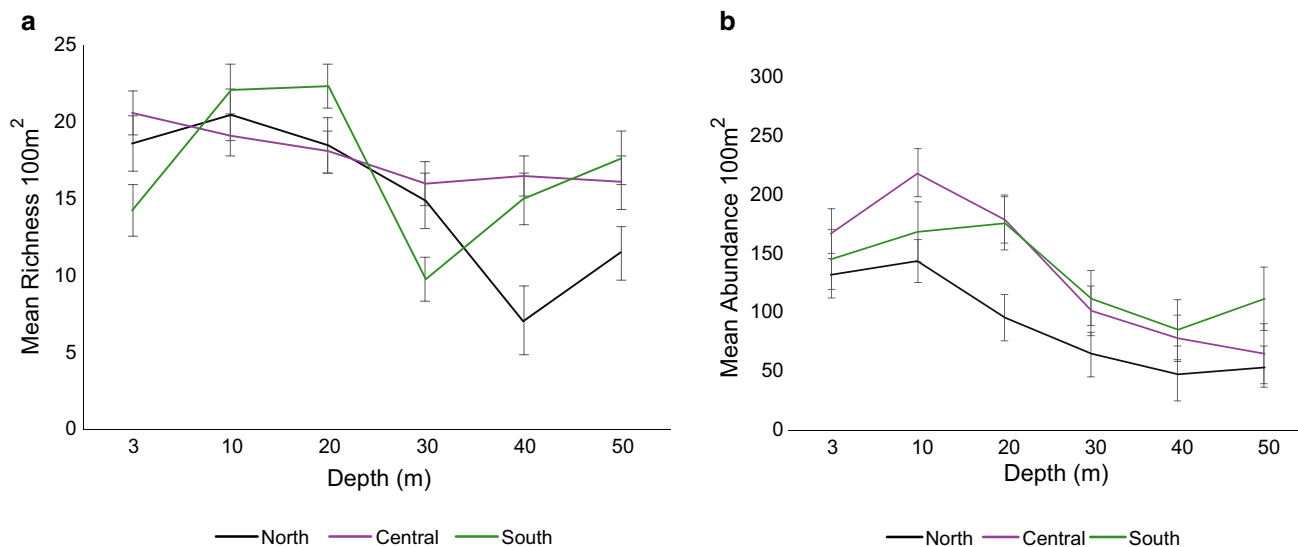
### Community composition

We recorded 26,553 fish from 150 species and 33 families within 212 transects at 11 sites along the West Hawaii coast. Species richness significantly differed across depths and regions sampled (GLM: depth  $\chi^2_{5,212} = 54.46$ ,  $P \leq 0.001$ ; region  $\chi^2_{2,212} = 7.95$ ,  $P = 0.019$ ; depth  $\times$  region  $\chi^2_{10,212} = 44.15$ ,  $P \leq 0.001$ ; Fig. 2a). Richness generally decreased from shallow (3–20 m) to mesophotic (30–50 m) depths. A significant interaction between depth and region occurred because of unexpectedly high richness at 40 and 50 m depths at one site (Kona Paradise) in the southern region. Overall fish abundance (Fig. 2b) significantly differed across depth (GLM:  $\chi^2_{5,212} = 59.01$ ,  $P \leq 0.001$ ) and regions sampled (GLM:  $\chi^2_{2,212} = 14.15$ ,  $P = 0.001$ ), but there was no depth  $\times$  region interaction (GLM:  $\chi^2_{10,211} = 7.61$ ,  $P = 0.67$ ). Overall fish abundance decreased with depth, with each region displaying similar declines with depth but slightly different overall abundances. Northern sites generally had lower abundance of fishes than central and southern sites. Fish abundance was significantly greater at 3–20 m than at mesophotic depths (30–50 m) (post hoc Tukey tests).

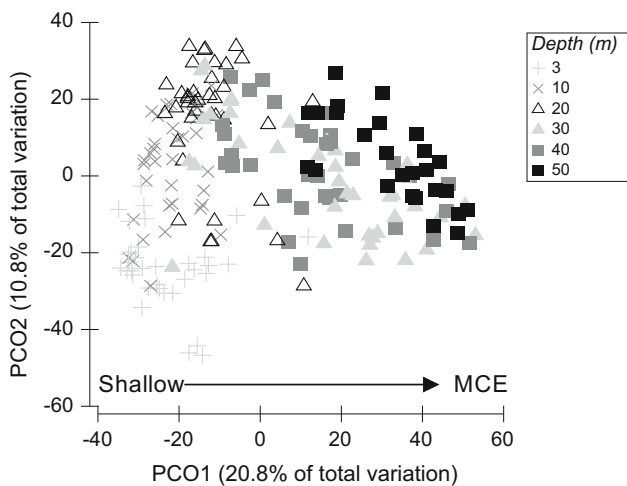
The community structure of reef fishes transitioned gradually with depth (PCO analysis; Fig. 3). Shallow reef-fish communities were more distinct (spatially separated groupings), while deeper communities were similar (groupings largely overlapping), particularly at 30–50 m. Axis 1 explained 21% of the total variation and corresponds most strongly with transect depth. PERMANOVA tests using species abundance data indicated that both region and depth were significant in structuring communities (depth: pseudo- $F_{5,212} = 18.47$ ,  $p(\text{perm}) = 0.001$ ; region: pseudo- $F_{2,212} = 6.06$ ,  $p(\text{perm}) = 0.001$ ; depth  $\times$  region: pseudo- $F_{10,212} = 3.13$ ,  $p(\text{perm}) = 0.001$ ).

### Patterns with depth

Species distributions varied greatly with depth (ESM Table S3), with some species found at only a single depth and others found at all six depths (Table 1). Depth-generalist species (observed at four or more depths,  $n = 79$ ) outnumbered depth-specialist species (found at one or two contiguous depths,  $n = 50$ ). Depth specialists were evenly divided between shallow specialists (<30 m;  $n = 21$ ) and



**Fig. 2** **a** Mean reef-fish species richness 100 m<sup>-2</sup> by depth. **b** Mean reef-fish abundance 100 m<sup>-2</sup> by depth. Error bars are SEs



**Fig. 3** Principal coordinates analysis ordination of square root-transformed fish community structure at different depths using Bray–Curtis similarity resemblance matrix. Axes describe percentage of variation in terms of the total fish community structure

**Table 1** Number of species observed from one to six depths (3, 10, 20, 30, 40 and/or 50 m), indicating the proportion of depth specialists (found at only one or two contiguous depths) to depth generalists (found at four or more depths)

#Depths	#Species	% of total
1	31	21
2	19	13
3	20	13
4	28	19
5	22	15
6	29	19

mesophotic specialists (>30 m; n = 21), and were not concordant with genus or family (ESM Table S3).

DistLM analysis indicated significant relationships between the reef-fish community structure and 20 of the 21

variables tested (pavement not statistically significant; Table 2). Depth accounted for the largest proportion of fitted variance in fish community structure (17%) while herbivore abundance and live coral cover accounted for ~10% each (Table 2). The decline in herbivore, detritivore and corallivore abundance with depth accounted for nearly 25% of the variation in community structure, while the decrease in live coral cover and increase in sand

**Table 2** Percentage of variation explained in a distance-based multivariate linear model of reef-fish communities

Variable	P	% Variation explained
Depth	0.001	16.89
Herbivore	0.001	10.31
Live coral	0.001	10.23
Sand/sediment	0.001	7.67
Detritivore	0.001	7.01
Corallivore	0.001	6.92
Rubble	0.001	6.24
Basalt	0.001	5.79
Macroalgae	0.001	5.43
Compressa bed	0.001	4.45
Zooplanktivore	0.001	3.7
Site	0.002	2.28
Invertivore	0.001	2.17
Turf algae	0.001	2.14
Carbonate	0.004	1.97
Boulder	0.006	1.65
Pebble/cobble	0.012	1.45
Omnivore	0.029	1.31
Piscivore	0.042	1.16
Pavement	0.454	0.67

accounted for approximately 18% of variation observed in the model. Axis 1 of the dbRDA accounted for 46% of fitted variation (18% of the total variation) and strongly correlated with depth (Fig. 4). Vector overlays indicate that sandy habitats increase with depth, while coral-dominated habitats are associated more strongly with shallow depths. Both herbivorous and corallivorous fishes are more closely associated with shallow depths. Axis 2 explained 14% of the fitted variation (5% of total variation) and appears largely associated with site-based differences.

Habitat analyses reveal significant increases in sand and macroalgal cover with depth (ANOVA; Macroalgae:  $F_{5,146} = 13.79$ ,  $P < 0.001$ ; Fig. 5a; Sand:  $F_{5,146} = 17.65$ ,  $P < 0.001$ ; Fig. 5d). While sand increased gradually with depth, macroalgae remained at low cover from 3 to 40 m depth and significantly increased at 50 m depth. Turf algae significantly differed among depths but did not exhibit any depth-related patterns (ANOVA:  $F_{5,146} = 3.7$ ,  $P = 0.004$ ; Fig. 5b). Coral cover peaked at 10 m and gradually but significantly decreased with depth; mesophotic depths had significantly less coral cover than shallower depths (ANOVA:  $F_{5,146} = 25.06$ ,  $P < 0.001$ ; Fig. 5c). Coral morphologies also differed significantly with depth (Fig. 5c). Branching/plating morphologies peaked in cover at 20 m and declined gradually with depth ( $F_{5,137} = 6.58$ ,  $P < 0.001$ ). Lobate morphologies also differed significantly with depth, peaking in percentage cover at 10 m and declining gradually with depth, with mesophotic depths having significantly lower lobate cover than 3–20 m depths ( $F_{5,137} = 20.9$ ,  $P < 0.001$ ). Encrusting morphologies

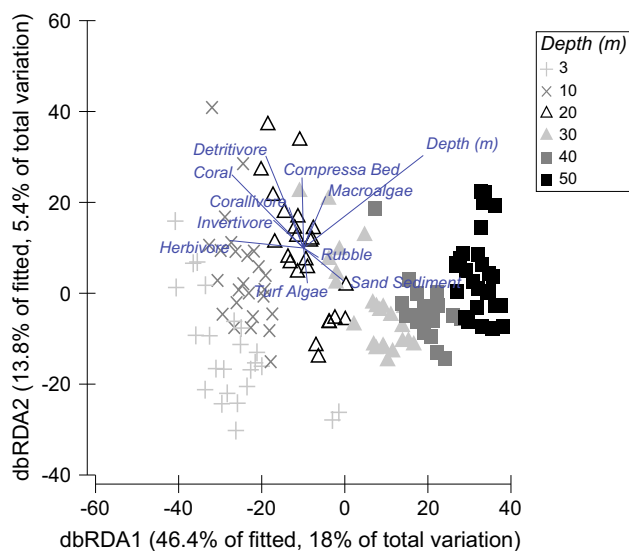
remained at low but consistent cover across depth ( $F_{5,137} = 1.92$ ,  $P = 0.11$ ).

Trophic composition varied significantly across depths. Abundance of fishes in nearly every trophic group significantly declined with depth (detritivores:  $F_{5,211} = 13.47$ ,  $P < 0.001$ ; herbivores:  $F_{5,211} = 24.25$ ,  $P < 0.001$ ; omnivores:  $F_{5,211} = 4.68$ ,  $P < 0.001$ ; zooplanktivores:  $F_{5,211} = 3.89$ ,  $P < 0.002$ ; corallivores:  $F_{5,211} = 24.36$ ,  $P < 0.001$ ; Fig. 6). The only exception were the invertivores, which differed significantly among depths but did not exhibit any directional pattern ( $F_{5,211} = 4.39$ ,  $P < 0.001$ ) and piscivorous fishes which did not differ significantly with depth ( $F_{5,211} = 1.3$ ,  $P = 0.27$ ). Trophic groups differed in the rate of decline between shallow (0–20 m) and mesophotic (30–50 m) depths. Detritivore (84%), corallivore (72%) and herbivore (68%) fish abundances declined nearly twice as much as zooplanktivore (40%) fishes from shallow to mesophotic depths.

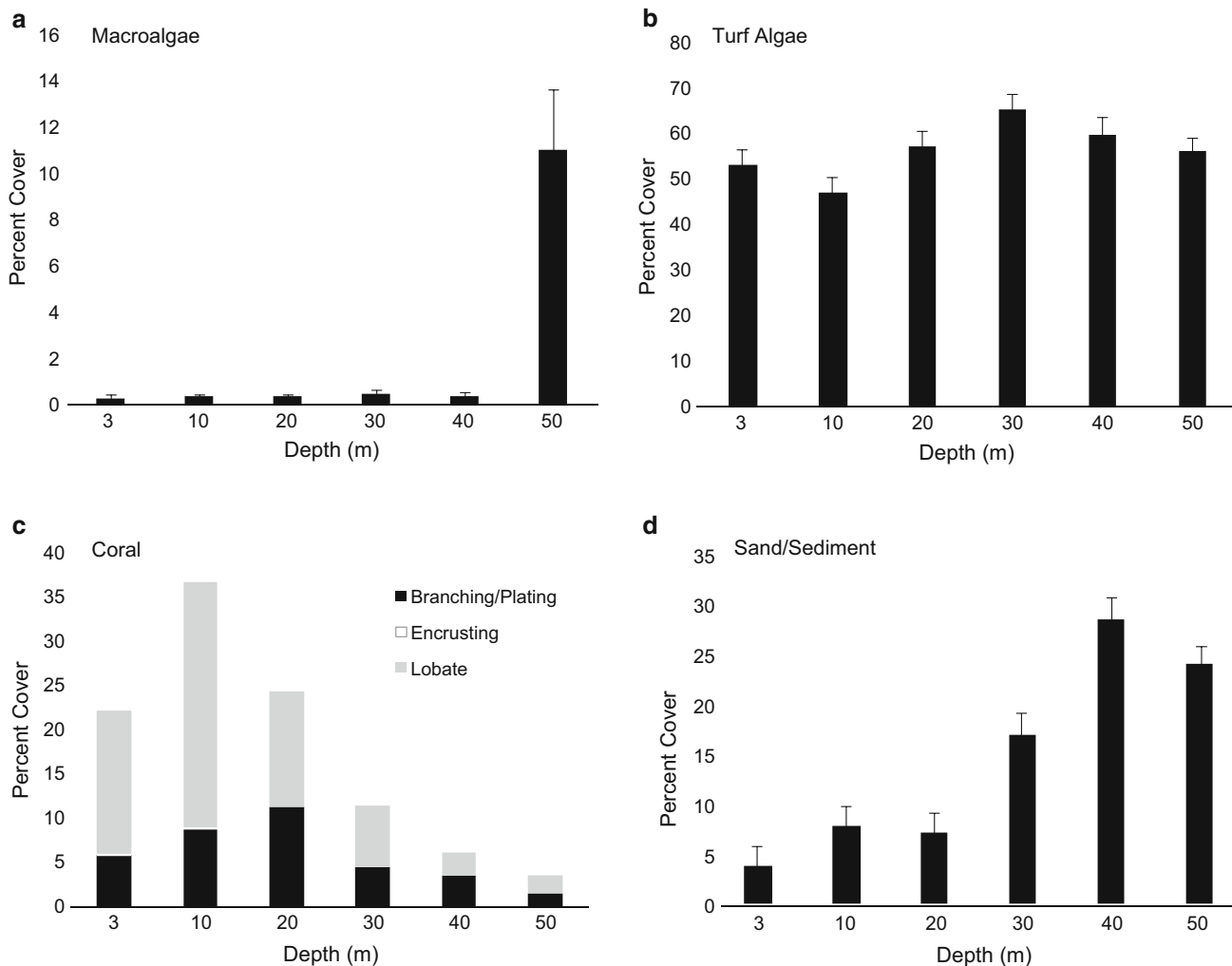
## Discussion

The mesophotic zone of coral reefs has been defined as beginning at 30 m and extending to the lower distributional limit of light-dependent coral reef communities (Hinderstein et al. 2010; Kahng et al. 2010). Our study highlights that while technically in the MCE range, the 30–50 m fish communities are largely extensions of shallow reef communities, with more than 78% of the fish species observed at MCE depths typically associated with shallow waters. Our data corroborate the few other mesophotic fish studies in that these shallow MCE regions act as transition zones between shallow and deep fish communities (Brokovich et al. 2008; Garcia-Sais 2010; Bejarano et al. 2014; Rosa et al. 2016). In particular, Rosa et al. (2016) found nearly identical overlaps of shallow fishes in upper mesophotic depths (80%) as our study (78%), indicating that the upper mesophotic zone (30–50 m) is still largely dominated by common shallow reef-fish species. The deep specialists noted here are species found commonly on mesophotic reefs in the Hawaiian Archipelago, indicating that the 40–50 m zone in West Hawaii acts as the upper limit for common mesophotic fish species and is congruent with results from other islands within the Hawaiian Archipelago (Pyle et al. 2016).

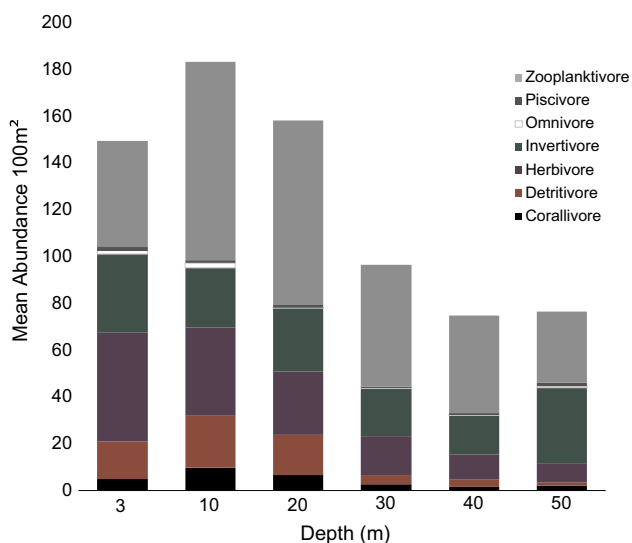
Trophic designation accounted for 33% of the variability in our model. Abundance analyses of trophic groups with depth indicate herbivores, detritivores and corallivores decreased significantly and accounted for 24% of the variation in community structure in this study. Comparisons of trophic assemblages indicate a shift from herbivore-dominated communities in shallow depths to zooplanktivore-dominated communities at mesophotic



**Fig. 4** Distance-based redundancy analysis ordination of reef-fish abundance using Bray–Curtis similarity resemblance matrix. Axes describe percentage of variation in terms of the total fish community structure. Vectors represent strength of variables in model



**Fig. 5** Mean percentage cover of **a** macroalgae, **b** turf algae, **c** coral morphologies, **d** sand/sediment along a depth gradient (in m). Error bars are SEs



**Fig. 6** Mean abundance ( $100\text{ m}^{-2}$ ) of reef-fish trophic groups by depth (m)

depths. Decreasing herbivorous fish abundances in mesophotic depths was first reported at Enewetak in the 1980s (Thresher and Colin 1986), but has received scant attention until recently; it has now been confirmed in the Red Sea, Caribbean and northwestern Hawaiian Islands (Brokovich et al. 2008, 2010b; Garcia-Sais 2010; Bejarano et al. 2014; Fukunaga et al. 2016).

The reduction in herbivorous fishes with depth does not appear to be related to food availability as we noted consistent turf algal cover across depth and significant increases in macroalgal cover at 50 m. In addition, many previous studies have reported significant increases in turf and macroalgae at mesophotic depths. Grazing pressure is reduced in mesophotic depths compared with shallow regions although grazing is still evident (Brokovich et al. 2010b; Kahng et al. 2010). Two main hypotheses explain the reduction in herbivorous fishes with depth: first, mesophotic temperatures may be too low for herbivores to

efficiently metabolize algae (Floeter et al. 2005); and second, deep algal species may be chemically defended and thus unpalatable for herbivorous fishes (Hay 1981, 1984). While herbivore abundances have been positively correlated with temperature across large latitudinal gradients (Floeter et al. 2005), the only mesophotic study of herbivory suggests that temperatures between shallow and upper mesophotic reefs are not substantially different (Brokovich et al. 2010b). Chemical defenses of mesophotic algal species have not been studied to date, but we have observed algal grazing by parrotfish and surgeonfish species at mesophotic depths, indicating that at least some of the algal community is edible. Decreases in herbivore abundance despite adequate food supply may be a result of differences in algal quality, not quantity. Studies in shallow systems have found that herbivore patchiness is strongly correlated with differences in algal productivity (Russ 2003; Tootell and Steele 2016). Although currently untested, it is plausible that productivity of turf and macroalgal resources decreases with depth given the low light availability at mesophotic depths, which could then account for observed declines in herbivorous fishes with depth.

While all trophic groups declined in abundance between shallow and mesophotic depths, herbivorous and detritivorous fishes declined at nearly twice the rate of zooplanktivorous fish abundances (herbivores 68%, detritivores 84%, zooplanktivores 40%). The dominance of zooplanktivorous fishes at mesophotic depths is supported at many locations worldwide (Thresher and Colin 1986; Brokovich et al. 2008; Garcia-Sais 2010; Bejarano et al. 2014) and has been hypothesized to result from higher zooplankton abundances and more nutrient-rich water at depth (Kahng et al. 2010). The only study to evaluate zooplankton communities at mesophotic depths reported negligible abundances but dramatic differences among locations, indicating that more study is needed (Rodriguez-Jerez 2004). Water clarity often increases in mesophotic depths (R. Pyle pers. comm.), but it is unclear whether zooplankton abundance is correlated with water clarity or phytoplankton abundance in tropical insular waters. We have observed increased water clarity at mesophotic depths in West Hawaii, likely a result from reduced turbidity and lower phytoplankton concentrations common in shallow waters. It is more likely, though, that zooplanktivorous fish dominance results from reductions in herbivorous fish abundance at mesophotic depths rather than increased habitat suitability or food availability in upper mesophotic depths. More investigation is needed to confirm or refute possible mechanisms underlying these observed trophic shifts.

The decline in coral cover and gradual increase in sand/sediment cover with depth indicate that habitat is more

patchily distributed at mesophotic sites in West Hawaii. Nine of the 11 sites surveyed in this study had reefs that ended in large sand beds at approximately 40–70 m depth. It is thus likely that reductions in overall abundance and species richness are linked with reduced habitat availability. Live coral cover is a significant predictor of reef-fish abundance and diversity in shallow reef systems (Williams 1991) but is not typically a strong predictor of fish assemblages within mesophotic systems, as coral habitat is greatly reduced at these depths. We found significant declines in cover of lobate and branching/plating coral morphologies at mesophotic depths, likely resulting in less suitable live coral habitat for many species of fishes. Brokovich et al. (2008) found declines in branching corals and live cover were the most pronounced habitat variables correlating with fish community structure in the Red Sea, while benthic habitat metrics accounted for little variation in fish community structure in Western Australia (Fitzpatrick et al. 2012). Our studies generally support those in the Red Sea, with reduced coral cover and increased sand cover explaining the most variability (17% combined) in fish communities with depth among the 11 benthic and structural variables tested. Overall colony size appeared smaller in mesophotic depths than in shallow waters—in shallow waters lobate colonies were often meters long while at mesophotic depths most colonies were less than 20 cm (pers. obs.). Reductions in size of colonies also likely influenced the size and species composition of fishes at mesophotic depths. While not ubiquitous across all mesophotic depths, many mesophotic reefs experience reduced coral cover and increased algal cover; thus, dissociation between coral cover and fish community structure is not unexpected. It is likely that the depth variable represents indirect effects on community structure through reductions in light availability which subsequently affect benthic cover and primary productivity, as well as predation success and behavior modifications among fishes in mesophotic systems (Brokovich et al. 2010a).

While not tested directly, habitat complexity may play a stronger role overall than benthic cover or general structure of the benthos. Variation within each depth is largely tied to differences between coral rich areas (% live coral cover) and highly complex coral matrices (*Porites compressa* beds) versus basalt regions and sand/sediment areas that lack complex interstitial spaces. While coral cover decreases significantly with depth and live coral dominance is rare in West Hawaii below depths of 20 m, it is likely that remnant reef structures and boulder habitats compensate for the complexity typically provided by branching corals in shallow regions. Numerous studies have shown that complexity, via the abundance and size of shelter holes, is important in characterizing fish assemblages at shallow depths (Hixon and Beets 1989; Friedlander and



Parrish 1998; Almany 2004). The prevalence of shallow reef-fish species to depths of 50 m is influenced by similarities in structural components but it is likely that mesophotic reefs lack the degree of fine-scale complexity found in shallow reefs resulting from complex matrices provided by branching corals, which may account for observed reductions in overall abundance and species richness at mesophotic depths in West Hawaii. Many MCE regions describe high coral cover to depths of 60 m or more, but these corals are largely comprised of mounding and plating morphologies, which provide far less complex shelter space than branching morphologies (Brokovich et al. 2008; Hinderstein et al. 2010; Kahng et al. 2010). The change in coral morphologies with depth results in changes in overall complexity and thus likely contributes to the variability in reef-fish composition between shallow and upper mesophotic systems.

Accumulating baseline information on mesophotic coral reefs is imperative to enhance both general knowledge and predictive capabilities regarding coral-reef fishes. While coral cover is one of the main drivers of reef-fish community composition in shallow waters, additional forces beyond live coral habitat appear to gain importance with depth; thus, more detailed studies of habitat complexity and niche availability would be very interesting. Trophic assemblages at mesophotic depths differ from those at shallow depths, and correlations between herbivorous fishes and algal abundance observed in shallow waters are not supported in mesophotic habitats (Choat 1991; Hughes et al. 2007; Brokovich et al. 2010b; Bejarano et al. 2014). It is therefore important to consider differential drivers of community structure with depth in future modeling efforts for population and community structure of reef fishes.

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## References

- Almany GR (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK
- Arreola-Robles JL, Elorduy-Garay JF (2002) Reef fish diversity in the region of La Paz, Baja California Sur, Mexico. *Bull Mar Sci* 70:1–18
- Bak RPM, Nieuwland G, Meesters EH (2005) Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs* 24:475–479
- Baker EK, Puglise KA, Harris PT (eds) (2016) Mesophotic coral ecosystems—A lifeboat for coral reefs?. The United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal, p 98
- Beijbom O, Edmunds PJ, Roelfsema C, Smith J, Kline DI, Neal BP, Dunlap MJ, Moriarty V, Fan TY, Tan CJ, Chan S, Treibitz T, Gamst A, Mitchell BG, Kriegman D (2015) Towards automated annotation of benthic survey images: variability of human experts and operational modes of automation. *PLoS One* 10:e0130312
- Bejarano I, Appeldoorn RS, Nemeth M (2014) Fishes associated with mesophotic coral ecosystems in La Parguera, Puerto Rico. *Coral Reefs* 33:313–328
- Boland RC, Parrish FA (2005) Description of fish assemblages in the black coral beds off Lahaina, Maui, Hawai'i. *Pacific Science* 59:411–420
- Bridge TCL, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. *Nat Clim Chang* 3:528–530
- Brokovich E, Baranes A, Goren M (2006) Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. *Ecol Indic* 6:494–507
- Brokovich E, Einbinder S, Kark S, Shashar N, Kiflawi M (2007) A deep nursery for juveniles of the zebra angelfish *Genicanthus caudovittatus*. *Environ Biol Fishes* 80:1–6
- 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, Ben-Ari T, Kark S, Kiflawi M, Dishon G, Iluz D, Shashar N (2010a) Functional changes of the visual system of the damselfish *Dascyllus marginatus* along its bathymetric range. *Physiol Behav* 101:413–421
- Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, Genin A, Kark S, Kiflawi M (2010b) 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
- Bryan DR, Kilfoyle K, Gilmore RG, Spieler RE (2013) Characterization of the mesophotic reef fish community in south Florida, USA. *J Appl Ichthyol* 29:108–117
- Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, CA, pp 120–155
- Colin PL (1974) Observation and collection of deep reef fishes off the coasts of Jamaica and Honduras. *Mar Biol* 24:29–38
- Donaldson TJ (2002) Habitat association and depth distribution of two sympatric groupers of the genus *Cephalopholis* (Serranidae: epinephelinae). *Ichthyological Research* 49:191–193
- Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Mar Biol* 161:599–607
- Feitoza B, Rosa R, Rocha L (2005) Ecology and zoogeography of deep-reef fishes in northeastern Brazil. *Bull Mar Sci* 76:725–742
- Fenner D (2005) *Corals of Hawaii: a field guide to the hard, black, and soft corals of Hawaii and the northwest Hawaiian Islands, including Midway*. Mutual Publishing, LLC, Honolulu, HI, p 144
- Fitzpatrick BM, Harvey ES, Heyward AJ, Twigg EJ, Colquhoun J (2012) Habitat specialization in tropical continental shelf demersal fish assemblages. *PLoS One* 7:e39634

- Floeter S, Behrens M, Ferreira C, Paddock M, Horn M (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar Biol* 147:1435–1447
- Fricke HW, Schumacher H (1983) The depth limit of Red Sea stony corals: an ecophysiological problem (a deep diving survey by submersible). *Mar Biol* 4:163–194
- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Bio Ecol* 224:1–30
- Fukunaga A, Kosaki RK, Wagner D, Kane C (2016) Structure of mesophotic reef fish assemblages in the Northwestern Hawaiian Islands. *PLoS One* 11:e0157861
- 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
- Goreau TF, Goreau NI (1973) The ecology of Jamaican coral reefs. II. Geomorphology, zonation, and sedimentary phases. *Bull Mar Sci* 23:399–464
- Gratwicke B, Speight M (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol* 66:650–667
- Hay M (1981) Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Am Nat* 118:520–540
- Hay M (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65:446–454
- Hill J, Wilkinson C (2004) Methods for ecological monitoring of coral reefs. Australian Institute of Marine Science, Townsville, Australia, p 117
- Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Theme section on mesophotic coral ecosystems: characterization, ecology, and management. *Coral Reefs* 29:247–251
- Hixon M (2011) 60 years of coral reef fish ecology: past, present, future. *Bull Mar Sci* 87:727–765
- Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull Mar Sci* 44:666–680
- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol Monogr* 63:77–101
- Hobson E (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin* 72:915–1031
- Hoey AS, Brandl SJ, Bellwood DR (2013) Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs* 32:973–984
- Hughes TP, Bellwood DR, Folke CS, McCook LJ, Pandolfi JM (2007) No-take areas, herbivory and coral reef resilience. *Trends Ecol Evol* 22:1–3
- Huisman JM, Abbott IA, Smith CM (2007) Hawaiian reef plants. University of Hawaii Sea Grant College Program, Honolulu, HI, p 264
- Kahng SE, Maragos JE (2006) The deepest, zooxanthellate scleractinian corals in the world? *Coral Reefs* 25:254
- Kahng SE, 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
- Kahng SE, Copus JM, Wagner D (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Curr Opin Environ Sustain* 7:72–81
- Kane C, Kosaki R, Wagner D (2014) High levels of mesophotic reef fish endemism in the Northwestern Hawaiian Islands. *Bull Mar Sci* 90:1–12
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24
- Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. *J Exp Mar Bio Ecol* 375:1–8
- Liddell WD, Ohlhorst SL (1988) Substrata community patterns, 1–120 m, North Jamaica. *Palaios* 3:413–423
- Liddell WD, Avery WE, Ohlhorst SL (1997) Patterns of benthic community structure, 10–250 m, the Bahamas. *Proc 8th Int Coral Reef Symp* 1:437–442
- Lindfield SJ, Harvey ES, Halford AR, McIlwain JL (2016) Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. *Coral Reefs* 35:125–137
- Maragos JE, Jokiel P (1986) Reef corals of Johnston Atoll—one of the World’s most isolated reefs. *Coral Reefs* 4:141–150
- McGehee M (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105:243–255
- Menza C, Kendall M, Rogers C, Miller J (2007) A deep reef in deep trouble. *Cont Shelf Res* 27:2224–2230
- Munday PL (2000) Interactions between habitat use and patterns of abundance in coral-dwelling fishes. *Environ Biol Fishes* 58:355–369
- Parrish FA, Boland RC (2004) Habitat and reef-fish assemblages of banks in the Northwestern Hawaiian Islands. *Mar Biol* 144:1065–1073
- Pyle RL (2000) Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-contained diving technology. *Marine Technology Society Journal* 34:82–91
- Pyle RL, Boland R, Bolick H, Bowen BW, Bradley CJ, Kane C, Kosaki RK, Langston R, Longenecker K, Montgomery A, Parrish FA, Popp BN, Rooney J, Smith CM, Wagner D, Spalding HL (2016) A comprehensive investigation of mesophotic coral ecosystems in the Hawaiian Archipelago. *PeerJ* 4:e2475
- Randall J (2007) Reef and shore fishes of the Hawaiian Islands. University of Hawaii Sea Grant College Program, Honolulu, HI
- Reaka M, Rodgers P, Kudla A (2008) Patterns of biodiversity and endemism on Indo-West Pacific coral reefs. *Proc Natl Acad Sci U S A* 105:11474–11481
- Rodriguez-Jerez Z (2004) Zooplankton communities of Isla Desecheo and adjacent waters of Mona Passage. MS Thesis, University of Puerto Rico, San Juan. 85 pp
- Rosa MR, Alves AC, Medeiros DV, Coni EOC, Ferreira CM, Ferreira BP, Rosa R, Souza R, Amado-Filho GH, de Moura RL, Thompson FL, Sumida PYG, Francini-Filho RB (2016) Mesophotic reef fish assemblages of the remote St. Peter and St. Paul’s Archipelago, Mid-Atlantic Ridge, Brazil. *Coral Reefs* 35:113–123
- Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* 22:63–67
- Sale P (1991) Ecology of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, pp 1–11
- Sandin SA, Smith JE, Demartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS One* 3:e1548
- Schultz AL, Malcolm HA, Bucher DJ, Linklater M, Smith SD (2014) Depth and medium-scale spatial processes influence fish assemblage structure of unconsolidated habitats in a subtropical marine park. *PLoS One* 9:e96798
- 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
- Thresher R, Colin P (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

- Tootell JS, Steele MA (2016) Distribution, behavior, and condition of herbivorous fishes on coral reefs track algal resources. *Oecologia* 181:13–24
- van Oppen MJH, Bongaerts P, Underwood JN, Peplow LM, Cooper TF (2011) The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. *Mol Ecol* 20:1647–1660
- Williams D (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale P (ed) *Ecology of coral reef fishes*. Academic Press, Cambridge, MA, pp 437–474
- Wilson SK, Depczynski M, Fisher R, Holmes TH, O’Leary RA, Tinkler P (2010) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. *PLoS One* 6:e15185