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# Changes in mesophotic reef fish assemblages along depth and geographical gradients in the Northwestern Hawaiian Islands

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**Abstract** Mesophotic coral ecosystems (MCEs) extend from 30 to 150 m in depth and support diverse communities of marine organisms. We investigated changes in the structure of mesophotic reef fish assemblages (27–100 m) in the Northwestern Hawaiian Islands (NWHI) along depth and geographical gradients using open- and closed-circuit trimix diving. There were clear changes in the assemblage structure from the southeastern to the northwestern end of the NWHI and from shallow to deep waters. Interactive effects of depth and location were also detected. MCEs in the NWHI can be treated as three regions: southeastern and mid regions primarily separated by the presence and absence, respectively, of the introduced species *Lutjanus kasmira*, and a northwestern region where fish assemblages are largely composed of endemic species. These spatial patterns may be explained, at least in part, by differences in temperature among the regions.

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## Introduction

Mesophotic coral ecosystems (MCEs) extend from 30 to 150 m in depth and support diverse communities of marine organisms (Kahng et al. 2010). Benthic communities of MCEs are mainly comprised of corals, macroalgae, sponges and bryozoans (Kahng and Kelley 2007). The dominant taxa change from photosynthetic organisms in shallower depths to obligate heterotrophs at greater depths (Kahng et al. 2014), and the amount of live benthic cover generally decreases with depth (Kahng and Kelley 2007; Rooney et al. 2010) although such a pattern can be site-specific and likely depends on depth ranges and intervals of analysis (e.g., Brokovich et al. 2008; Eyal et al. 2016). Fish assemblages on mesophotic reefs are characterized by relatively high abundances of planktivores and relatively low abundances of herbivores (Brokovich et al. 2010; Fukunaga et al. 2016; Rosa et al. 2016). Species richness of fish generally correlates with live coral cover and therefore decreases with depth (reviewed by Kahng et al. 2014).

Mesophotic habitat has received increased attention as a potential refugium for biodiversity threatened in shallow waters by global and local disturbances (Baker et al. 2016; Lindfield et al. 2016). Physical characteristics of MCEs, in comparison to their shallower counterparts, include reduced photosynthetically active radiation, decreases in seawater temperature and greater protection from strong wave action and thermal stress (Lesser et al. 2009; Pyle et al. 2016). These physical factors affect benthic

community composition and habitat complexity (Magalhães et al. 2015; Heyns et al. 2016), and in turn, they all affect the structure of reef fish assemblages (McGehee 1994; Friedlander and Parrish 1998). Water temperature has been suggested as a particularly important environmental factor that could restrict distributions of fish and other ectothermic organisms through effects on physiological processes (Pörtner 2002; Behrens and Lafferty 2007; Kahng et al. 2012).

The Northwestern Hawaiian Islands (NWHI) are ten major islands or atolls that span approximately 2000 km northwest of the inhabited main Hawaiian Islands (Fig. 1). The NWHI are part of the Papahānaumokuākea Marine National Monument (PMNM), a marine protected area originally established in 2006 encompassing 362,073 km$^2$ of fully protected area and expanded in 2016 to 1,508,870 km$^2$ with specific regulations currently being established. Kure Atoll is the farthest north (28°25.28′N) and the oldest (29.8 million years) of the NWHI, while Nihoa is the farthest south (23°3.73′N) and the youngest (7.2 million years) (reviewed by Rooney et al. 2008). Thus, the longitudinal and latitudinal gradient of the NWHI reflects their differences in geological ages and underwater topography, as well as changes in water temperature due to latitudinal differences, ranging in average sea surface temperature in winter from below 20 °C at the northern end to ~23 °C at the southern end (Grigg et al. 2008; Rooney et al. 2010).

Here, we investigated changes in the structure of mesophotic reef fish assemblages in the NWHI across depth and geographical gradients, using data collected at 27–100 m depth. A recent study showed gradual changes in the structure of fish assemblages in the NWHI along a depth gradient of 1–67 m (Fukunaga et al. 2016). Thus, our primary focus here was to investigate the structure of reef fish assemblages along a geographical gradient. We hypothesized that the assemblage structure would change from the southeastern to northwestern ends of the NWHI, with different fish species being numerically dominant and characterizing assemblages at different islands/atolls due to changes in environmental conditions.

## Materials and methods

Annual summer surveys were performed during seven expeditions to the NWHI aboard the NOAA ship *Hiʻialakai* from 2010 to 2016. Surveyors used open-circuit trimix diving from 2010 to 2012 and closed-circuit rebreathers from 2013 to 2016. Survey sites were haphazardly chosen from potential survey areas with hard-bottom slopes, ledges or other distinguishing features of fish habitats within allowable diving depths (<100 m). At each site, divers identified and counted all conspicuous, diurnally active fishes along a 25 × 2 m belt transect (Kane et al. 2014). There was generally one belt transect survey per site, with
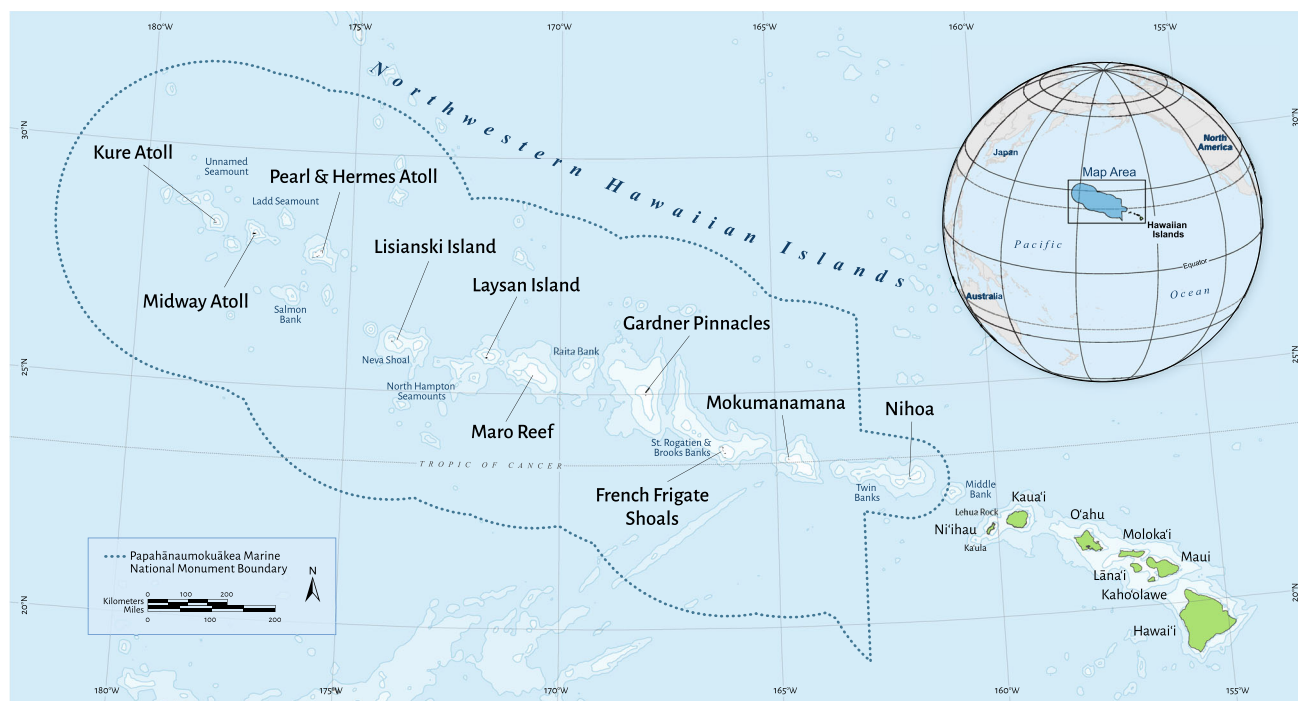


Fig. 1 Map of the Hawaiian Archipelago including the Northwestern Hawaiian Islands

exceptions in earlier years, particularly 2010, in which multiple transect surveys were performed at the same site on the same day, during either one dive or two separate dives (Table 1). In those cases, fish counts were averaged among transects to obtain fish abundance per site. Note that this process averages fish counts per site but not the number of species, thereby potentially increasing the number of species for sites with multiple transect surveys compared to those with a single transect survey. Nevertheless, there was no strong evidence for such an increase, with the number of species per site mostly similar among years; our statistical analysis also accounted for year-to-year variability (see below) if there was an overall increase in the number of species in 2010 resulting from the multiple transects per site. We used GPS coordinates to mark the survey sites, and the same sites were never surveyed on different days. In total, 161 sites were surveyed at nine islands and atolls: Nihoa, French Frigate Shoals (FFS), Gardner Pinnacles, Maro Reef, Laysan Island, Lisianski Island, Pearl and Hermes Atoll (PHA), Midway Atoll and Kure Atoll (Table 1).

Reef fish assemblages were compared using the software package PRIMER 6 with the PERMANOVA + add-on. The structure of fish assemblages was measured on the basis of Bray–Curtis similarity after square root transformation of fish abundance data. Changes in the structure of fish assemblages were examined along depth and geographical gradients using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) with 4999 permutations of residuals under a reduced model. Here, we used a model analogous to a univariate general linear model with mixed effects by including both categorical (factors) and quantitative (covariates) explanatory variables. Terms included as factors were Method (fixed with two levels, open-circuit and rebreather) and Year (random with seven levels, nested

in Method) to account for any effects of survey methods and year-to-year variability. Terms included as covariates were Location, Depth and Location × Depth. As latitudinal and longitudinal coordinates were highly correlated (Pearson's $r = 0.97$), we used principal components analysis of the coordinates and used the first principal component scores as a single location variable.

To investigate further details of the depth and location effects found in the PERMANOVA analysis, canonical analysis of principal coordinates (CAP; Anderson and Robinson 2003; Anderson and Willis 2003) was used to obtain a constrained ordination by finding axes through the multivariate data cloud that had maximum correlations with depth and location. This method allows for analysis of relationships between the structure of fish assemblages and the explanatory variables of interest in the presence of other potentially important variables (e.g., year-to-year variability). To avoid over-parameterization, the appropriate number of principal coordinate axes ($m$) was chosen by minimizing a leave-one-out residual sum of squares. To explore which species were associated with patterns observed in the CAP ordination, we examined Spearman rank correlations of individual fish species with canonical axes by superimposing correlation vectors on the CAP ordination. We chose the top 15 species that had the highest correlations with the depth or location variable and individually confirmed their occurrence and abundance at different islands/atolls or depths.

## Results and discussion

In total, 13,975 individuals from 162 reef fish taxa were identified from 161 mesophotic sites in the NWHI (Electronic supplementary material, ESM, Table S1). There was relatively high temporal variability in the structure of

**Table 1** Number of survey sites at each island/atoll during seven separate cruises to the NWHI

| | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | Total (survey sites) | Total (transects) |
|---|---|---|---|---|---|---|---|---|---|
| Nihoa | 1 (2) | | 2 (2) | 6 (6) | | | | 9 | 10 |
| French Frigate Shoals | 7 (10) | 7 (7) | 2 (2) | 6 (6) | 7 (7) | 4 (4) | 7 (7) | 40 | 43 |
| Gardner Pinnacles | | 6 (6) | 1 (2) | | | | | 7 | 8 |
| Maro Reef | | 3 (3) | 2 (2) | | | 3 (3) | | 8 | 8 |
| Laysan Island | | | | 4 (4) | | 1 (1) | | 5 | 5 |
| Lisianski Island | | 9 (9) | 4 (4) | | 6 (6) | 5 (5) | 3 (3) | 27 | 27 |
| Pearl and Hermes Atoll | 7 (11) | 7 (8) | 8 (9) | | 9 (9) | 4 (4) | 4 (4) | 39 | 45 |
| Midway Atoll | 6 (10) | | 1 (1) | | 3 (3) | 1 (1) | 2 (2) | 13 | 17 |
| Kure Atoll | 1 (3) | | | | | 8 (8) | 4 (4) | 13 | 15 |
| Depth range (m) | 39–68 | 27–40 | 51–68 | 43–68 | 53–88 | 52–92 | 42–100 | | |

The number of belt transect surveys at each island/atoll is shown in parenthesis. Depth ranges of surveys shown at the bottom of the table

mesophotic fish assemblages, but no strong evidence for differences between the two diving methods (Table 2). Location, Depth and Location × Depth interaction each explained a significant proportion of the variation in the structure of fish assemblages (Table 2).

CAP analysis also showed strong correlations between the assemblage structure and the two explanatory variables; the two canonical axes had squared canonical correlations of $\delta_1^2 = 0.89$ and $\delta_2^2 = 0.75$, using $m = 32$ principal coordinate axes that explained 99.86% of the variability in the original assemblage structure data. Constrained CAP ordination showed changes in the assemblage structure along both depth and geographical gradients (Fig. 2).

Fishes that were associated with depth in the CAP analysis decreased in abundance from shallower to deeper mesophotic sites. These included six invertivores (*Thalassoma duperrey*, *Coris venusta*, *Oxycheilinus bimaculatus*, *Parupeneus multifasciatus*, *Pseudocheilinus evanidus* and *Sufflamen bursa*), two herbivores (*Centropyge potteri* and *Ctenochaetus strigosus*) and a planktivore (*Chromis hanui*) (Fig. 2). In particular, *Ctenochaetus strigosus* was only present at depths <45 m, *Coris venusta* at depths <54 m and *T. duperrey*, *O. bimaculatus*, *P. evanidus* and *S. bursa* at depths <70 m. *Pseudocheilinus evanidus*, *S. bursa* and *Parupeneus multifasciatus* were also associated with the geographical gradient; these species were more abundant at the southeastern end than northwestern end of the NWHI and were only present up to PHA with an exception of one individual (*P. multifasciatus*) at 48 m depth at Midway. Therefore, on mesophotic (27–100 m) reefs of the NWHI, changes in fish assemblages along a depth gradient were largely characterized by decreases in abundance of invertivores and herbivores. Decreases in the abundances of herbivores with depth are consistent with previous studies in other locations (Brokovich et al. 2010; Rosa et al. 2016).

Fish species that contributed to differentiating fish assemblages among islands/atolls were *Genicanthus personatus*, *Pseudanthias thompsoni*, *Centropyge interrupta* and *Lutjanus kasmira* (Fig. 2). The two locations at the southeastern end of the NWHI (Nihoa and FFS) were

**Table 2** PERMANOVA based on the Bray–Curtis similarity after square root transformation of fish abundance data

|                    | df | MS     | Pseudo-F | p      |
|--------------------|----|--------|----------|--------|
| Method             | 1  | 7884   | 1.59     | 0.0962 |
| Year (method)      | 5  | 6443   | 2.14     | **0.0002** |
| Location           | 1  | 13,176 | 4.37     | **0.0002** |
| Depth              | 1  | 11,174 | 3.71     | **0.0002** |
| Location × Depth   | 1  | 12,267 | 4.07     | **0.0002** |

Significant *p* values at $\alpha = 0.05$ are in bold

primarily separated from other locations by relatively high abundances of the introduced species *L. kasmira*; this species was only recorded at these two locations with an exception of one individual at Lisianski. The three atolls at the northwestern end of the NWHI (PHA, Midway and Kure) had higher abundances of two Hawaiian endemic planktivores, *G. personatus* and *P. thompsoni*, and a temperate herbivore (*C. interrupta*) than other locations. The endemic invertivore *Bodianus sanguineus* was also abundant at depths >50 m at these three northernmost locations where >75% of all individuals were recorded. Similarly, the endemic planktivore *Chromis struhsakeri* was only recorded at these locations at depths >80 m. Both *B. sanguineus* and *C. struhsakeri* are mesophotic specialists previously reported to have distribution ranges of 32–168 m and 85–302 m in depth, respectively (Chave and Mundy 1994; Randall 2007).

High levels of endemism among mesophotic fish assemblages in the NWHI have previously been reported (Kane et al. 2014); the level of endemism is highest at the northern end of the island chain (Kosaki et al. 2016). In this study, four of the five fish species that separated the three northernmost atolls from the rest of the NWHI in terms of the assemblage structure were endemic to the Hawaiian Islands. Calculating the proportion of endemics based on fish abundance per site also resulted in, on average, over 80% of reef fish at these atolls being endemic to the Hawaiian Islands (ESM Fig. S1). In addition, *Centropyge interrupta*, a temperate species from southern and central Japan, was exclusively found at these atolls with an exception of one individual at Lisianski. In contrast, *L. kasmira*, a tropical species with a wide natural range in the Indo-Pacific, was limited to mesophotic reefs of the two southernmost locations (with an exception of one individual at Lisianski). This species was intentionally introduced to the main Hawaiian Island of Oahu in 1958 and has previously been found in shallow (≤30 m) waters of Midway (Randall et al. 1993) and Kure (Gaither et al. 2010), both over 2000 km from the site of introduction.

Thus, MCEs in the NWHI can be separated into three regions for the purpose of reef fish monitoring and management. The northwestern region includes PHA, Midway and Kure where fish assemblages are largely composed of endemic species and potentially influenced by relatively cool temperatures. The southeastern region (from Nihoa to FFS) and the mid region (from Gardner to Lisianski) are primarily separated by the presence and absence, respectively, of the introduced species *L. kasmira*. It is possible that this species is still in the process of spreading to deeper waters of the mid- and northwestern regions of the NWHI. If this is the case, however, the process seems to be relatively slow given that they were already present in shallow waters of Laysan in 1980 (Oda and Parrish 1981) and of

**Fig. 2** Canonical analysis of principal coordinates constrained ordinations based on Bray–Curtis similarity in assemblage structure showing separation of samples (sites) along depth and geographical gradients. Vector overlays in main figure show depth and location variables. Depth increases from the top right to the bottom left and the location variable increases from top left (northwest) to the bottom right (southeast). Vector overlays in the top right show 15 fish species with the highest Spearman rank correlations ($\rho$) with canonical axes
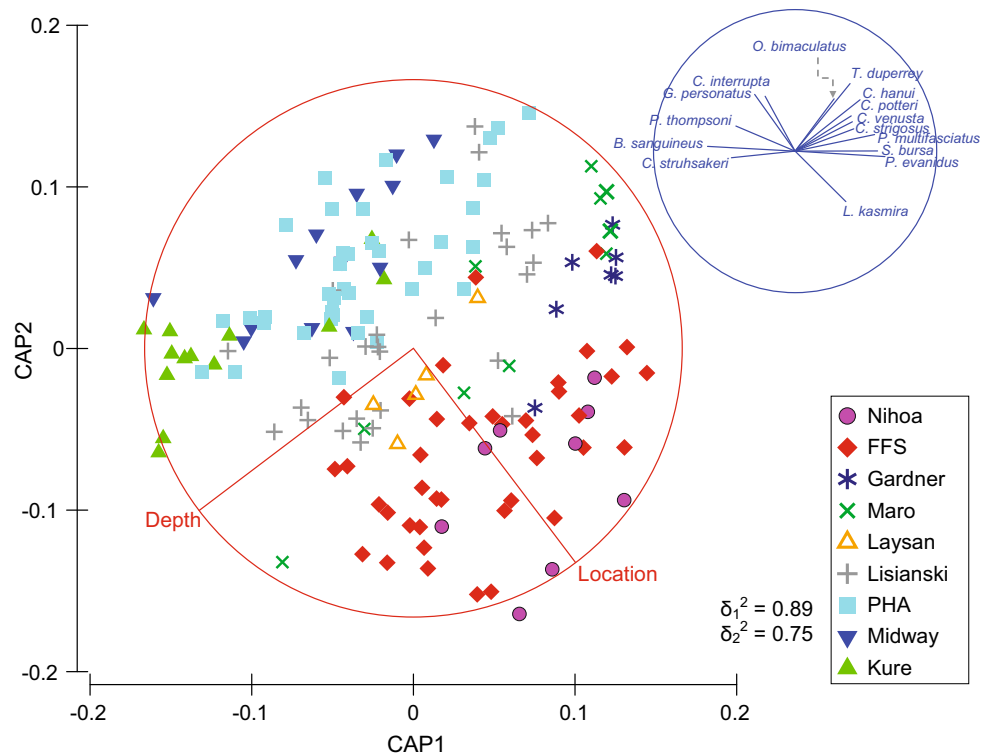
Midway by 1992 (Randall et al. 1993). Note that species identified in the CAP analysis were those that contributed to differentiating fish assemblages among islands/atolls, not necessarily the most numerically dominant species in each region. Nevertheless, post hoc comparisons using similarity percentage analysis (SIMPER; Clarke 1993) among these three regions showed that species typifying each region included those contributing to differentiating them (ESM Table S2).

While the causes of the observed differences in the assemblage structure among the three regions cannot be determined, the grouping of fish assemblages corresponds to latitudinal and, therefore, water temperature gradients in the NWHI. In winter, average sea surface temperature is $\sim 23\ ^\circ$C at Nihoa and FFS (23–24°N), $\sim 22\ ^\circ$C at Maro, Laysan and Lisianski (25–26°N) and reaches below 20 °C at the three northernmost atolls (28°N) (Rooney et al. 2008). Even in late summer to early fall, water temperatures at 100 m depth are below 19 °C at the three northernmost atolls while those at the southern end (Nihoa and FFS) are $\sim 23\ ^\circ$C (Grigg et al. 2008). In addition, the distributions of subtropical Hawaiian endemics *B. sanguineus* and *Chromis struhsakeri* on deeper mesophotic reefs of northwestern (i.e., cooler) locations and the abundance of the widespread species *Pseucocheilinus evanidus*, *S. bursa* and *Parupeneus multifasciatus* on shallower mesophotic reefs of southeastern (i.e., warmer) locations seem to support the idea that water temperature

acts as a barrier for vertical and horizontal distributions of certain tropical reef fishes in the NWHI. Future studies on mesophotic reefs of the NWHI should include hypothesis-driven investigations into the factors that regulate vertical and horizontal distributions of reef fish, such as water temperature, changes in reef complexity and benthic cover associated with depth and geological ages of islands/atolls, trophic interactions and habitat area/species richness relationships. Such studies would provide important information for effective management of the PMNM.

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