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Dominance of endemics in the reef fish assemblages of the Hawaiian Archipelago

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Abstract

Aim: Species ranges provide a valuable foundation for resolving biogeographical regions, evolutionary processes and extinction risks. To inform conservation priorities, here we develop the first bioregionalization based on reef fish abundance of the Hawaiian Archipelago, which spans nearly 10° of latitude across 2,400 km, including 8 high volcanic islands in the populated main Hawaiian Islands (MHI), and 10 low islands (atolls, shoals and islets) in the remote northwestern Hawaiian Islands (NWHI).

Location: The Hawaiian Archipelago.

Taxon: Fishes (276 taxa).

Methods: We compiled 5,316 visual fish surveys at depths of 1–30 m from throughout the Hawaiian Archipelago. Geographical range (km^2) for each species was measured as extent of occurrence (EOO) and area of occurrence (AOO). PERMANOVA and PCO were used to investigate drivers of fish assemblage structure. Distance-based multivariate analyses were used to evaluate the relationship between fish assemblage structure and predictor variables including latitude, reef area, temperature, chlorophyll-*a*, wave energy and human population density.

Results: Distinct fish assemblages exist in the MHI and NWHI, with two additional faunal breaks driven primarily by endemic species abundance. Latitude explained 37% of the variability in fish assemblages, with reef area accounting for an additional 9%. EOO showed a significant correlation with latitude. Endemics comprised 52%–55% of the numerical abundance at the northern end of the archipelago but only 17% on Hawai'i Island in the extreme south. Maximum size and activity regime (day vs. night) explained the most variation in the abundance of endemics.

Main conclusions: The Hawaiian fish assemblages are strongly influenced by endemic species, affirming the archipelago as a biodiversity hotspot of high conservation value. The higher abundance of endemics in the NWHI may represent preadaptation to oceanic (oligotrophic) conditions. Resolution of distinct bioregions across the archipelago provides a better understanding of reef fish macroecology, with implications for management at the archipelago scale.

KEYWORDS
biodiversity, endemism, fish assemblage structure, Hawaiian Archipelago, latitudinal gradient, life-history attributes, marine conservation

1 | INTRODUCTION

Delineating species ranges is essential for understanding the biogeography and ecology of faunal assemblages, as well as the evolutionary forces shaping biodiversity patterns (Briggs & Bowen, 2012; Floeter et al., 2008; Ricklefs & Renner, 2012). This delineation also provides a framework for identifying priority areas for conservation (Rondinini, Rodrigues, & Boitani, 2011). Reef fishes are an excellent group to quantitatively assess biogeographical boundaries due to their conspicuousness, diversity, advanced taxonomy and well-documented distributions (Kulbicki et al., 2013).

Determining concordant geographical ranges within a species assemblage can define biogeographical regions and launch theories about demographic and evolutionary processes (Schurr et al., 2012). Geographical range size is a central ecological and evolutionary characteristic, and a strong predictor of extinction risk (Gaston, 2003). Greater abundance as a function of increasing geographical range size is a widely reported pattern (Gaston, Blackburn, & Lawton, 1997) and the basis for one of the fundamental laws in macroecology (Lawton, 1999).

Endemism is a key feature of biotic communities that is relevant to both evolution and conservation. Endemic species contribute to the biodiversity of their respective geographical regions, and endemism hotspots are vital to our understanding of speciation and the maintenance of biodiversity (Brooks et al., 2006; Moritz, 2002). Isolated endemic faunas also contribute to our understanding of self-recruitment to local populations (Hixon & Webster, 2002; Mora & Sale, 2002). The restricted geographical ranges inherent to endemic species make them particularly vulnerable to habitat loss (Hawkins, Roberts, & Clark, 2000; Hobbs, Jones, & Munday, 2011). As coral reef health declines globally, understanding the distribution and richness of key contributors to biodiversity, including endemism, has taken on a new urgency (Allen, 2008; Fautin et al., 2010; Hughes et al., 2017).

Marine centres of endemism predominate in locations isolated by geography or oceanography (Roberts et al., 2002; Thornhill, Mahon, Norenburg, & Halanych, 2008). Unlike terrestrial ecosystems, these centres of marine endemism are often peripheral to centres of biodiversity (Bellwood, Renema, & Rosen, 2012; Bowen et al., 2016). Oceanic island endemics may comprise a small fraction of species diversity, but they can be locally abundant, often exceeding the densities of widespread congeners (DeMartini & Friedlander, 2004). Hence, endemic reef fishes at oceanic islands have attributes that promote high local abundance (Hobbs et al., 2011; Jones, Caley, & Munday, 2002; Randall, 1973). This high abundance may buffer them from stochastic processes, such as recruitment failure and climatological variability (Hobbs et al., 2011); However, most of the recorded extinctions in the marine environment have been species with small range sizes (Dulvy, Sadovy, & Reynolds, 2003).

Endemic species are often representative of the regional species pool (Ruttenberg & Lester, 2015), and share many biological attributes with widespread species, including trophic group, body size, larval duration and reproductive type (Robertson, 2001). Yet, island endemics may have subtle specializations for insular life, since some are found on multiple oceanic islands that are separated by greater distances than the mainland, implying that differences between insular and continental environments might be involved in the persistence of island endemics (Mora & Robertson, 2005; Rocha, Robertson, Roman, & Bowen, 2005).

The Hawaiian Archipelago is one of the most isolated on earth, with the North American continent lying some 4,100 km to the east, and the nearest emergent land (Johnston Atoll) lying ~800 km away. This archipelago comprises two regions defined by geography and geology: 8 high volcanic islands in the populated main Hawaiian Islands (MHI), and 10 largely uninhabited low islands (atolls, shoals and islets) in the remote northwestern Hawaiian Islands (NWHI). The Hawaiian ichthyofauna includes ~1,473 species (Mundy, 2006), with ~622 shorefish species (Randall, 2007). Hawaiʻi's high proportion of endemic shorefishes (25%) is rivalled by only Easter Island with 22% and the Marquesas Islands with 14% (Delrieu-Trottin et al., 2015). Previous work has shown that Hawaiian endemics accounted for 21% of the individuals observed in visual censuses of the NWHI, increasing in numerical abundance towards the northern end of the archipelago (DeMartini & Friedlander, 2004; Kane, Kosaki, & Wagner, 2014).

Our study used underwater-visual survey data to develop a biogeographical framework to examine factors that influenced reef fish assemblage structure across the entire Hawaiian Archipelago. We combined observational data with life-history information and known geographical distributions to examine spatial patterns of abundance along latitudinal and oceanographic gradients. This work serves to identify faunal breaks and spatial patterns of fish assemblage structure that can inform regional management strategies in Hawaiʻi and contribute to our understanding of reef fish macroecology. In addition to resolving ecoregions defined by differences in community structure, we address the long-standing question about why endemic reef fishes have higher abundance in the atolls and islets of the NWHI, relative to the MHI.

2 | MATERIALS AND METHODS

2.1 | Study area

This study incorporated data from the entire Hawaiian Archipelago spanning nearly 10° latitude and over 2,400 km (Figure 1). The high islands range in age from active lava flows on Hawaiʻi Island to Niʻihau, which formed 5.6 million years ago (Fletcher et al., 2008; Juvik & Juvik, 1998). The NWHI represent the older portion of the Hawaiian Archipelago, beginning at Nihoa (7 mya) and extending to Midway and Kure atolls (28 mya) (Grigg, 1997; Rooney et al., 2008). For most of the last 100,000 years, sea level has been lower than at present day (Miller, Mountain, Wright, & Browning, 2011). As recently as 20,000 years ago, sea level was 120 m lower than present levels, and this usually (but not always) reduces the shallow and littoral habitat available for reef organisms (Ávila et al., 2019).

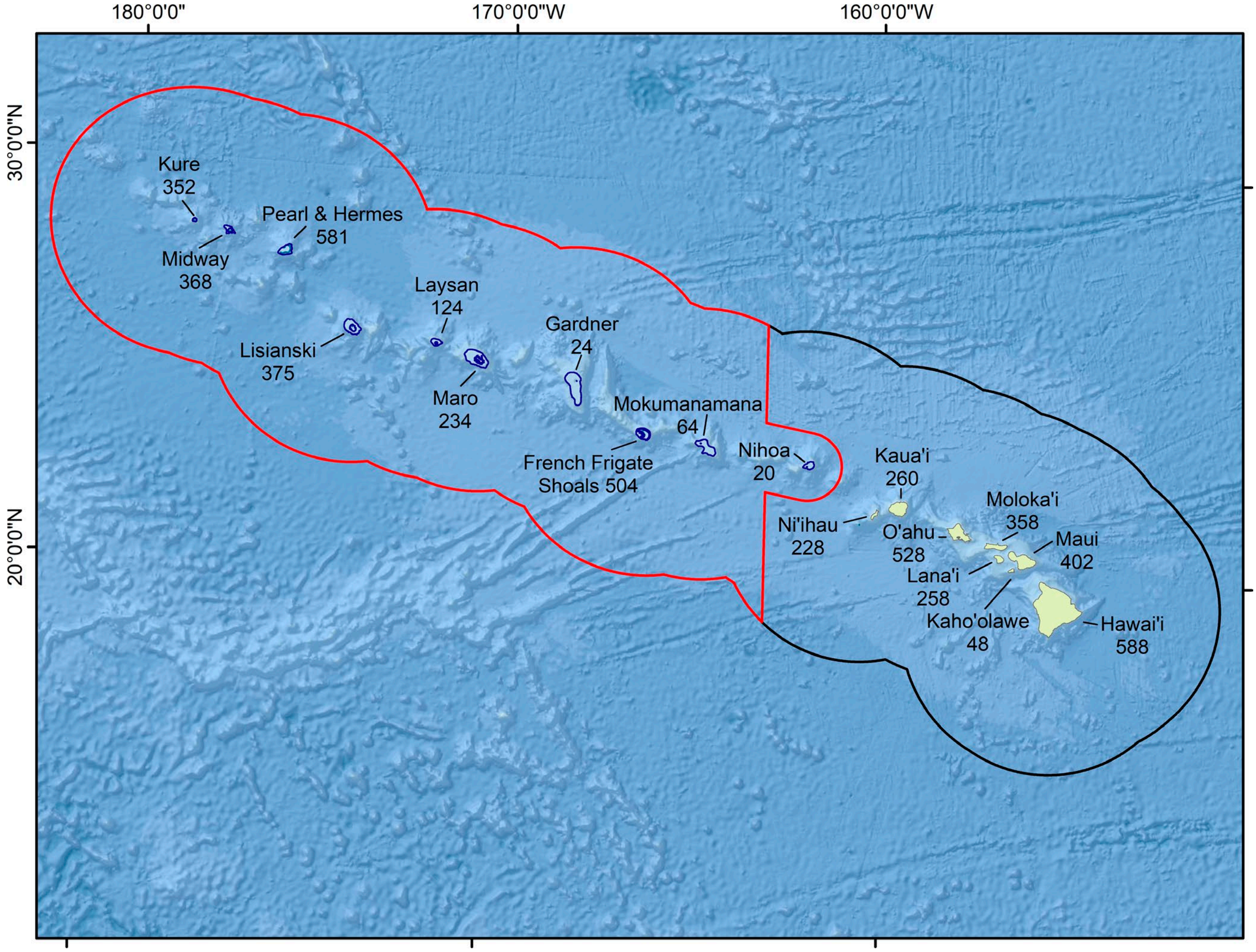

FIGURE 1 Sampling location and number of surveys across the Hawaiian Archipelago. Papahānaumokuākea Marine National Monument (PMNM) boundary is indicated with red line. NWHI 100 m bathymetric contour lines in purple [Colour figure can be viewed at wileyonlinelibrary.com]

The amount of potential coral reef habitat in <18 m (10 fathoms) is comparable between the MHI (1,231 km^2) and NWHI (1,595 km^2) (Rohmann, Hayes, Newhall, Monaco, & Grigg, 2005). Long-term mean sea surface temperature (SST) is 23.1°C at Kure Atoll in the extreme north and 25.3°C at Hawaii Island in the extreme south, with the range nearly twice higher in the NWHI (5.40°C ± 1.51) compared to the MHI (2.72°C ± 0.25) (Gove et al., 2013).

2.2 | Fish sampling methods

Fish surveys were conducted throughout the Hawaiian Archipelago from 2007 to 2016 by the US National Oceanic and Atmospheric Administration's Ecosystem Sciences Division, using a stratified random sampling design (Heenan et al., 2017). A total of 5,316 surveys were conducted at 2,108 locations, across a depth range of 1–30 m. Only forereef locations were used to control for differences in habitat types. Each survey consisted of two divers, collecting data at adjacent survey areas using a modification of the paired stationary point count (SPC) method (Heenan et al., 2017). For the SPC, the divers conducted simultaneous counts in estimated 15 m diameter cylinders extending from the substrate to the limits of vertical visibility. Each SPC consisted of two components: a 5-min species enumeration period in which divers recorded all species present or moving through their cylinder, followed by a tallying portion, in which divers systematically recorded the number and size (total length to nearest cm) of each taxon on their list. The tallying portion was conducted as a series of rapid visual sweeps, with one species grouping counted per sweep.

2.3 | Geographical range index

We used a geographical range index based on species' range sizes (Kulbicki et al., 2013; Parravicini et al., 2013). Geographical range estimates were based on the extent of occurrence (EOO), drawn from polygons encompassing locations where the species are known to occur based on 169 checklists (Kulbicki et al., 2013). When discontinuities were detected, the initial convex hull was divided into multiple polygons to avoid merging disjointed distributions. Species composition was extracted for each 5° × 5° grid cell, corresponding to ~550 × 550 km at the equator. We calculated the area occupied by each polygon and produced a distribution of EOOs in 10 quantiles. Distributions in the smallest quantile represents endemic species limited to the Hawaiian Archipelago (and in some cases adjacent Johnston Atoll).

EOO is defined as the outermost geographical limits to the occurrence of a species (Gaston & Fuller, 2009). EOO is typically used to determine species distribution limits, geographical range dynamics and likelihood of extinction. Another measure of geographical range is the area of occurrence (AOO), the subset of EOO wherein the species actually occurs. There is a debate in the literature about which method is most appropriate (Gaston & Fuller, 2009) so we examined both measures.

2.4 | Predictor variables

We examined environmental and anthropogenic variables known to influence reef fish assemblages in Hawaiʻi (Friedlander, Brown, Jokiel, Smith, & Rodgers, 2003; Friedlander et al., 2018; Williams et al., 2015). Sea-surface temperature (SST, °C), chlorophyll-*a* (CHL, mg/m^3) and derived wave energy (WV, kW/m) were taken from satellite observations and model outputs to develop time series datasets, long-term means, range limits, and the magnitude and occurrence of anomalous climatological events (Gove et al., 2013). The amount of potential coral reef habitat <20 m depth was taken from Rohmann et al. (2005). Anthropogenic influence was indexed as the human population for each island from 2010 US census data (http://www.census.gov/2010census/) divided by the total (potential) coral reef habitat (Williams et al., 2015).

2.5 | Statistical analysis

Pelagic and coastal pelagic species were excluded from all analyses as the focus was on reef and reef-associated assemblage structure. Two coastal pelagic species, *Atherinomorus insularum* and *Encrasicholina purpurea*, are endemic but accounted for <0.5% combined of total numerical abundance in the study. An index of relative dominance (IRD) for each species was created by multiplying the per cent frequency of occurrence on all transects by the relative per cent numerical abundance (Greenfield & Johnson, 1990).

Drivers of fish assemblage structure were investigated using PERMANOVA. A Bray–Curtis similarity matrix was created from numerical density of fish species. Locations (MHI and NWHI) was treated as a fixed factor in the PERMANOVA. Fish numerical abundances were $\ln(x + 1)$ transformed. Principal Coordinate Analysis (PCO) was used to display fish assemblage structure between locations in ordination space. The primary taxa vectors driving the ordination (Pearson product-moment correlations ≥ 0.8) were overlaid on the PCO plots to visualize the major taxa that explained spatial distribution patterns. All PERMANOVAs and PCOs were conducted using Primer v6 (https://primer-demo.software.informer.com/6.1/).

We used a distance-based multivariate analysis for a linear model (DISTLM, McArdle & Anderson, 2001) to measure the relationship between fish assemblage structure and predictor variables (latitude, reef area, CHL, WV, SST, human population density/reef area). Predictor variables were centred and standardized, and a Euclidian Distance Matrix was calculated prior to analyses. A stepwise selection procedure was employed using the Akaike Information Criterion (AIC) for best model solution. Latitude and longitude were highly correlated ($\rho = 0.993$, $p < .001$) so longitude was excluded from statistical analyses.

Relationships between EOO and AOO with latitude were examined with linear models using the lm function in R. We used a generalized additive model (GAM) to examine the relationship between latitude and density of endemics (No. m^{-2}) by island using the gam function in the mgcv package in R (Hastie, 1992). The GAM model was fitted with a Gaussian distribution using an identity link function. To examine the relationships between latitude and relative abundance of species from four taxonomic families (Acanthuridae, Scaridae, Labridae, and Pomacentridae) that contain endemic species, we constructed linear models fitted with binomial distributions using the glm function in R.

K-means cluster analysis was used to group islands based on the average numerical density of endemic and non-endemic species. The optimal number of clusters was determined based on the largest Cubic Clustering Criterion (CCC) statistic.

Boosted regression trees (BRT) was used to examine the relationship between average numerical density of endemic species by island and species life-history attributes, including trophic group (herbivore, planktivore, invertivore and piscivore), mobility (resident, S1 = 10 s m^2 daily movement, S2 = 100 s m^2 daily movement), maximum size, activity (day, night), schooling (solitary, small groups [3–20 individuals], large groups [>20 individuals]), and water column position (bottom, above reef). Mobility followed Friedlander and Parrish (1998). Schooling and water column position were adapted from Mouillot et al. (2014). Numerical density of endemic species by island was 4th root transformed prior to analysis. Learning rate was set at 0.1. Prior to model fitting, survey data were randomly divided into model training (70%) and test (30%) subsets. The test dataset was used only to evaluate predictive performance.

3 | RESULTS

3.1 | Composition of fish fauna

We detected 276 reef-associated taxa from 47 families on SPC surveys. Sixty of these species from 22 families are endemic to Hawaiʻi (21.7%). The most speciose families are Labridae (*N* = 36, 44.4% endemic), Acanthuridae (*N* = 27, 7.4% endemic), Chaetodontidae (*N* = 21, 14.3% endemic), Holocentridae (*N* = 18, 5.6% endemic), Pomacentridae (N = 15, 46.7% endemic) and Muraenidae (N = 15, 6.7% endemic).

Non-endemics accounted for 61.9% of total numerical abundance whereas endemics comprised 38.1%. However, endemics were not distributed evenly across the archipelago. The highest percentage of endemics were at Kure (65.9%), Lisianski (62.7%), Pearl & Hermes (62.4%) and Midway (62.1%), whereas the lowest percentage of endemics were at Nihoa (8.9%), Kaua‘i (22.9%), Kaho‘olawe (13.5%) and Hawai‘i (19.7%).

Based on IRD, endemics accounted for 5 of the top 10 species, comprising 42.9% of the numerical abundance in this group (Table 1). The convict tang is an endemic subspecies (*Acanthurus triostegus sandvicensis*) and accounted for an additional 2.5% of total numerical abundance. The endemic saddle wrasse, *Thalassoma duperrey*, was the second most abundant species overall but was the most frequently encountered, occurring at 94.4% of survey sites.

3.2 | Spatial patterns of the Hawaiian fish fauna

Fish assemblage structure based on numerical abundance (number of individuals × m^{-2}) was significantly different between the MHI and NWHI (pseudo-$F_{1,17}$ = 6.45, p = 0.001). There was clear separation in ordination space between the MHI and NWHI based on PCO (Figure 2). The 1st PCO axis explained 42.1% of total variation in assemblage structure; MHI locations plotted towards the lower end of this axis. The more densely populated MHI sites clustered together, while the less populated islands of Ni‘ihau, Kaho‘olawe, and Hawai‘i were located towards the higher end of PCO_2, which explained an additional 19.6% of total variation. Most locations in the NWHI tended towards the higher end of PCO1. Five endemic species *Thalassoma ballieui*, *Acanthurus nigroris*, *Thalassoma duperrey*, *Stegastes marginatus* and *Chromis ovalis* were highly correlated with locations in the NWHI along PCO1. None of the species that showed high correlations with locations in the MHI were endemic.

Over 46% of the variation in the fish assemblage was attributed to two measured variables (DISTLM; Table 2). Latitude accounted for 37.2% of the explained variation and reef area accounted for 9.2%. Axis 1 explained 81.4% of variation, with the remaining 18.6% explained by Axis 2.

3.3 | Distribution of endemics

There was a significant negative linear relationship between latitude and mean range size measured as extent of occurrence (EOO) (Figure S1, $F_{1,16}$ = 83.8, R^2 = 0.840, p < 0.001). The relationship between latitude and AOO was similar, although the model fit was poorer ($F_{1,16}$ = 49.3, R^2 = 0.755, p < 0.001). Average density of endemic species by island was positively but nonlinearly related to latitude, with a notable increase in density of endemics above 23° latitude (Figure 3, Figure S2). The GAM was highly significant (F = 36.4, p < 0.001, adj. R^2 = 0.894) and explained 91.5% of the deviation. The distribution of species abundance by range size showed a striking pattern with endemics dominating numerically in the NWHI, particularly around the three northernmost islands (Figure 4).

Endemics dominated over related non-endemic species (in four taxonomic families) at higher latitudes. However, the transitions from non-endemic to endemic occurred at different latitudes, depending on the family (Figure 5). The transition from non-endemic to endemic for the damselfishes *Chromis vanderbilti* (non-endemic) to *C. ovalis* (endemic) occurred below the three northern atolls (Kure, Midway and Pearl & Hermes; 27 ° latitude). The transition for the surgeonfishes *Acanthurus nigrofuscus* (non-endemic) and *A. nigroris* (endemic) occurred farther south at Maro Reef (25.4° latitude). The transition from the non-endemic wrasse *Coris gaimard* to the endemic *C. flavovittata* also occurred farther south between Gardner Pinnacles and FFS (25.0°–23.8° latitude). Finally, the two parrotfishes, *Scarus rubroviolaceus* (non-endemic) and the endemic *Chlorurus perspicillatus*, reversed in abundance at Nihoa (23.1° latitude), the southernmost island in the NWHI.

Species	Abundance (No. m^{-2})	% Total abundance	% freq.	IRD	% IRD
Chromis vanderbilti	0.063 (0.156)	16.63	57.40	954.54	20.73
Thalassoma duperrey	0.032 (0.034)	8.51	94.35	802.73	17.43
Acanthurus nigrofuscus	0.021 (0.034)	5.52	70.35	388.68	8.44
Ctenochaetus strigosus	0.017 (0.034)	4.55	59.87	272.57	5.92
Chromis hanui	0.014 (0.049)	3.67	44.17	162.17	3.52
Stegastes marginatus	0.011 (0.019)	2.87	54.46	156.25	3.39
Paracirrhites arcatus	0.008 (0.014)	2.22	64.80	144.02	3.13
Acanthurus triostegus sandvicensis*	0.009 (0.041)	2.45	45.49	111.42	2.42
Parupeneus multifasciatus	0.005 (0.006)	1.31	83.35	109.55	2.38
Stethojulis balteata	0.006 (0.012)	1.50	63.24	95.09	2.07

TABLE 1 Top 10 fish species overall from visual surveys. Values for abundance (No. m^{-2}) are means with standard deviations in parentheses. Freq. = frequency of occurrence (N = 2,108). IRD = index of relative dominance (% freq. × % total abundance). Endemic species are in bold. *Acanthurus triostegus sandvicensis** is considered an endemic subspecies

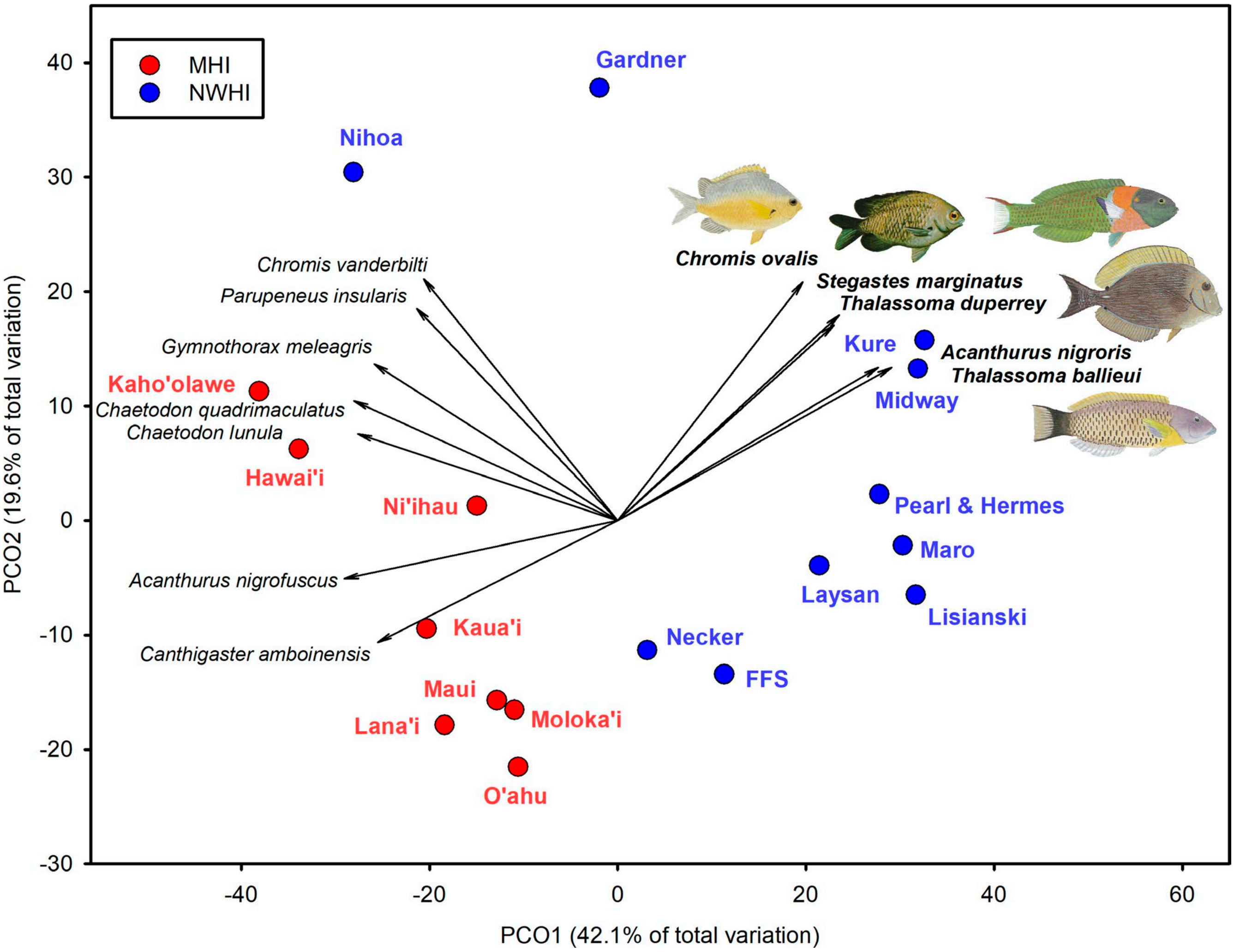

FIGURE 2 Principle coordinates analysis of fish species numerical abundance by region in the Hawaiian Archipelago. Data were ln(x + 1)-transformed prior to analyses. Vectors are the primary taxa driving the ordination (Pearson product-moment correlations ≥ 0.8). Endemic species are in bold. MHI = main Hawaiian Islands, NWHI – Northwestern Hawaiian Islands [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Results of distance-based multivariate linear model (DIST-LM) for species abundance showing percent variation explained by significant variables

Variable	AIC	SS (trace)	Pseudo-F	p	%	Cumulative %
Latitude	125.2	8,958.2	9.481	0.001	37.21	37.21
Reef area (km^2)	124.3	2,219.5	2.581	0.022	9.22	46.43

Based on the numerical abundance of endemic and non-endemic species, the optimal number of clusters from the *k-means* analysis was six (CCC = 1.85). When these clusters are overlaid onto the archipelago map, several clear faunal breaks are evident (Figure 6). The three northern atolls (Kure, Midway, Pearl & Hermes) form a distinct unit, as does the central portion of the NWHI except for the Gardner Pinnacles outlier. The northern and central regions of the MHI, along with Mokumanamana in the southern portion of the NWHI, cluster together, with Nihoa Island as an outlier within this geographical group. The two southernmost islands of Kahoʻolawe and Hawaiʻi form a distinct cluster from the rest of the MHI.

3.4 | Life-history attributes

Endemic species were significantly smaller ($\overline{X}$ = 8.85 ± 9.52) than non-endemics ($\overline{X}$ = 11.02 ± 22.45, t = 52.69, p < 0.001). The BRT had a training R^2 = 0.493 (RMSE = 0.079, N = 747) and a validation R^2 of 0.475 (RMSE = 0.086, N = 333). Maximum size had the greatest relative contribution (0.347) to the model, followed by activity (0.210; directly related to body size), and schooling (0.167; inversely related to size) (Table 3). The first split in the BRT separated nocturnal from diurnal endemic species (Figure S3). For diurnally active species, there was a split between species above and below <35 cm maximum size. Species ≥ 35 cm split between those with mobility of

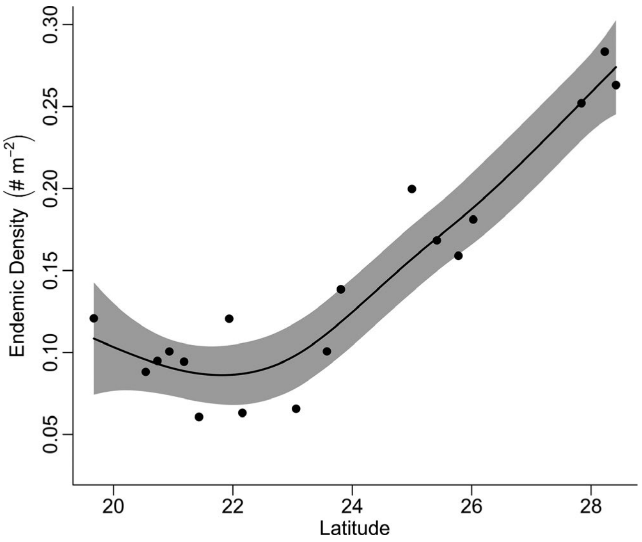

FIGURE 3 Relationship between latitude and density of endemic species (No. m^{-2}) by island in the Hawaiian Archipelago. Results of general additive model ($F = 36.4$, $p < 0.001$, adj. R$^2 = 0.894$). Shaded areas show 95% confidence interval

S1 (10 s m^2) and S2 (100 s m^2). Species < 35 cm showed a split between solitary and schooling species. Solitary species split between those above and below 9 cm maximum size.

4 | DISCUSSION

A remarkable 25% of Hawaiian shore fishes are endemic (Randall, 2007). In contrast, endemic fishes comprised 38% of the numerical abundance of all fishes on shallow (1–30 m depth) visual surveys, with a gradient of higher abundance towards the northern end of the archipelago. While estimates of endemism abundance based on visual observations cannot be directly compared with estimates of taxonomic endemism, diver observations allow us to quantitatively examine the abundance of the conspicuous fauna, and therefore one aspect of the ecological function of endemics.

Prior to extrapolating trends from our results, we review the evolutionary context for endemic Hawaiian reef fishes residing on islands aged 0.5–32 MY. Overwhelming evidence indicates that isolation and reduced gene flow are the most important mechanisms for maintaining reef fish endemism on oceanic islands (Hachich et al., 2015). Multiple genetic comparisons of Hawaiian Islands to other Central/West Pacific locations corroborate this conclusion (e.g. DiBattista, Wilcox, Craig, Rocha, & Bowen, 2011). Hawaiian endemics are the product of rare colonization events, mostly during sea level fluctuations within the Pleistocene, but with a few earlier contributions (Craig, Eble, & Bowen, 2010; Hodge, van Herwerden, & Bellwood, 2014; see also Pinheiro et al., 2017). With a few exceptions, Hawaiian endemic fishes occur throughout the archipelago, and connectivity is sufficient to preclude allopatric or parapatric radiations within the archipelago (Bowen et al., 2020).

Our examination of reef fish abundance in Hawaiʻi clearly substantiates separation between the MHI and NWHI. Fish species endemic to Hawaiʻi are greatly more common at the northern end of the chain, and this is strongly correlated across latitude (DeMartini & Friedlander, 2004; this study). Endemic fishes comprised 50% of the numerical abundance of reef fishes surveyed in the NWHI compared to 20% in the MHI. This represents an important zoogeographical break in reef fishes within the archipelago.

In addition to the MHI-NWHI partition, a faunal break separates the three northern atolls that are dominated by endemics. Another break is evident at the southern end of the archipelago (Hawaiʻi and Kahoʻolawe) dominated by non-endemics. The faunal break in the central archipelago is less precisely defined, partially because of the small reef area of several of the islands (e.g. Gardner = 0.7 km^2, Nihoa = 5.6 km^2).

Many endemic fishes of Hawaiʻi occur at shallow (<20 m) depths in the NWHI but are restricted to much deeper waters in the MHI (>100 m). For example, the endemic Hawaiian grouper (*Hyporthodus quernus*) is abundant on shallow reefs in the far NWHI but is rarely found shallower than 100 m in the MHI. This depth gradient from cooler to warmer waters in some endemic species is a foundation for the hypothesis that temperature influences EOO.

Surveys of mesophotic (30–90 m) coral reefs in the NWHI document 179 species, of which 46% are endemic to Hawaiʻi (Kane et al., 2014). Like the shallow-water assemblages, endemism of the mesophotic fish assemblages increases with latitude, as relative abundances of endemic reef fishes range from 16% at the southernmost end of the NWHI to upwards of 92% at the northernmost NWHI (Kane et al., 2014). Surveys conducted at Kure Atoll (86–91 m) recorded 22 species, all endemic (Kosaki et al., 2017). This unprecedented endemism indicates that mesophotic reefs in the NWHI are reservoirs of biodiversity, and further underscores the need for protection. The effect of temperature on the relative abundances of endemic and non-endemic reef fishes needs further quantitative exploration across all depths, including mesophotic depths.

On land, small-range-specialized endemics are major contributors to tropical diversity (Blackburn & Gaston, 2006; Stevens, 1989). However, for Indo-Pacific reef fishes, centres of high species richness are not concordant with centres of high endemicity. Peaks in species richness occur near the equator and the Central Indo-Pacific biodiversity hotspot, with only minor contributions from endemics (Hughes, Bellwood, & Connolly, 2002). Medium and low diversity regions on the periphery of the Indo-Pacific basin, such as Hawaiʻi and the Red Sea, have disproportionately more endemic corals and fishes (DiBattista et al., 2011; Hughes et al., 2002).

Contrary to macroecological theory, range size is negatively correlated with abundance of reef fishes in the NWHI but positively correlated with abundance in the MHI. Endemic reef fishes are consistently among the most abundant within their taxon or ecological guild in local assemblages (DeMartini & Friedlander, 2004; Jones et al., 2002). Greater abundances of endemics at higher-latitude reefs in Hawaiʻi may be related to better survivorship after settlement onto reefs, higher levels of within-reef and

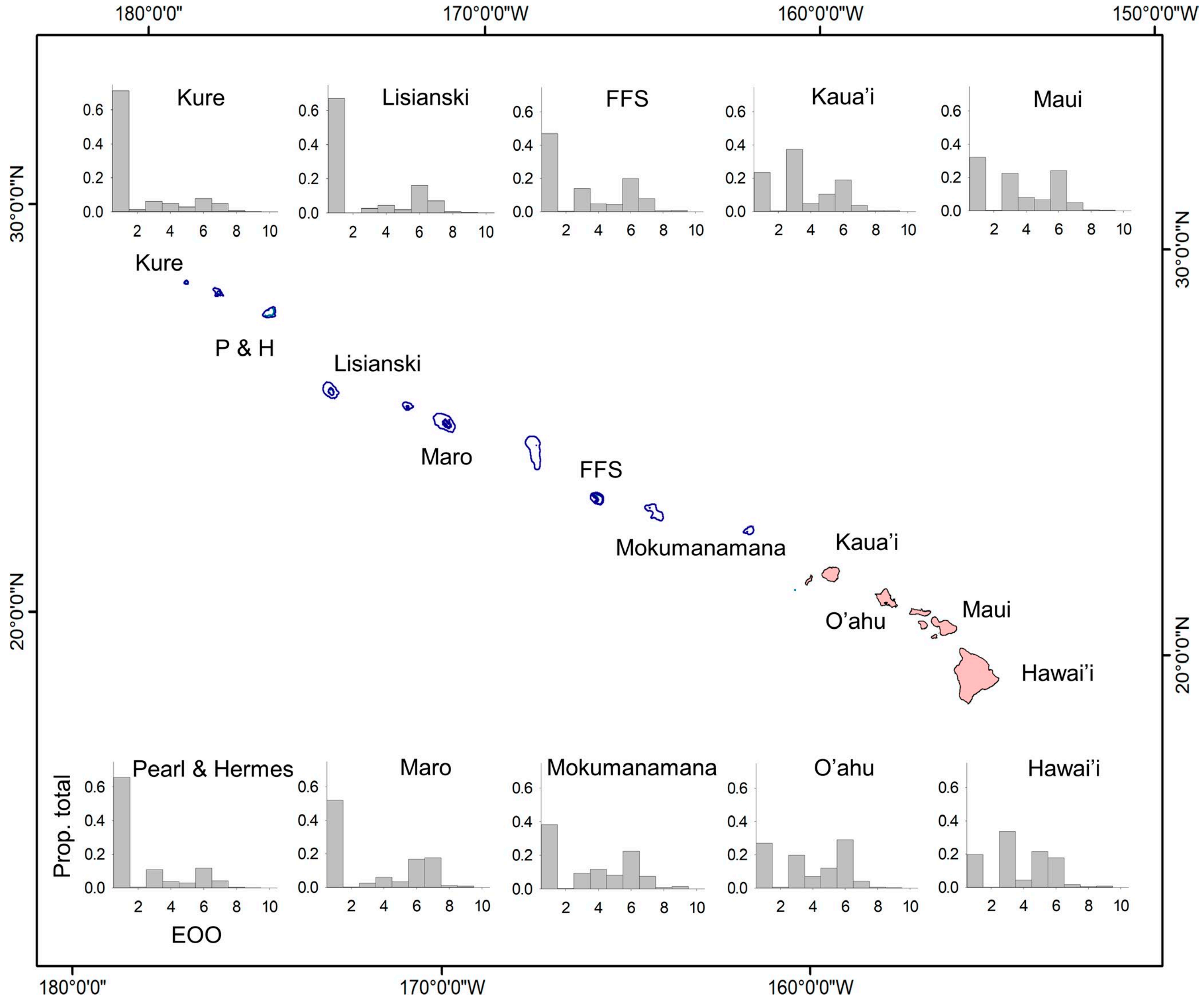

FIGURE 4 Spatial presentation of the distribution of proportional numerical abundance of fishes across geographical range sizes for a subset of islands within the Hawaiian Archipelago. Geographical range estimates based on the extent of occurrence (EOO), drawn from polygons encompassing locations where the species are known to occur based on 169 checklists (Kulbicki et al., 2013) and divided into 10 quantiles. Distributions in the smallest quantile represent endemic species limited to the Hawaiian Archipelago. FFS = French Frigate Shoals, P & H = Pearl and Hermes [Colour figure can be viewed at wileyonlinelibrary.com]

regional self-recruitment, or response to the oligotrophic oceanic conditions of the NWHI (DeMartini & Friedlander, 2004; Robertson, 2001).

Endemic reef fishes of Hawai'i appear to have restricted dispersal (Eble, Toonen, & Bowen, 2009; Ramon, Nelson, DeMartini, Walsh, & Bernardi, 2008; Tenggardjaja, Bowen, & Bernardi, 2018) and higher recruitment compared to widespread congeners (DeMartini, 2004; DeMartini & Friedlander, 2004), which may explain why they maintain high local abundances. In a review of population genetic structure in 35 species in Hawaiian coral reef communities, Selkoe, Gaggiotti, Bowen, and Toonen (2014) found genetic partitioning was highest in endemic and specialist species. These data support the hypothesis that Hawai'i's contemporary endemic species evolved from ancestors with reduced dispersal, and this may be a general feature of ocean island endemics (Hachich et al., 2015; Pinheiro et al., 2017; see also Floeter & Gasparini, 2000). These fishes are unable to maintain connectivity with the parent populations after rare colonization events, as indicated by low genetic connectivity across the Hawaiian Archipelago. Strong selection on larvae from isolated islands to return to their natal reefs may help maintain consistently high recruitment (Gerlach, Atema, Kingsford, Black, & Miller-Sims, 2007; Jones et al., 2009).

Endemic reef fishes associated with isolated islands may have attributes that promote high local abundance and may buffer them from low genetic diversity and stochastic processes, such as recruitment failure and climatological variability (Hobbs et al., 2011; Jones et al., 2002; Randall, 1973). Despite their high adaptive capacity and abundance conducive to oceanic island conditions, most of the recorded extinctions in the marine environment have been those species with small range sizes (Dulvy et al., 2003).

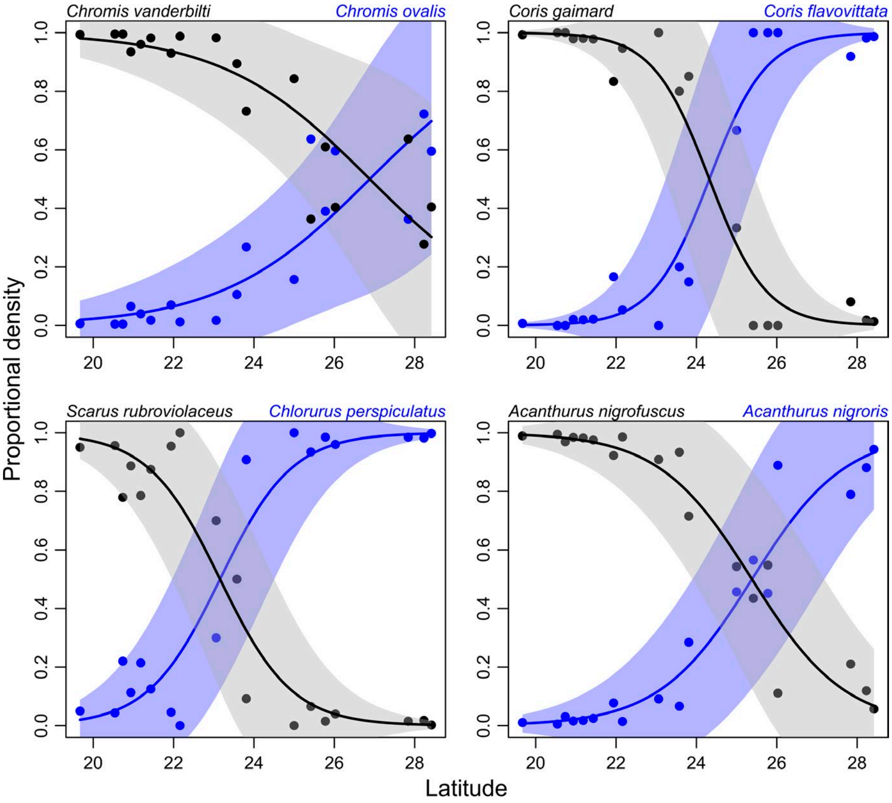

FIGURE 5 Relative density of endemic species (blue) compared to their wide-ranging relatives (black) across a latitudinal gradient in the Hawaiian Archipelago. The Y-axis is the relative numerical density for each species. Lines are fits of a logistic regression for endemic species (blue) and non-endemics (black). Shaded areas show 95% confidence [Colour figure can be viewed at wileyonlinelibrary.com]

Range-restricted species are generally considered to be at increased extinction risk due to localized human or natural disturbances (Brooks et al., 2006; Quimbayo et al., 2019; Selig et al., 2014). Conserving places with high endemism are therefore critical for preventing biodiversity loss and maintaining genetic diversity (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). In this case, endemic species may be more susceptible in the MHI compared with the NWHI due the numerous anthropogenic threats found in the former (Friedlander & Brown, 2019).

A number of behavioural and life-history attributes are correlated with range size, including habitat specificity, degree of environmental tolerance, fecundity, generation time and larval duration (Brown, Stevens, & Kaufman, 1996; Gaston, 1996; Kunin & Gaston, 1993). Like island endemics elsewhere, the endemic fishes of Hawai'i are small bodied (Roberts et al., 2002), possibly in response to high predation pressure (Reznick, Butler IV, & Rodd, 2001), and this might help explain our observations that mobility and associative (schooling) behaviours are positively and inversely related to body size, respectively, as anti-predatory measures in Hawaiian endemics. Small body size per se may be associated with higher extinction risk because small-bodied species tend to have narrower habitat requirements (Hawkins et al., 2000). Therefore, both body size and endemic status argue for the conservation of these species.

5 | CONCLUSIONS

Our results reveal distinct bioregions across the Hawaiian Archipelago based on the abundance of endemic species, providing a better understanding of reef fish macroecology with implications for management. Notably, partitions defined by assemblage structure are concordant with population genetic breaks in a suite of reef fauna (Toonen et al., 2011), including partitions in the north and in the south, with a genetically homogeneous region in the middle of the archipelago.

The primary faunal break between the MHI and NWHI coincides with the transition from volcanic basaltic high islands to calcareous low islands, lagoons and atolls. High islands have freshwater runoff, sedimentation and nutrient loads; their coastlines thus partially mimic continental margins. Nonetheless, oligotrophic conditions dominate—a characteristic of true oceanic atolls. We suggest that the higher abundance of endemics in the NWHI is because these species first colonized the oligotrophic portion of the archipelago. Substantial genetic and oceanographic evidence indicates that the NWHI is the entry point for colonization of reef biodiversity into Hawai'i (Bowen et al., 2016). For the most part, successful colonization into Hawaiian reefs entails preadaptation to oligotrophic oceanic island conditions, and this may explain the higher abundance of endemics in the NWHI.

The large proportions of endemic shore fish species in Hawai'i, particularly in the NWHI, highlight the uniqueness and irreplaceable nature of these fish assemblages. Endemic species pose a special management challenge because their inherently limited distributions puts them at greater risk of extinction from natural or anthropogenic hazards (Gaston, 1994). Many endemic fishes preferentially recruit to rugose corals habitats of Hawai'i (DeMartini, Anderson, Kenyon, Beets, & Friedlander, 2010), and increasing stressors on corals impact the replenishment of endemic fishes. Management should note that

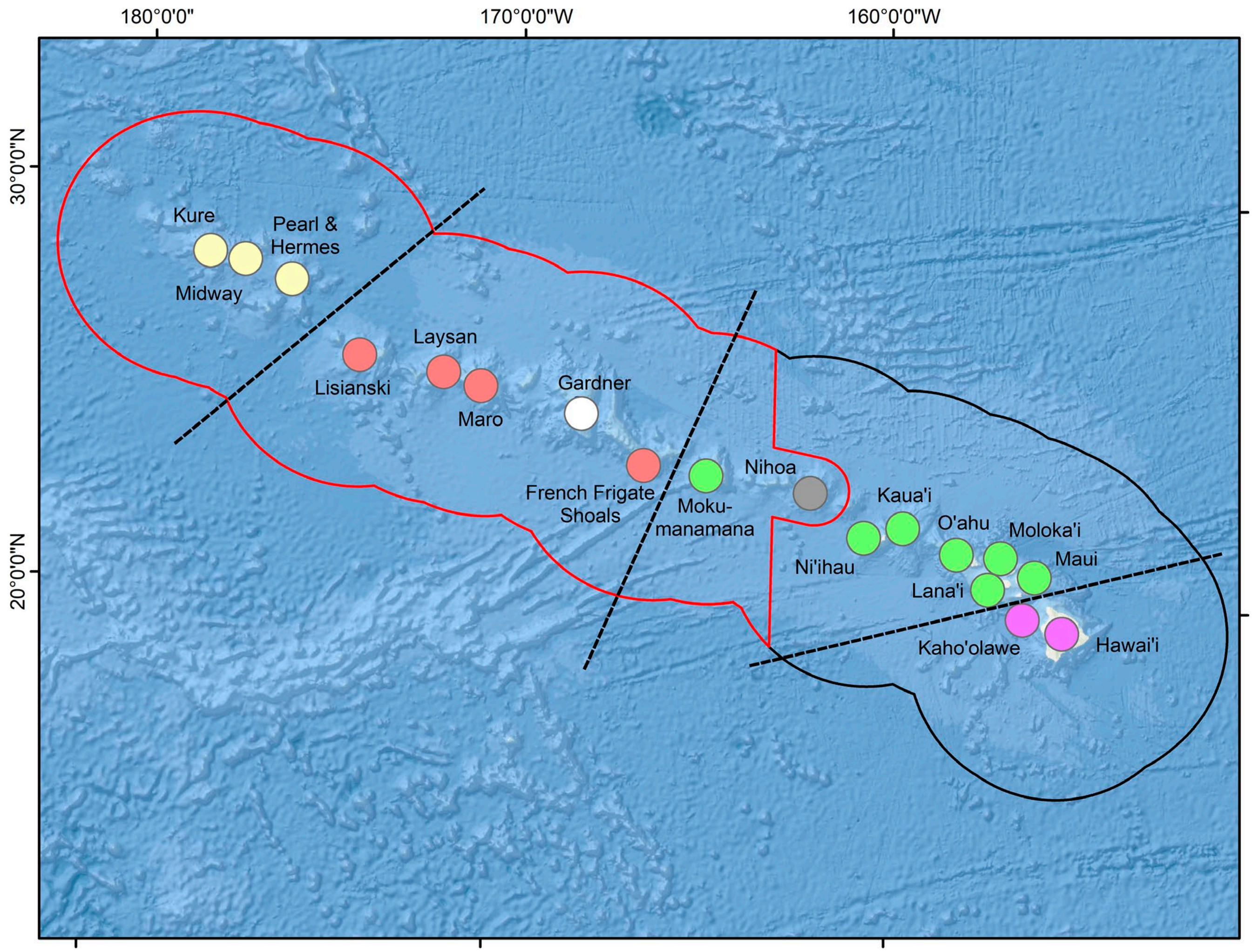

FIGURE 6 Faunal breaks across the Hawaiian Archipelago based on the numerical abundance of endemic and non-endemic species. The optimal number of clusters from the *k-means* analysis was six (CCC = 1.85). Clusters are colour coded and overlaid onto the archipelago map. Dashed lines represent clear faunal breaks [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Results of boosted regression trees (BRT) used to examine the relationship between average numerical density of endemic species by island and species life history characteristics

Term	Number of splits	SS	Portion
Maximum size	94	8.397	0.347
Activity	29	5.095	0.210
Schooling	32	4.017	0.166
Mobility	37	3.887	0.161
Level-water	34	1.893	0.078
Trophic level	24	0.934	0.039

SS, sum of squares. The BRT had a training $R^2 = 0.493$ (RMSE = 0.079, $N = 747$) and a validation R^2 of 0.475 (RMSE = 0.086, $N = 333$).

reef fishes unique to Hawai‘i have less gene flow across the archipelago than more broadly distributed Indo-Pacific species (Tenggardjaja et al., 2018). Because small islands have persistent self-sustaining populations of endemic species, a regional system of small MPAs could effectively preserve endemic biodiversity (Robertson, 2001). The State of Hawai‘i has recently committed to effectively manage 30% of its nearshore waters by 2030 and our identification of bioregions for endemic species can inform this process.

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AUTHORS’ CONTRIBUTIONS

A.M.F. conceived the project. M.K.D. and A.M.F. organized and analysed the transect data, E.E.D. contributed expertise on fish life history and conservation ecology, and B.W.B. contributed expertise on genetic connectivity and phylogeography. All authors contributed to the writing and commented on the final draft.

DATA AVAILABILITY STATEMENT

Our data are publicly available at Data Dryad: https://doi.org/10.5061/dryad.wh70rxwkf.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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