Received: 26 January 2017 | Revised: 7 July 2017 | Accepted: 18 July 2017
DOI: 10.1002/aqc.2832

WILEY

RESEARCH ARTICLE

Human-induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries

Alan M. Friedlander[1,2] | **Mary K. Donovan**[1] | **Kostantinos A. Stamoulis**[1] | **Ivor D. Williams**[3] | **Eric K. Brown**[4] | **Eric J. Conklin**[5] | **Edward E. DeMartini**[6] | **Kuulei S. Rodgers**[6] | **Russell T. Sparks**[7] | **William J. Walsh**[8]

[1] Fisheries Ecology Research Lab, Department of Biology, University of Hawai'i at Mānoa, Honolulu, Hawai'i, USA
[2] Pristine Seas, National Geographic Society, Washington, District of Columbia, USA
[3] National Oceanic and Atmospheric Administration Fisheries, Pacific Islands Fisheries Science Center, Inouye Regional Center, Honolulu, Hawai'i, USA
[4] National Park Service, Kalaupapa National Historical Park, Kalaupapa, Hawai'i, USA
[5] The Nature Conservancy of Hawai'i, Honolulu, Hawai'i, USA
[6] Hawai'i Institute of Marine Biology, Kaneohe, Hawai'i, USA
[7] Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources, Wailuku, Hawai'i, USA
[8] Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources, Kailua-Kona, Hawai'i, USA

Correspondence
Alan M. Friedlander, Fisheries Ecology Research Lab, Department of Biology, University of Hawaiʻi at Mānoa, Honolulu, Hawaiʻi, 96822, USA.
Email: alan.friedlander@hawaii.edu

Funding information
The National Oceanic and Atmospheric Administration's Coral Reef Conservation Program; Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources, Grant/Award Number: #C30597

Abstract

1. Large declines in reef fish populations in Hawaiʻi have raised concerns about the sustainability of these resources, and the ecosystem as a whole. To help elucidate the reasons behind these declines, a comprehensive examination of reef fish assemblages was conducted across the entire 2500 km Hawaiian Archipelago.
2. Twenty-five datasets were compiled, representing >25 000 individual surveys conducted throughout Hawaiʻi since 2000. To account for overall differences in survey methods, conversion factors were created to standardize among methods.
3. Comparisons of major targeted resource species (N = 35) between the densely populated main (MHI) and remote north-western Hawaiian Islands (NWHI) revealed that 40% of these species had biomass in the MHI below 25% of NWHI levels. In total, 54% of the species examined had biomass <50% of NWHI biomass.
4. The moku or district was a basic unit of resource management in pre-contact Hawaiʻi and was used as a unit of spatial stratification for comparisons within the MHI. Biomass of resource species was negatively correlated with human population density within moku boundaries, with extremely low biomass in areas with highest human population densities. No such relationship was found for species not targeted by fishing.
5. A number of remote areas with small human populations in the MHI still support high standing stock of fished species, and these areas are likely important refugia for maintaining fisheries production and biodiversity functioning.
6. These results highlight the large gradient of human impacts on fish assemblages across the Hawaiian Archipelago and the potential in using landscape and seascape units, such as those that are watershed and bio-physically-based, when managing in part based on a framework of traditional ecological knowledge.

KEYWORDS
archipelago, conservation evaluation, ecological status, fish, fisheries sustainability, overfishing, reef fish production, reef fish trophic structure

1 | INTRODUCTION

The Hawaiians of old had a sophisticated understanding of the natural processes regulating resource abundance and used this knowledge to develop effective strategies to manage those resources (ʻĪʻI, 1959; Kahāʻulelio, 2006; Kamakau, 1976; Malo, 1951). In pre-contact Hawaiian society (<1778), the basic unit of land division and socio-economic organization was the watershed or ahupuaʻa, which was nested within districts (moku) that were roughly aligned to bio-physical attributes of island ecosystems (e.g. windward /leeward and wet/dry districts of islands, Kaneshiro et al., 2005; Malo, 1951). Customary fisheries management was specific to each moku and even ahupuaʻa, with fishing activities and catch strictly disciplined by rules and regulations that were embedded in socio-political structures and religious systems (Kirch, 1989; Titcomb, 1972).

The breakdown of this traditional fisheries management system after Western contact led to extensive exploitation of marine resources fuelled by a cash-based economy, which was centred on large and increasing urban demands (Cobb, 1901; Kuykendall, 1938; Schug, 2001). Reef fish populations and their associated fisheries have declined dramatically around Hawaiʻi over the past hundred years owing to a growing human population, destruction of habitat, introduction of new and unsustainable fishing techniques, and loss of traditional conservation practices (Friedlander & DeMartini, 2002; Friedlander, Stamoulis, Kittinger, Drazen, & Tissot, 2014; McClenachan & Kittinger, 2013; Smith, 1993). Although many people acknowledge declines in certain reef fishes in Hawaiʻi over time, there is little agreement on the causes (Kittinger et al., 2011; Williams et al., 2008). To make matters worse, there is poor compliance with fishing laws and regulations coupled with insufficient enforcement due to lack of resources and political will (Capitini, Tissot, Carroll, Walsh, & Peck, 2004; Stevenson & Tissot, 2013; Tissot, Walsh, & Hixon, 2009).

In contrast to the main Hawaiian Islands (MHI), the nearshore fish populations of the remote north-western Hawaiian Islands (NWHI) have been largely unfished for decades, in what is now the Papahānaumokuākea Marine National Monument (PMNM), which is currently the single largest conservation area in the USA, and one of the largest in the world (Kittinger, Dowling, Purves, Milne, & Olsson, 2010; Toonen et al., 2013) Previous comparisons between the MHI and NWHI have revealed dramatic differences in the abundance, size, and biomass of the shallow reef fish assemblages, with both severe depletion of top predators and heavy exploitation of lower trophic levels in the MHI compared with the largely unfished NWHI (Friedlander & DeMartini, 2002; Williams et al., 2010, 2015). A previous study comparing fish assemblages within the MHI showed a strong negative effect of human population density on fisheries resource species (Williams et al., 2008); however, these data were limited in spatial extent, habitat diversity, and did not incorporate other available datasets. In addition, data collection efforts of fish assemblages around the entire archipelago have greatly expanded in spatial and temporal scope since 2006 when that study was conducted.

Hawaiʻi's coral reef fisheries provide livelihoods, sustenance, recreation, and help perpetuate customary cultural practices (Friedlander, Shackeroff, & Kittinger, 2013; McClenachan & Kittinger, 2013; Smith, 1993). The dramatic declines seen in these resources are therefore negatively affecting the goods and services that are essential to the people of Hawaiʻi. One of the major obstacles to wise management of coral reef fisheries resources is the lack of good information on population abundance at spatial scales commensurate with the uses of these resources (Cinner et al., 2012; Hilborn, Orensanz, & Parma, 2005).

Localized differences in the abundances of coral reef fishes can result from varying environmental factors (e.g. habitat quality, reef zone, productivity, sea surface temperature), as well as the magnitude of human extraction (Darling et al., 2017; Pinca et al., 2012; Williams et al., 2015). This information is critical to developing sustainable fisheries management strategies, which includes improving management of existing marine protected areas (MPAs), designing future MPA networks, and aiding in the development of comprehensive marine spatial planning.

All available reef fish visual census data from Hawaiʻi were compiled into a single dataset in order to assess the patterns of reef fish biomass across the entire Hawaiian Archipelago in relation to both bio-physical and human factors. The unpopulated NWHI and the MHI were compared in terms of resource fish biomass and densities were examined for a number of key resource species between regions. Human influence on resource fish biomass was further investigated, while accounting for bio-physical variation to highlight locations with the least and greatest impacts.

2 | METHODS

Twenty-five datasets were compiled, representing more than 25 000 individual fish surveys at 6468 unique survey locations from throughout the entire Hawaiian Archipelago since 2000. This study incorporated data from 18 islands spanning nearly 10° of latitude and >2500 km (Figure 1). Data sets were identified from around the archipelago that collectively represented a variety of habitats, depths, and human influences. These data were rigorously checked for errors and integrated into a common database with a standardized structure.

2.1 | Fish sampling methods

A number of underwater visual census (UVC) methods were used to assess fish populations across the Hawaiian Archipelago. Methods consisted of belt transects of various dimensions (e.g. 25 × 5 m, 25 × 4 m, and 25 × 2 m) and stationary point counts (15 m diameter). Details of each method are described in Table S1, Supporting information.

2.2 | Biomass estimates

The biomass of individual fishes was estimated using the allometric length–weight conversion: $W = a\mathrm{TL}^b$, where parameters a and b are species-specific constants, TL is total length (cm), and W is weight (g). Length–weight fitting parameters were obtained from a comprehensive assessment of Hawaiʻi length–weight fitting parameters (Froese & Pauly, 2009). The cross-product of individual weights and numerical densities was used to estimate biomass by species.

Fishes were categorized into four trophic groups (top predators, invertivores, planktivores, and herbivores) after DeMartini, Friedlander, Sandin, and Sala (2008) and Sandin et al. (2008). Top predators, primarily reef sharks and jacks, were enumerated on all surveys, when present. Total biomass was examined both with and without these top predators to enable comparisons with other studies (MacNeil et al., 2015; Williams et al., 2010, 2015). Analyses of top predators, whether including or excluding reef sharks and jacks, excluded apex predators (e.g. tiger shark [*Galeocerdo cuvier*] and the great hammerhead shark [*Sphyrna mokkaran*]), owing to the large uncertainties in quantifying the abundances of these highly mobile,

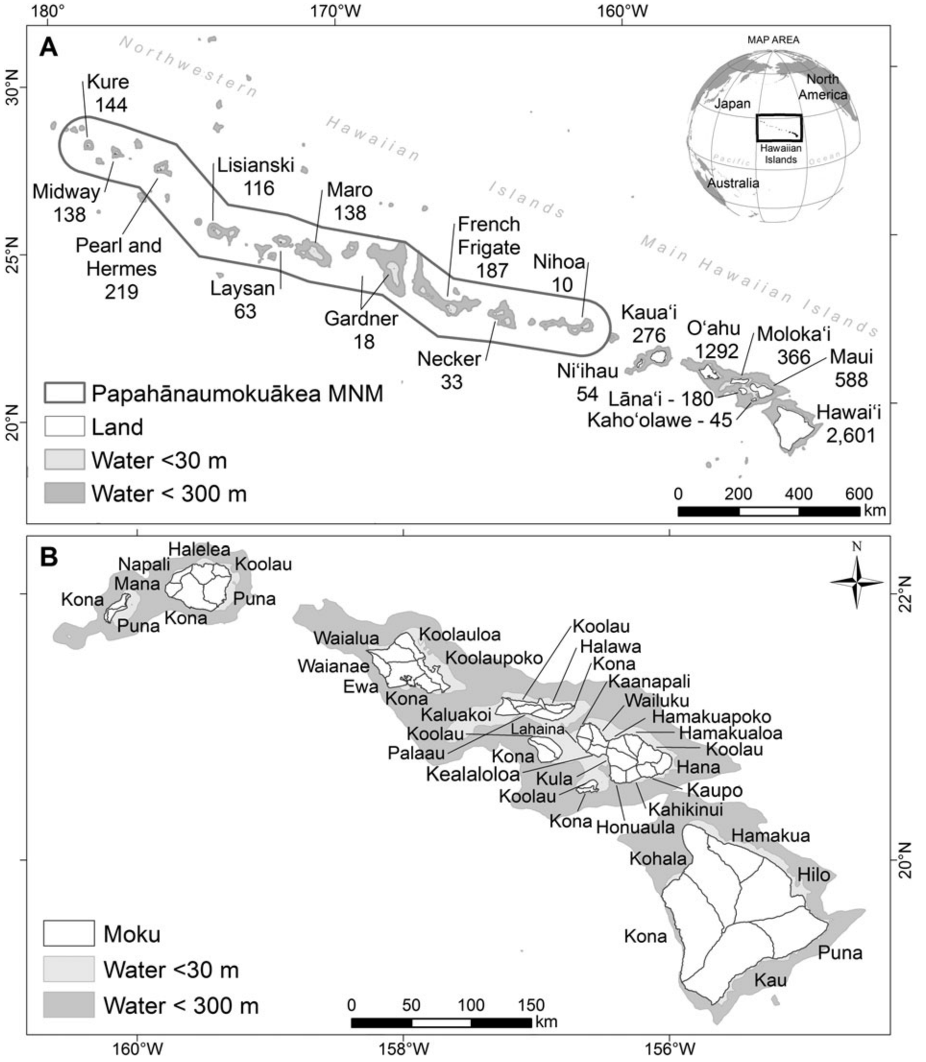

FIGURE 1 (a). Map of Hawaiian archipelago with islands labelled including sample sizes by island. (b) Map of moku across the main Hawaiian islands

large-bodied species (Roff et al., 2016; Ward-Paige, Flemming, & Lotze, 2010). Each trophic group was divided into resource and non-resource species, where resource species were defined either as those species having ≥450 kg of average annual commercial or recreational harvest for the past 10 years (2000–2010) or as recognized species that are important to the local subsistence or cultural sectors (http://dlnr.hawaii.gov/dar/fishing/hmrfs/, Table S2). A subset of resource species was also examined without reef sharks and jacks, as estimates of these latter taxa can be highly variable for several reasons (Ward-Paige et al., 2010). Several species were removed from biomass calculations if aspects of their life history led to inaccurate counts with visual surveys, such as cryptic benthic species (e.g. blennies and gobies), nocturnal species, and pelagic schooling species.

2.3 | Methods calibration

Underwater visual survey methods of fishes all have their own inherent biases (Colvocoresses & Acosta, 2007; Edgar, Barrett, & Morton, 2004; McClanahan et al., 2007), and differences in the performance of these different methods means that survey data gathered by multiple methods should be standardized before being combined for analysis (Maunder & Punt, 2004). To account for overall differences in survey methods, conversion factors were calculated to standardize each method to the NOAA Biogeography Program belt transect (Table S3). This was done using general linear models and Monte Carlo simulations to calculate methods calibration factors (Nadon, 2014). Calibrations were calculated by species, where possible, using the following decision rules: (1) ≥ 10 paired observations were available within an island; (2) if the proportion of zeros was high (> 15%), a delta model was run where occurrences were modelled separately from non-occurrences; (3) the fit was checked for normally distributed residuals, and if this check failed the model was rerun and checked with log-transformed data. If a species did not pass this series of rules then a calibration factor was not calculated, and a calibration factor for each combination of family and trophic level was calculated and applied instead. If a calibration factor could not be calculated at the combined family–trophic level, then a global calibration was used that considered all species pooled for each method. For all subsequent analyses, density estimates were based on calibrated densities of raw data (Table S3).

One important consideration when accounting for differences across datasets is how schooling species are counted. To account for exaggerated counts of schooling species, exploratory analyses were conducted to identify extreme observations in the database and subsequently adjust those observations to dampen their effect on the calculations of biomass. Extreme observations were defined by calculating the upper 0.1% of all individual observations (e.g. one species, size, and count on an individual transect) resulting in 26 observations out of >0.5 million, and comprising 11 species. The distribution of individual counts in the entire database for those 11 species was then used to identify individual observations that fell above the 99.9% quantile of counts for each species individually. The counts for these individual observations were then capped to the value of the 99.9% quantile for biomass calculations.

2.4 | Spatial stratification (moku)

For the purpose of providing potentially informative, within-island spatial comparisons for the MHI, the traditional Hawaiian district or moku was chosen as a unit of spatial stratification. Although the Hawaiʻi statewide GIS program (http://planning.hawaii.gov/gis/) provides a GIS shapefile of ahupuaʻa and moku boundaries, there is no definitive source for this information. The difficulty arises from several factors: (1) early Hawaiians left few maps; (2) several volcanic eruptions have modified or destroyed ahupua'a and/or moku boundaries; (3) boundaries were well established at the shoreline but were more ambiguous offshore; (4) the conquest and unification of the islands destroyed sovereign boundaries; and (5) current boundaries set by various indigenous and historical authorities sometimes conflict (Gonschor & Beamer, 2014). For these reasons, the most reliable source for this information was found to be the Island Breath organization (http://www.islandbreath.org/), who conducted a detailed survey using historical documents, early Hawaiian maps, USGS survey maps, and individual accounts. Using these moku maps, each site location was attributed to the nearest moku land division (Figure 1).

Spatial dependence was tested within and among moku by constructing an experimental variogram of resource fish biomass with 25 m distance bins to correspond with the length of the fish transects. A theoretical variogram was fitted using weighted least squares and spherical covariance to obtain an estimate for the sill and corresponding lag distance, which is the maximum distance between points exhibiting spatial dependence (Fortin & Dale, 2005). This value was compared to the minimum distance between any two points between adjacent moku to determine if spatial dependence occurred across moku.

Human population was used as a proxy for human impact and was calculated at the moku scale for analytical purposes. Average human population for each moku was calculated using 2010 census data (www.census.hawaii.gov). Because census blocks did not correspond with moku boundaries, a 1 ha resolution grid was developed where each cell contained the average population density (number of people ha^{-1}) for that census block. The cells corresponding to each moku were summed to calculate the total population for each moku. Total human population within each moku was divided by the shoreline length of that moku to provide an index of human population pressure (Williams et al., 2008). Thus, moku with large populations and small shorelines were weighted more heavily. Wave exposure for each moku was described by the aspect, which was defined individually for each moku based on the dominant cardinal direction (north, south, east, and west) of the coastline (Table S4).

2.5 | Comparing species-level biomass in the MHI and the NWHI

The abundance of major targeted resource species, as defined above, was compared between the NWHI and MHI. Since some species naturally have tropical or subtropical affinities, the correlation between latitude and biomass density (g m^{-2}) of these species was examined only in the NWHI using Spearman Rank Correlation. This analysis was restricted to the NWHI to remove any effect of fishing within the MHI. Species that showed a significant correlation with latitude or had inadequate sample size to test this correlation (≤ 20 sites in the NWHI) were excluded from the NWHI vs. MHI comparison. For the adequately sampled species that did not show a latitudinal bias, density in the MHI was estimated and then measured as a percentage of unfished biomass by dividing the mean biomass density observed within the MHI by the density within the NWHI. No major resource species were restricted to the MHI.

2.6 | Statistical analyses

Patterns of fish biomass across moku, islands, and region (NWHI and MHI) were analysed using generalized linear mixed models (GLMM, Zuur, Ieno, Walker, Saveliev, & Smith, 2009), using the R package *glmmADMB* (Skaug & Fournier, 2006) in the R statistical program version 3.0.2. Owing to the skewed nature of the biomass estimates, models were fitted using a gamma error structure with an inverse link function suitable for continuous-positive data (Crawley, 2012). Models of moku and region accounted for spatial dependence, and differences in sampling strategies were accounted for by including datasets nested within islands as random effects, since data from the same islands are assumed to be more similar than data among islands. Similarly, the island model included a random effect of dataset. Surveys from inside fully-no-take reserves were removed before all analyses to avoid confounding effects of spatial protection on patterns of fish biomass. Model fits were assessed by visual inspection of residuals, and goodness of fit (R^2) was calculated following methods described by Nakagawa and Schielzeth (2013). Hypothesis tests for fixed effects were based on likelihood ratio tests using the *Anova* function in the *car* package in R. Comparisons of resource fish biomass by trophic group (top predators, herbivores, planktivores, and invertivores) between the MHI and NWHI were conducted using Mann–Whitney rank sum tests with a Bonferroni correction ($P = 0.05/4$) for multiple comparisons (Sokal & Rohlf, 1981).

To examine the influence of bio-physical factors on resource fish biomass between regions, a GLMM was conducted with gamma error using sea surface temperature (SST), chlorophyll-*a*, and coral cover as covariates in the model. Long-term means of SST and chlorophyll-*a* were obtained from published satellite-derived data at the island scale, as this was the finest scale available for the NWHI (Gove et al., 2013). Long-term means, rather than metrics such as anomaly frequencies, were used since interest was in comparing overall conditions across islands and these metrics have previously been shown to reflect differences across islands in the Hawaiian Archipelago (Gove et al., 2013). Coral cover at the island scale was derived from estimates used in Williams et al. (2015). All variables were centred and scaled so that coefficients in the GLMM were comparable.

Several additional analyses were conducted in order to test for the sensitivity of the model results to the year of sampling. GLMM models were rerun with an additional random effect of year and compared with models without year using likelihood ratio tests. In addition, the effect of year on resource fish biomass was tested alone using a generalized linear gamma mixed effect model with moku, island, and dataset as random effects to test whether the spatial results observed were sensitive to the effects of time.

The relationship between resource fish and non-resource fish biomass and human population density km^{-1} of shoreline by moku was assessed using a GLMM with Gaussian error, where resource fish biomass was ln (x + 1) transformed to meet the assumptions of linear modelling. Human population density was fourth-root transformed to reduce the mean–variance relationship given the large variance. Similar to the above, island was included as a random effect in the model to account for spatial dependence of moku within islands.

To describe the pattern of variation in fish assemblage structure and their relationship to bio-physical and human gradients, linear ordination methods were used. Linear models are appropriate for these data because a preliminary detrended correspondence analysis showed short gradient lengths along the ordination axes (< 2 SD, ter Braak & Smilauer, 2012). To explore the spatial distribution of fish assemblage structure among moku within the MHI and its relationship with bio-physical and human gradient variables, a direct gradient analysis (redundancy analysis: RDA) was performed using the ordination program CANOCO for Windows version 5.0 (ter Braak, 1994). The RDA introduces a series of explanatory (physical and human) variables, analogous to a model of multivariate multiple regression, which identifies the linear combinations of variables that determine the gradients. Data from all taxa were pooled into biomass for each of the four trophic groups to facilitate large-scale analysis. Data were standardized, centred, and log-transformed for analysis. The bio-physical and human data matrix included the following variables: island, aspect (north, south, east, west), SST, chlorophyll-*a*, coral cover, and scaled human population density by moku. Environmental variables, SST, and chlorophyll-*a*, were obtained from published data (Gove et al., 2013), and coral cover by moku was calculated from a synthesis of benthic data (Bauer et al., 2016). For consistency with the fish survey data, these bio-physical and human variables were quantified for each survey location and averaged to obtain a value for each moku. To rank bio-physical and human variables in their importance for being associated with the structure of the fish assemblage, forward selection was used where the statistical significance of each variable was judged by a Monte-Carlo permutation test (ter Braak & Verdonschot, 1995). In addition, patterns of resource fish biomass among moku within the MHI was also assessed using a GLMM as described above using the same covariates as the redundancy analysis with covariates summarized to the moku scale. Throughout the text, all values are means and one standard deviation unless otherwise noted.

3 | RESULTS

3.1 | Comparisons between the MHI and NWHI

Total resource fish biomass in the NWHI (294.6 g m^{-2}, 95% C.I. 290.5–303.2) was 5.9 times higher, on average, than in the MHI (50.0 g m^{-2}, 95% C.I. 13.1–117.7, Gamma GLMM: $\chi^2_{1,\,3907} = 84.1$, $P < 0.01$). When sharks and jacks are removed from the analysis, resource fish biomass in the NWHI (154.9 g m^{-2}, C.I. 152.6–159.7) was still 3.3 times higher, on average, than in the MHI (47.1 g m^{-2}, C.I. 12.6–111.5, Gamma GLMM: $\chi^2_{1,\,3907} = 25.6$, $P < 0.01$). Total resource fish biomass in the NWHI ranged from a high of 389.9 (± 388.8) at Gardner Pinnacles to 142.8 (± 183.7) at Mokumanamana (Necker). In the MHI, resource fish biomass was highest at the uninhabited island of Kaho'olawe (104.1 ± 37.3), which was an order of magnitude greater than on O'ahu (11.8 ± 22.2), where the lowest biomass was found.

In the GLMM of fish resource biomass and environmental and habitat variables, all variables in the model were significant, except for SST (Table 1). Region had the largest relative influence, followed by chlorophyll-*a*, and coral cover. Chlorophyll-*a* and coral cover had a positive relationship with resource fish biomass, while the interaction of region and chlorophyll-*a* had a negative correlation with resource fish biomass. After accounting for the environmental covariates by holding all values at their means, resource fish biomass in the NWHI was 3.2 times higher than in the MHI.

More than 53% of the total resource fish biomass in the NWHI consisted of top predators, primarily sharks and jacks, while this trophic group accounted for only 10.8% of the total resource fish biomass in the MHI. Absolute biomass of top predators was nearly 32 times greater in the NWHI compared with the MHI (Mann–Whitney U = 30.2, $P < 0.001$). Herbivores, primarily parrotfishes and surgeonfishes, accounted for 39% of resource biomass in the NWHI and more than 61% in the MHI. Total biomass of herbivores was more than 4 times higher in the NWHI compared with the MHI (Mann–Whitney U = 23.7, $P < 0.001$). Invertivores included a diverse suite of species and comprised 22% of the biomass in the MHI compared with 6% in the NWHI; absolute biomass of this trophic group was 72% higher in the NWHI (Mann–Whitney U = 14.6, $P < 0.001$). Finally, planktivore biomass was 61% higher in the NWHI compared with the

TABLE 1 Results of generalized linear mixed-effects model of resource fish biomass and environmental and habitat variables between the MHI and NWHI. χ^2 and *P* values are from likelihood ratio tests. Explanatory variables were centred and scaled before analysis. Region - NWHI and MHI, SST – Long-term mean sea surface temperature (°C), Chl a – Long-term mean chlorophyll-α. Only significant interactions are shown

	Beta	Std error	χ^2	p-value
Intercept (MHI)	4.067	0.777		
Region (NWHI)	1.435	0.782	3.982	0.046
SST	−0.968	0.880	1.198	0.274
Chl *a*	0.770	0.164	17.709	<0.01
Coral cover	0.760	0.131	32.864	<0.01
Region × Chl *a*	−0.774	0.249	9.693	0.002

MHI (Mann–Whitney U = 7.2, $P < 0.001$), accounting for 1.6% of the total in the former and 6.3% in the latter.

3.2 | Comparing MHI fish species using the NWHI as a reference

There were 55 resource species that had mean landings >450 kg yr^{-1} during the past 10 years from either the commercial (CML) or recreational (MRIP) databases. After applying the aforedescribed filter for latitudinal bias and sample size, a total of 35 major targeted resource species were left for our comparison between the NWHI vs MHI (Figure 2, Table S2). Of these species, 23% had biomass densities in the MHI < 10% of the NWHI, 40% had biomass <25%, and 54% had less than 50% of the unfished biomass in the NWHI.

3.3 | Moku descriptions

In total, 37 of the 41 moku in the MHI had fish data that could be used for the analysis. These moku ranged in size from 2335 km^2 at Ka'u on Hawai'i Island, to 53 km^2 on the small island of Ni'ihau (Table 2, Figure 1b). One third of the moku have southern aspects, with 27% exposed to the north, 20% with windward eastern aspects, and 22% with leeward western aspects. Human population density averaged *c.* 32 625 people moku^{-1} or 834 people km^{-1} of shoreline, with an average of 3529 (± 3986) people km^{-1} of shoreline on O'ahu to just slightly more than 2 people km^{-1} on Ni'ihau, and no permanent residents on the island of Kaho'olawe.

Spatial dependence within and among moku was tested by examination of the sill and corresponding lag distance of the variogram (Figure S1). The distance corresponding to the variogram sill was estimated at 120.5 m between site coordinates for resource fish biomass. This small distance between spatially dependent survey points indicated that the fish assemblages were similar at the moku scale. This finding supports the use of moku-scale subdivisions of habitat because the closest distance between two points in adjacent moku was 129 m.

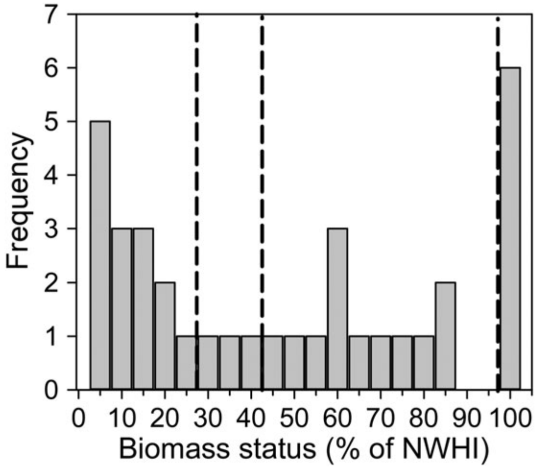

FIGURE 2 Biomass density of 35 resource fish species in the MHI compared with the NWHI as an unfished reference area. Vertical dashed lines delineate the 14 (40%), 3 (9%), and 12 (34%) of the 35 species for which respective biomass values were ≤25%, 25–40%, and 40–95% of the NWHI, respectively. Biomass ratios for individual species are presented in Table S2

3.4 | Resource fish biomass among moku

Within the MHI, mean moku resource fish biomass ranged from 5.8 g m^{-2} to 144.4 g m^{-2}, with the lowest biomass in moku around populated areas of O'ahu and Maui, and the highest biomass in more remote locations, such as the northern coastline of Moloka'i and uninhabited Kaho'olawe (Figure 3). Resource fish biomass was negatively and significantly related to human population density among moku ($\chi^2_{1,33} = 10.29$; $P = <0.01$; $R^2 = 0.64$, Figure 4), while non-resource fish biomass showed no correlation with human population density ($\chi^2_{1,33} = 0.29$; $P = 0.59$; $R^2 = 0.01$). An additional random effect of year resulted in a greater AIC (likelihood ratio test, $P = 0.01$), thus supporting the exclusion of a year effect. In addition, no effect of year was found when modelled independently against resource fish biomass (Gamma GLMM, $P = 0.51$), suggesting that little change in patterns of overall biomass occurred over the study period.

Using the NWHI as an unfished reference, only six (16.2%) of the moku in the MHI had resource fish biomass >25% of unfished biomass and only two (5.4%) had resource fish biomass >40% of that found within the NWHI. However, using the uninhabited island of Kaho'olawe as an unfished reference revealed that 27 of the 37 moku (73%) would be above the 25% threshold, while 20 (54.0%) would be above 40%. If sharks and jacks were excluded from these calculations, 20 (54.0%) of the moku in the MHI had resource fish biomass >25% of that found in the NWHI and eight (21.6%) had resource fish biomass >40% of that found within the NWHI. The values for Kaho'olawe stayed the same since there was only a 4.6% difference in total biomass vs biomass without sharks and jacks at this island.

3.5 | Influence of physical and human factors

In the GLMM of resource fish biomass and environmental and habitat variables among moku, all variables in the model were significant (Table 3). Resource fish biomass was negatively correlated with human population density, chlorophyll-*a*, and SST, and positively related to coral cover. No interactions among these variables were significant.

Ordination of fish trophic biomass showed a strong gradient along RDA axis 1, with islands having low human populations well separated in ordination space from the more heavily populated islands (Figure 5). The first two axes of the RDA biplot explained 67% of the trophic group variance and 92% of the trophic groups and bio-physical-human relationship (Table 4). The main factor influencing this ordination was the island of Kaho'olawe, which explained 15.3% of variation in the fish trophic structure and physical-human matrix. This was followed by human population density per moku, which explained an additional 14.4% of the variation. The heavily populated island of O'ahu accounted for an additional 13.3% of the variation in trophic structure, followed by the island of Maui (8.3%), and SST (6.6%).

Trophic biomass was highly variable among moku and islands (Figure 6). Herbivores accounted for 56.2% of total resource biomass, with the islands of Moloka'i, Kaho'olawe, Lānai, and Ni'ihau all having herbivore biomass >40 g m^{-2}, while herbivore biomass averaged only 9.4 g m^{-2} on O'ahu. Biomass of top predators was highest on Kaho'olawe, where it accounted for 23.0% of the total resource biomass, and lowest on O'ahu, were top predator biomass was nearly

TABLE 2 Geographic and demographic attributes by island, averaged by district (moku). N = number of moku by island. Values are means with standard deviations in parentheses. * several moku within these islands were combined owing to confidentiality concerns or excluded because of low sample size

Island	N	Area (km^2)	Shoreline (km)	Human population	People km^{-1}
Hawai‘i	6	1745.7 (591.1)	81.3 (24.1)	30,422.5 (19,905.4)	374.0
Kaho‘olawe	2	58.0 (7.1)	26.5 (0.7)	0	0
Kaua‘i	5	239.7 (172.0)	27.5 (10.6)	10,864.3 (13,432.3)	395.1
Lana‘i	2	183.0 (9.9)	39.0 (1.4)	1,410.0 (1989.8)	36.2
Maui	9*	145.5 (62.6)	17.8 (5.8)	10,947.0 (15,365.4)	616.1
Moloka‘i	5	135.8 (34.9)	31.2 (13.7)	1,427.0 (1,553.4)	45.7
Ni‘ihau	2*	61.7 (46.8)	24.7 (12.6)	56.0 (41.2)	2.3
O‘ahu	6	258.3 (118.0)	47.5 (25.0)	156,244.8 (147,819.5)	3,289.4
Grand means		388.4 (598.0)	35.6 (25.2)	31,107.5 (73,627.3)	874.3

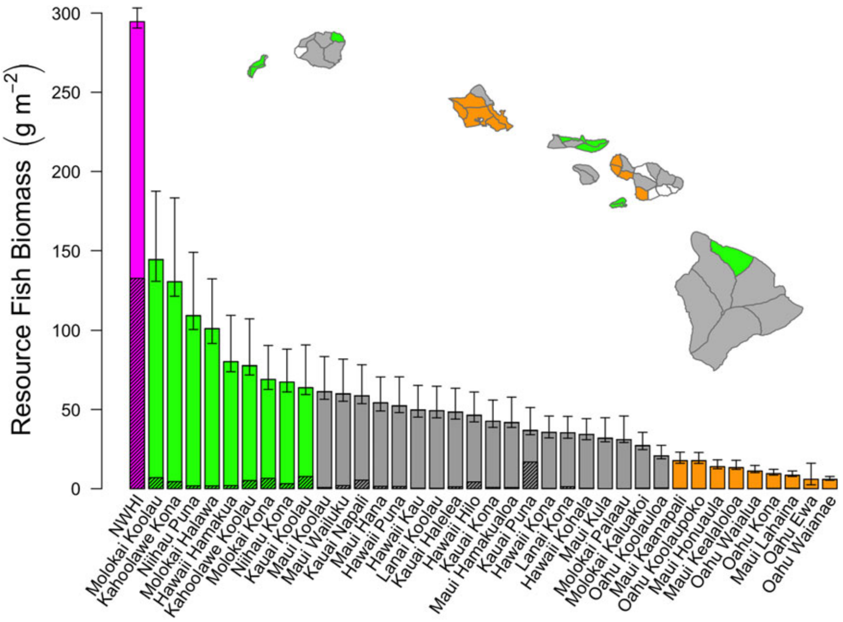

FIGURE 3 Resource fish biomass (g m^{-2}) for each moku in the MHI compared with NWHI, ordered by resource fish biomass. Colours represent the lower (orange), and upper (green) quantiles of resource fish biomass in the MHI. Error bars are 95% confidence intervals based on gamma GLMM. Cross-hatched areas represent proportion of biomass comprising reef sharks and jacks. Inset is a map of moku coloured according to lower (orange), and upper (green) quantiles of resource fish biomass; data from moku coloured in white moku were insufficient for estimating biomass

35 times lower than at Kaho‘olawe. Planktivore biomass was low overall, only accounting for 7.4% of total resource biomass, with the exception of Kaho‘olawe where this trophic group accounted for 18.8% of total resource biomass.

4 | DISCUSSION

The findings from this study highlight the negative impacts of human population pressure on reef fishes in Hawai‘i, which are particularly evident around the densely populated islands of O‘ahu and Maui. Large differences in resource fish biomass were observed between the MHI and NWHI, with the greatest differences observed for top predators, which are among the major targeted resource species in the MHI. These findings are similar to those found in previous studies (Friedlander & DeMartini, 2002; Williams et al., 2010, 2015) at different spatial scales and reinforce the dramatic differences in biomass and trophic structure between these regions. Results of the GLMM showed region had the most influence on resource fish biomass, although chlorophyll-*a* and coral cover also contributed significantly. After accounting for the influence of chlorophyll-*a* and coral cover, resource fish biomass in the NWHI was still > 3 times higher than in the MHI. Although habitats differ between the NWHI and MHI, greater nutrient input and the presence of estuaries in the windward and vegetated MHI should result in a more, not less, productive ecosystem compared with the smaller low islands and atolls of the NWHI (Friedlander & DeMartini, 2002). The NWHI is a large-scale, intact, predator-dominated ecosystem that represents an important baseline for comparisons with the heavily fished MHI. In other parts of the Indo-Pacific, remote wilderness areas have been shown to support ecosystems that are distinctly different even from those in large and well-managed marine reserves (Cinner et al., 2016; D'agata et al., 2016; Graham & McClanahan, 2013).

Scientific management advice is lacking for most tropical marine fisheries because of the exacting data requirements and many assumptions of conventional stock assessment models. Comparisons of biomass abundance for 35 species within the MHI and unfished NWHI were conducted. Examination of major targeted resource species revealed that of the 35 species examined, 40% had biomass in the MHI below 25% of the NWHI level, suggesting that biomass of many MHI resource species are below levels that are generally considered sustainable (Hilborn, 2011; Worm et al., 2009). In total, ~ 54% of the species examined had biomass <50% of the NWHI biomass. A recent length-based assessment of reef fishes in the MHI found similar

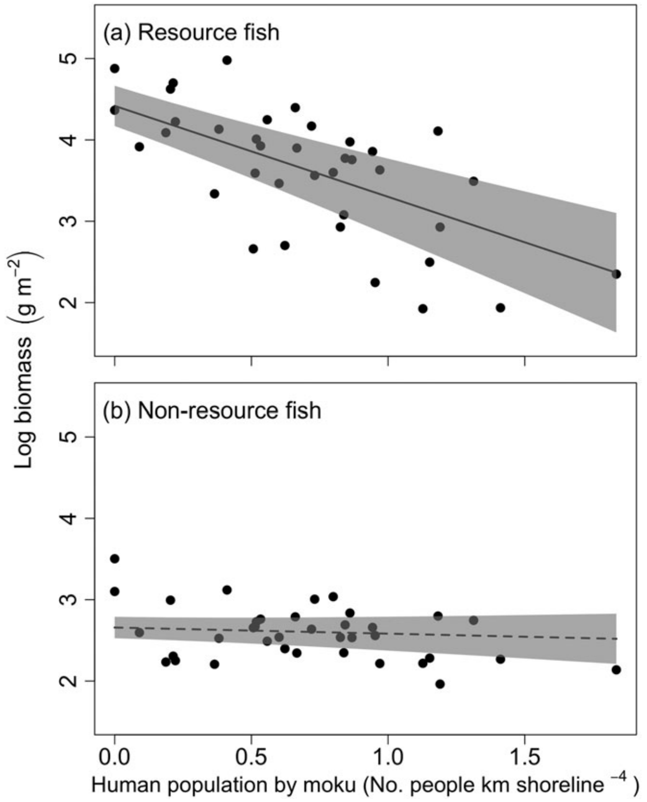

FIGURE 4 Relationship between scaled human population density and (a) resource fish biomass (y = 4.42 + −1.12×, $X^2_{1,33}$ = 10.29; P = <0.01; R^2 = 0.64) and (b) non-resource biomass (y = 2.66 + −0.08×, $X^2_{1,33}$ = 0.29; P = 0.59; R^2 = 0.01). Lines are predicted fits from a general linear mixed model with island as a random effect where grey bars are 95% confidence intervals. Biomass is ln(x + 1) transformed and human population density is 4th root transformed

TABLE 3 Results of generalized linear mixed-effects model of resource fish biomass and environmental and habitat variables among moku within the MHI. χ^2 and P values are from likelihood ratio tests. Explanatory variables were centred and scaled before analysis. SST – Long-term mean sea surface temperature (°C), Chl *a* – Long-term mean chlorophyll a. No interactions were significant

	Beta	Std error	χ^2	p-value
Intercept	4.952	0.252		
SST	−1.655	0.230	51.872	<0.001
Chl *a*	−0.703	0.181	15.025	<0.001
Coral cover	0.938	0.160	34.575	<0.001
Human pop. Density	−0.901	0.289	9.750	<0.001

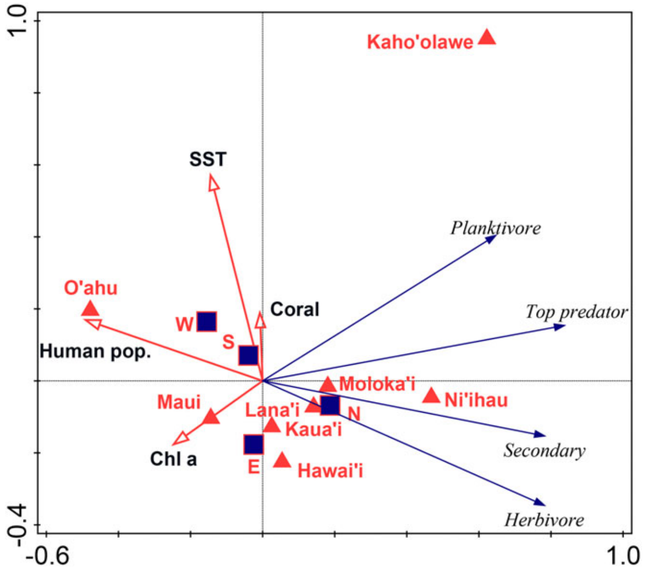

FIGURE 5 Biplot of results of redundancy analysis on fish biomass of trophic groups with physical-human variables (island, aspect [e.g., north, south, east, west], and scaled human population density by moku)

TABLE 4 (a) Results of redundancy analysis (RDA) on log-transformed fish biomass data for trophic groups with physical–human variables (island, aspect [north, south, east, west], and scaled human population density by moku). TG = trophic groups. (b) conditional effects of Monte-Carlo permutation results on the RDA. Is. = island, asp. = aspect, scaled human population = scaled human population density by moku

(A) axes	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.58	0.08	0.04	0.02
TG & physical-human correlations	0.90	0.72	0.70	0.63
Cumulative percentage variance				
Of trophic biomass &	58.52	66.76	70.30	72.40
Physical–human relation	80.83	92.22	97.11	100.00

(B) variable	Pseudo-F	P	% variance explained
Is.Kahoʻolawe	7.4	0.002	15.3
Human pop.	5.9	0.004	14.4
Is.Oʻahu	7.5	0.004	13.3
Is.Maui	5.4	0.010	8.3
SST	4.8	0.010	6.6

results, with nine of the 17 native species examined having spawning potential ratios close to or below the 30% recruitment overfishing threshold (Nadon, Ault, Williams, Smith, & DiNardo, 2015).

The concept of B_{MMSY} is the biomass that allows for maximum sustainable yield (MSY) from the entire community (Hilborn, 2010). For coral reef fishes, there is insufficient empirical information to establish a single reference point, therefore a broad range of yield estimates are warranted, particularly given the high uncertainty in these populations and the growing consensus that the exploitation rates that achieve MSY should be reinterpreted as an upper limit rather than as management targets (Worm et al., 2009). A range of biomass-based multispecies MSYs (B_{MMSY} ~ 0.25–0.50 of B_0) were established for targeted fish biomass in the western Indian Ocean (McClanahan et al., 2011). Using the NWHI as an unfished reference revealed that 84% of the moku would be below the 25% threshold, and 48% would be below this threshold if sharks and jacks are excluded from the calculation. Using Kahoʻolawe as an unfished reference would result in 27% of the moku being below this threshold. Regardless of whether the NWHI or Kahoʻolawe is used as a reference area, none of the moku on Oʻahu (n = 6), the most populated island, have resource fish biomass above the 25% threshold. Of the nine moku on Maui, none are above the NWHI 25% threshold and five are above this threshold using Kahoʻolawe as a reference area.

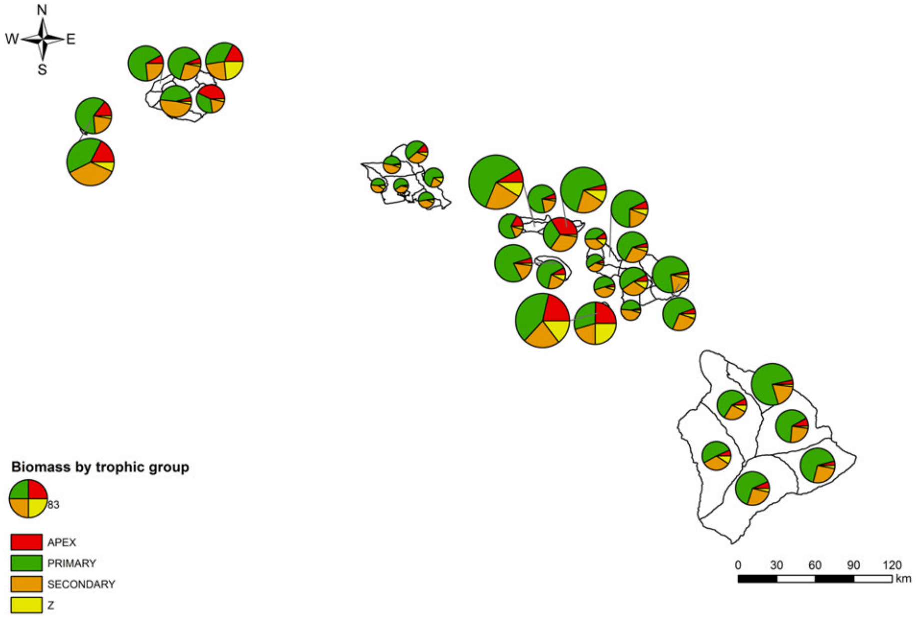

FIGURE 6 Trophic biomass by moku. Pie sizes are proportional to total biomass for each moku

For 50 years, the island of Kahoʻolawe functioned as a de facto natural no-take reserve where public access was restricted while the island served as a military bombing range until 1990. Since 1993, the Kahoʻolawe Island Reserve Commission (KIRC) has managed the island allowing subsistence fishing and marine gathering only by participants in cultural activities organized by a stewardship organization for consumption and offerings restricted to visits to the island (Friedlander et al., 2013). This modest take allows this large island to function as a no-take reserve. Kahoʻolawe had the highest resource biomass among all islands in the MHI and represents the largest no-take coral reef reserve in the MHI (42.25 km^2). However, remoteness and limited enforcement has resulted in a moderate level of poaching (KIRC, unpublished data) and the biomass observed therefore does not represent truly unfished biomass. In addition, Kahoʻolawe is too small an area to fully protect many species of roving predators such as reef sharks and jacks (Lowe, Wetherbee, & Meyer, 2006; Wetherbee, Holland, Meyer, & Lowe, 2004).

Within the MHI, a number of moku were found to have high biomass relative to the unfished NWHI that were comparable with that of the uninhabited island of Kahoʻolawe. These remote areas may provide natural refugia that help sustain fish stocks and therefore are likely important conservation hotspots. No correlation between human population density and non-resource fish biomass was found, which strongly suggests that fishing, rather than other anthropogenic influences (e.g. pollution, habitat degradation) or intrinsic differences in local productivity or habitat quality is probably primarily responsible for the observed differences in fish biomass among moku. Top predators account for a small proportion of total fish biomass in the MHI, and this may account for the lack of a significant release effect on non-resource prey.

Ordination of fish trophic biomass by moku showed large separations between islands with low human populations and the more heavily populated islands of Oʻahu and Maui. Top predators, which are the most heavily targeted trophic group by fishers, were most abundant around the unpopulated island of Kahoʻolawe and the sparsely populated island of Niʻihau. Moku with northerly and easterly aspects harboured higher resource fish biomass, likely owing to rougher sea conditions, which limits fishing effort during much of the year. In addition to human population density, SST and chlorophyll-α also had negative influences on resource fish biomass, while coral cover was positively related with this variable. These factors have been shown to be important drivers of resource fish biomass throughout the Pacific (Williams et al., 2015). At finer scales, structural complexity and reef zone have been shown to be important drivers of fish reef assemblage structure in Hawai'i and throughout the Indo-Pacific (Darling et al., 2017; Friedlander & Parrish, 1998; Graham & Nash, 2013), and these need to be considered when assessing and managing such resources at these scales.

Spatial variation in fish assemblages is evident throughout the archipelago and has been previously shown to correlate with human population pressure (Friedlander, Brown, Jokiel, Smith, & Rodgers, 2003; Williams et al., 2008). The status and structure of fish assemblages across a human impact gradient is extended by comparing metrics based on customary Hawaiian management boundaries (moku). Moku roughly correspond to bio-physical attributes of island ecosystems and represent a spatial scale that is relevant to humans, thus providing ideal units for examining patterns and managing marine resources. This builds on evidence from a number of locations around the world that are integrating traditional ecological knowledge and customary management practices into contemporary marine management (Aswani & Hamilton, 2004; Cinner et al., 2009; Johannes, 2002; Jokiel, Rodgers, Walsh, Polhemus, & Wilhelm, 2011; Olsson, Folke, & Berkes, 2004).

Our findings also reinforce a growing belief that smaller-than-regional scale factors importantly influence the demographics and abundances of coral reef fishes (D'agata et al., 2016; MacNeil & Connolly, 2015; Pinca et al., 2012; Williams et al., 2015). These local factors are both environmental and anthropogenic and include differences in habitat quality, benthic or planktonic productivity, the direct or indirect effects of fishing and other imposed stressors like pollution or sedimentation, or combinations thereof (DeMartini & Smith, 2015; Taylor, Lindfield, & Choat, 2015; Williams et al., 2015). These local influences can translate to spatial differences in growth rates and maturation schedules of reef fishery resources (Donovan, Friedlander, DeMartini, Donahue, & Williams, 2013; Gust, 2004; Taylor et al., 2015). Western scientific management guidelines and customary management practices thus converge on the need for management at the local scale.

Friedlander et al. (2003, 2013) have shown that in Hawai'i, community-based resource management areas can harbour fish biomass that is equal to or greater than that in no-take reserves. Adaptive community-based resource management has the potential for improving fisheries management and ecosystem health in Hawai'i through the development of proper fishing practices and traditional stewardship (Jupiter, Cohen, Weeks, Tawake, & Govan, 2014; Tissot, Walsh, & Hallacher, 2004). Local-scale management represents a form of traditional management practices that is adapted to a contemporary governance structure. Management at a spatial scale compatible with the scale of these community managed areas would be consistent with bio-physical features that make them useful management units, and are easily understood and accepted by local communities. The current results may provide an impetus to better extend the renaissance of community-based fisheries management already seen elsewhere throughout the Indo-Pacific region (Cinner et al., 2009; Johannes, 2002; Jupiter et al., 2014). Many communities already use customary practices to adaptively restrict gears and spatial areas as ecological and social conditions require (Cinner, Marnane, McClanahan, & Almany, 2006; Johannes, 2002). Customary knowledge is currently used throughout the Indo-Pacific to inform proper harvest seasons and strategies and to identify no-take periods during critical times of development and reproduction (Friedlander, 2015; Johannes, 1980; Poepoe, Bartram, & Friedlander, 2007).

The results of this study strongly suggest that fishing intensity, as proxied by human population density, has greatly reduced reef fish biomass around the more populated areas of Hawai'i, but the results also show the likely positive influence that remote and inaccessible areas within the MHI have on resource fish biomass. No-take reserves have been shown to conserve reef fish assemblages in Hawai'i but most are too small and poorly enforced to be fully effective (Friedlander, Brown, & Monaco, 2007; Friedlander et al., 2014). The findings from this study demonstrate that the island of Kaho'olawe represents a scale at which no-take reserves might be more effective in Hawai'i.

In recognition of the importance of moku-scale management in the past, the State of Hawai'i has created a moku advisory committee to counsel the government on the integration of indigenous resource management practices into contemporary management practices (Hawaii State House Bill 2806). At the IUCN World Conservation Congress in September 2016, Governor Ige of Hawai'i announced an initiative to effectively manage 30% of Hawai'i's nearshore waters by 2030, and a working group tasked with helping to measure progress towards this goal has highlighted moku as a useful scale for this evaluation as it matches the ecological, social, and cultural aspects of Hawai'i. Based on the long history of knowledge and continued practice, future marine resource management in Hawai'i might benefit from operating at less-than statewide (and smaller than island-specific) levels, and by increasing the involvement of local communities within these smaller management units.

ACKNOWLEDGEMENTS

This work was funded under subcontract from The National Oceanic and Atmospheric Administration's Coral Reef Conservation Program to the Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources (#C30597). We thank the ~120 divers working for the various programmes and agencies that collected the data used in this study. Data sharing and collaboration among the various agencies (e.g. NOAA, DAR, UH) and programs (e.g. TNC Marine Program, NPS Inventory and Monitoring Program) were recognized as key components in enabling the method calibration and ultimate publication. Michael Lameier from the NOAA Fisheries Pacific Islands Regional Office and the Hawaii Coral Reef Working Group were big proponents of this project.

ORCID

Alan M. Friedlander http://orcid.org/0000-0003-4858-006X

REFERENCES

Aswani, S., & Hamilton, R. J. (2004). Integrating indigenous ecological knowledge and customary sea tenure with marine and social science for conservation of bumphead parrotfish (*Bolbometopon muricatum*) in the Roviana lagoon, Solomon Islands. *Environmental Conservation*, *31*, 69–83.

Bauer, L., Poti, M., Costa, B. M., Wagner, D., Parrish, F., Donovan, M., & Kinlan, B. (2016). Benthic habitats and corals. In B. M. Costa, & M. S. Kendall (Eds.), *Marine biogeographic assessment of the main Hawaiian Islands* (pp. 57–136). Silver Springs, MD: Bureau of Ocean Energy Management and National Oceanic and atmospheric administration. OCS study BOEM 2016-035 and NOAA technical memorandum NOS NCCOS 214.

Capitini, C. A., Tissot, B. N., Carroll, M. S., Walsh, W. J., & Peck, S. (2004). Competing perspectives in resource protection: The case of marine protected areas in west Hawai 'i. *Society and Natural Resources*, *17*, 763–778.

Cinner, J., Marnane, M., McClanahan, T., & Almany, G. (2006). Periodic closures as adaptive coral reef management in the indo-Pacific. *Ecology and Society*, *11*, 31.

Cinner, J. E., Huchery, C., MacNeil, M. A., Graham, N. A., McClanahan, T. R., Maina, J., … Allison, E. H. (2016). Bright spots among the world's coral reefs. *Nature*, *535*, 416–419.

Cinner, J. E., McClanahan, T. R., Daw, T. M., Graham, N. A., Maina, J., Wilson, S. K., & Hughes, T. P. (2009). Linking social and ecological systems to sustain coral reef fisheries. *Current Biology*, *19*, 206–212.

Cinner, J. E., McClanahan, T. R., MacNeil, M. A., Graham, N. A., Daw, T. M., Mukminin, A., … Campbell, S. J. (2012). Comanagement of coral reef social-ecological systems. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 5219–5222.

Cobb, J. N. (1901). *Commercial fisheries of the Hawaiian Islands*. Washington, DC: Government Printing Office. U.S. Fish Commission Report for 1901.

Colvocoresses, J., & Acosta, A. (2007). A large-scale field comparison of strip transect and stationary point count methods for conducting length-based underwater visual surveys of reef fish populations. *Fisheries Research*, *85*, 130–141.

Crawley, M. J. (2012). *The R book*. Chichester, UK: John Wiley & Sons.

D'agata, S., Mouillot, D., Wantiez, L., Friedlander, A. M., Kulbicki, M., & Vigliola, L. (2016). Marine reserves lag behind wilderness in the conservation of key functional roles. *Nature Communications*, *7*, 12000. https://doi.org/10.1038/ncomms12000

Darling, E. S., Graham, N. A., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*, 561–575.

DeMartini, E. E., Friedlander, A. M., Sandin, S. A., & Sala, E. (2008). Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series*, *365*, 199–215.

DeMartini, E. E., & Smith, J. E. (2015). Effects of fishing on the fishes and habitat of coral reefs. In C. Mora (Ed.), *The ecology of coral reef fishes* (pp. 135–144). Cambridge, UK: Cambridge University Press.

Donovan, M. K., Friedlander, A. M., DeMartini, E. E., Donahue, M. J., & Williams, I. D. (2013). Demographic patterns in the peacock grouper (*Cephalopholis argus*), an introduced Hawaiian reef fish. *Environmental Biology of Fishes*, *96*, 981–994.

Edgar, G. J., Barrett, N. S., & Morton, A. J. (2004). Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *Journal of Experimental Marine Biology and Ecology*, *308*, 269–290.

Fortin, M. J., & Dale, M. R. T. (2005). *Spatial analysis: A guide for ecologists*. Cambridge, UK: Cambridge University Press.

Friedlander, A. M. (2015). A perspective on the management of coral reef fisheries. In C. Mora (Ed.), *Ecology of fishes on coral reefs* (pp. 208–214). Cambridge, UK: Cambridge University Press.

Friedlander, A. M., Brown, E. K., Jokiel, P. L., Smith, W. R., & Rodgers, K. S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs*, *22*, 291–305.

Friedlander, A. M., Brown, E. K., & Monaco, M. E. (2007). Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. *Ecological Applications*, *17*, 715–730.

Friedlander, A. M., & DeMartini, E. E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. *Marine Ecology Progress Series*, *230*, 253–264.

Friedlander, A. M., & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, *224*, 1–30.

Friedlander, A. M., Shackeroff, J. M., & Kittinger, J. N. (2013). Customary marine resource knowledge and use in contemporary Hawai'i. *Pacific Science*, *67*, 441–460.

Friedlander, A. M., Stamoulis, K. A., Kittinger, J. N., Drazen, J., & Tissot, B. N. (2014). Understanding the scale of marine protection in Hawai'i: From community-based management to the remote northwestern Hawaiian Islands Marine National Monument. *Advances in Marine Biology*, *69*, 153–203.

Froese, R., & Pauly, D. (2009). FishBase. www.fishbase.org [accessed 9 Sep 2016].

Gonschor, L., & Beamer, K. (2014). Toward an inventory of ahupua'a in the Hawaiian kingdom: A survey of nineteenth- and early twentieth-century cartographic and archival records of the island of Hawai'i. *Hawaii Journal of History*, *48*, 53–87.

Gove, J. M., Williams, G. J., McManus, M. A., Heron, S. F., Sandin, S. A., Vetter, O. J., & Foley, D. G. (2013). Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. *PLoS ONE*, *8*, e61974.

Graham, N. A., & McClanahan, T. R. (2013). The last call for marine wilderness? *Bioscience*, *63*, 397–402.

Graham, N. A. J., & Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, *32*, 315–326.

Gust, N. (2004). Variation in the population biology of protogynous coral reef fishes over tens of kilometres. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*, 205–218.

Hilborn, R. (2010). Pretty good yield and exploited fishes. *Marine Policy*, *34*, 193–196.

Hilborn, R. (2011). Future directions in ecosystem based fisheries management: A personal perspective. *Fisheries Research*, *108*, 235–239.

Hilborn, R., Orensanz, J. M., & Parma, A. M. (2005). Institutions, incentives and the future of fisheries. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*, 47–57.

'I'I, J. P. (1959). *Fragments of Hawaiian history*. Honolulu, Hawaii: Bishop Museum Press.

Johannes, R. E. (1980). Using knowledge of the reproductive behavior of reef and lagoon fishes to improve fishing yields. In J. E. Bardach, J. J. Magnuson, R. C. May, & J. M. Reinhart (Eds.), *Fish behaviour and its use in the capture and culture of fishes* (pp. 247–270). Manila, Philippines: ICLARM conference proceedings no. 5.

Johannes, R. E. (2002). The renaissance of community-based marine resource management in Oceania. *Annual Review of Ecology and Systematics*, *33*, 317–340.

Jokiel, P. L., Rodgers, K. S., Walsh, W. J., Polhemus, D. A., & Wilhelm, T. A. (2011). Marine resource management in the Hawaiian archipelago: The traditional Hawaiian system in relation to the western approach. *Journal of Marine Biology*, *2011*, 151682.

Jupiter, S. D., Cohen, P. J., Weeks, R., Tawake, A., & Govan, H. (2014). Locally-managed marine areas: Multiple objectives and diverse strategies. *Pacific Conservation Biology*, *20*, 165–179.

Kahā'ulelio, D. (2006). In M. P. Nogelmeier (Ed.), *Ka 'oihana lawai'a: Hawaiian fishing traditions*. Translated by Mary Kawena Pūkui. Honolulu, Hawaii: Bishop Museum Press and Awaiaulu Press.

Kamakau, S. M. (1976). In D. B. Barrere (Ed.), *The works of the people of old: Na hana a ka po'e kahiko*. Translated by Mary Kawena Pūkui. Honolulu, Hawaii: Bishop museum press.

Kaneshiro, K. Y., Chinn, P., Duin, K. N., Hood, A. P., Maly, K., & Wilcox, B. A. (2005). Hawai'i's mountain-to-sea ecosystems: Social–ecological microcosms for sustainability science and practice. *EcoHealth*, *2*, 349–360.

Kirch, P. V. (1989). *The evolution of the Polynesian chiefdom*. Cambridge, UK: Cambridge University Press.

Kittinger, J. N., Dowling, A., Purves, A. R., Milne, N. A., & Olsson, P. (2010). Marine protected areas, multiple-agency management, and monumental surprise in the northwestern Hawaiian Islands. *Journal of Marine Biology*, *2011*, 241374.

Kittinger, J. N., Pandolfi, J. M., Blodgett, J. H., Hunt, T. L., Jiang, H., Maly, K., … Wilcox, B. A. (2011). Historical reconstruction reveals recovery in Hawaiian coral reefs. *PLoS ONE*, *6*, e25460.

Kuykendall, R. S. (1938). The Hawaiian Kingdom. In *Foundation and transformation* (Vol. I) (pp. 1778–1854). Honolulu, Hawaii: University of Hawaii Press.

Lowe, C. G., Wetherbee, B. M., & Meyer, C. G. (2006). Using acoustic telemetry monitoring techniques to quantify movement patterns and site fidelity of sharks and giant trevally around French frigate shoals and midway atoll. *Atoll Research Bulletin*, *543*, 281–303.

MacNeil, M. A., & Connolly, S. R. (2015). Multi-scale patterns and processes in reef fish abundance. In C. Mora (Ed.), *Ecology of fishes on coral reefs* (pp. 116–124). Cambridge, UK: Cambridge University Press.

MacNeil, M. A., Graham, N. A., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., … McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. *Nature*, *520*, 341–344.

Malo, D. (1951). *Hawaiian antiquities (Mo'olelo Hawai'i)*. Honolulu, Hawaii: Bernice P. Bishop Museum Press.

Maunder, M. N., & Punt, A. E. (2004). Standardizing catch and effort data: A review of recent approaches. *Fisheries Research*, *70*, 141–159.

McClanahan, T. R., Graham, N. A., MacNeil, M. A., Muthiga, N. A., Cinner, J. E., Bruggemann, J. H., & Wilson, S. K. (2011). Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 17230-17233.

McClanahan, T. R., Graham, N. A. J., Maina, J., Chabanet, P., Bruggemann, J. H., & Polunin, N. V. C. (2007). The influence of instantaneous variation on estimates of coral reef fish populations and communities. *Marine Ecology Progress Series*, *340*, 221–234.

McClenachan, L., & Kittinger, J. N. (2013). Multicentury trends and the sustainability of coral reef fisheries in Hawai ʻi and Florida. *Fish and Fisheries*, *14*, 239–255.

Nadon, M. O. (2014). Improving stock assessment capabilities for the coral reef fishes of Hawaii and the Pacific Region (PhD thesis). University of Miami, Coral Gables, Florida.

Nadon, M. O., Ault, J. S., Williams, I. D., Smith, S. G., & DiNardo, G. T. (2015). Length-based assessment of coral reef fish populations in the main and northwestern Hawaiian islands. *PLoS ONE*, *10*, e0133960.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.

Olsson, P., Folke, C., & Berkes, F. (2004). Adaptive comanagement for building resilience in social–ecological systems. *Environmental Management*, *34*, 75–90.

Pinca, S., Kronen, M., Magron, F., McArdle, B., Vigliola, L., Kulbicki, M., & Andréfouët, S. (2012). Relative importance of habitat and fishing in influencing reef fish communities across seventeen Pacific Island countries and territories. *Fish and Fisheries*, *13*, 361–379.

Poepoe, K., Bartram, B., & Friedlander, A. (2007). The use of traditional Hawaiian knowledge in the contemporary management of marine resources. In N. Haggan, B. Neis, & I. Baird (Eds.), *Fishers' knowledge in fisheries science and management* (pp. 117–141). Paris, France: UNESCO.

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y. M., Krueck, N. C., Aurellado, E., … Mumby, P. J. (2016). The ecological role of sharks on coral reefs. *Trends in Ecology & Evolution*, *31*, 395–407.

Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., … Pantos, O. (2008). Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE*, *3*, e1548.

Schug, D. M. (2001). Hawai'i's commercial fishing industry: 1820-1945. *Hawaii Journal of History*, *35*, 15–34.

Skaug, H. J., & Fournier, D. A. (2006). Automatic approximation of the marginal likelihood in non-gaussian hierarchical models. *Computational Statistics & Data Analysis*, *51*, 699–709.

Smith, M. K. (1993). An ecological perspective on inshore fisheries in the main Hawaiian islands. *Marine Fisheries Review*, *55*, 34–49.

Sokal, R. R., & Rohlf, F. J. (1981). *Biometry: The principles and practice of statistics in biological research* (2nd ed.). San Francisco, CA: WH Freeman.

Stevenson, T. C., & Tissot, B. N. (2013). Evaluating marine protected areas for managing marine resource conflict in Hawaii. *Marine Policy*, *39*, 215–223.

Taylor, B. M., Lindfield, S. J., & Choat, J. H. (2015). Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography*, *38*, 520–530.

ter Braak, C. (1994). Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience*, *1*, 127–140.

ter Braak, C. J. F., & Smilauer, P. (2012). *Canoco reference manual and user's guide: Software for ordination*. Ithaca, NY: Microcomputer Power.

ter Braak, C., & Verdonschot, P. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences*, *57*, 1–35.

Tissot, B. N., Walsh, W. J., & Hallacher, L. E. (2004). Evaluating effectiveness of a marine protected area network in west Hawai'i to increase productivity of an aquarium fishery. *Pacific Science*, *58*, 175–188.

Tissot, B. N., Walsh, W. J., & Hixon, M. A. (2009). Hawaiian islands marine ecosystem case study: Ecosystem-and community-based management in Hawaii. *Coastal Management*, *37*, 255–273.

Titcomb, M. (1972). *Native use of fish in Hawaii*. Honolulu, Hawaii: University of Hawaiʻl Press.

Toonen, R. J., Wilhelm, T. A., Maxwell, S. M., Wagner, D., Bowen, B. W., Sheppard, C. R., … Friedlander, A. M. (2013). One size does not fit all: The emerging frontier in large-scale marine conservation. *Marine Pollution Bulletin*, *77*, 7–10.

Ward-Paige, C., Flemming, J. M., & Lotze, H. K. (2010). Overestimating fish counts by non-instantaneous visual censuses: Consequences for population and community descriptions. *PLoS ONE*, *5*. e11722

Wetherbee, B. M., Holland, K. N., Meyer, C. G., & Lowe, C. G. (2004). Use of a marine reserve in Kaneohe Bay, Hawaii by the giant trevally, *Caranx ignobilis*. *Fisheries Research*, *67*, 253–263.

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015). Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS ONE*, *10*, e0120516.

Williams, I. D., Richards, B. L., Sandin, S. A., Baum, J. K., Schroeder, R. E., Nadon, M. O., … Brainard, R. E. (2010). Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western Pacific. *Journal of Marine Biology*, *2011*, 826234.

Williams, I. D., Walsh, W. J., Schroeder, R. E., Friedlander, A. M., Richards, B. L., & Stamoulis, K. A. (2008). Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation*, *35*, 261–272.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., … Jensen, O. P. (2009). Rebuilding global fisheries. *Science*, *325*, 578–585.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Science & Business Media.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Friedlander AM, Donovan MK, Stamoulis KA, et al. Human-induced gradients of reef fish declines in the Hawaiian archipelago viewed through the lens of traditional management boundaries. *Aquatic Conserv: Mar Freshw Ecosyst*. 2018;28:146–157. https://doi.org/10.1002/aqc.2832