



FEATURE ARTICLE

Fishing and environmental influences on estimates of unfished herbivorous fish biomass across the Hawaiian Archipelago

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ABSTRACT: A longstanding goal in coral reef ecology is to estimate the baseline states of ecological communities and the extent to which human activities have perturbed them. Often, baseline estimates rely upon observations from remote, uninhabited areas, highlighting dramatic differences in fish communities compared to populated areas. However, previous studies have focused on island- and archipelago-wide comparisons of reef communities that may mask finer-scale spatial variability. Here we describe spatial patterns of herbivorous fish biomass across fished and unfished regions of the Hawaiian Archipelago to evaluate whether accounting for environmental variability between these regions alters estimates of unfished biomass (B_{unfished}) and fisheries depletion. We found environmental factors were strongly associated with 4 measures of herbivorous fish community biomass (total, scraper, grazer, and browser), and failure to account for these influences on B_{unfished} resulted in different conclusions about herbivore depletion in Hawaii, USA. Overall, depletion estimates that controlled for environmental differences indicated that biomasses of the 4 herbivorous fish groups across much of Hawaii are near or above a commonly used sustainability reference point ($0.5 \times B_{\text{unfished}}$). However, scraper and browser biomass on Oahu, the island with the highest human population density, were near or below 15% of B_{unfished} , highlighting the potential importance of spatial and functional group variability when assessing fishing effects on coral reefs. These findings are of immediate use to resource managers in Hawaii and applicable to other reef systems where embracing spatial variability can aid in identification of conservation targets on coral reefs.



Unfished reefs in Hawaii can support large biomasses of herbivorous fishes, such as these surgeonfish at Kure Atoll, but environmental factors also have an important influence.

Photo: Jason Helyer

KEY WORDS: Coral reef · Baseline · Reference point · Unfished biomass

INTRODUCTION

A fundamental goal in coral reef ecology is to estimate the baseline states of ecological communities and the extent to which human activities have perturbed them. This question is all the more pressing in the face of global change. On coral reefs and in other systems subject to human exploitation, a critical component of defining baselines is accurate assessment

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of unfished biomass (B_{unfished}). B_{unfished} represents the expected biomass of a population or community that is not exploited (Hilborn & Walters 1992, Quinn & Deriso 1999). While there is strong evidence that environmental forcing can influence fish biomass in addition to fishing (Williams et al. 2015), the incorporation of environmental variability into estimates of unfished reference points and assessments of fisheries depletion have been limited (Haltuch et al. 2009, King et al. 2015). When studies have controlled for environmental influences on fish biomass, there were marked improvements in estimates of B_{unfished} (Williams et al. 2015) and detectability of fishing effects (Hamilton et al. 2010, Caselle et al. 2015). Thus, properly accounting for environmental variability may increase the accuracy of assessing fisheries resources.

The paucity of long-term catch and biomass data in coral reef fisheries has limited the application of traditional stock-assessment methods for estimating unfished reference points (Zeller et al. 2015). Instead, first-order approximations of B_{unfished} are typically generated from current biomass estimates at unfished locations such as remote, unpopulated areas or long established marine protected areas where the effects of fishing are minimal (McClanahan et al. 2007, Williams et al. 2011, Edwards et al. 2014, but see Ault et al. 2008, Nadon et al. 2015 for alternatives using length-based methods). Consequently, past studies of fishing effects on coral reef fishes have generally had 2 key ingredients for depletion estimates: (1) current estimates of fish biomass in populated, fished areas, and (2) current estimates of fish biomass in unpopulated areas or regions where fishing is prohibited. However, biomass at unfished locations may not be a reasonable proxy for unfished biomass at locations where fishing is currently nonzero, especially if environmental conditions vary between fished and unfished areas (Hamilton et al. 2010, Caselle et al. 2015). Thus, a third key ingredient for estimating depletion of fish biomass when implicit space-for-time substitutions are used to approximate B_{unfished} is a proper accounting of environmental factors that might differ between fished and unfished locations.

In this study we describe spatial patterns of herbivorous fish biomass across fished and unfished regions of the Hawaiian Archipelago to evaluate whether accounting for environmental variability between these regions alters estimates of B_{unfished} and fisheries depletion. We focus on herbivorous fishes because of their importance in maintaining the function and resilience of coral reef benthic communities and because they are a common target of subsistence and

recreational fishing (Mumby et al. 2007, Hughes et al. 2010). Across the Hawaiian Archipelago, substantial declines of herbivorous fish biomass have been reported along gradients of human population density (Williams et al. 2008), and biomass levels in fished locations have been estimated to be less than 35 % of biomass at unfished locations (Williams et al. 2011). These estimated differences in fish biomass, however, did not account for spatial variability in environmental factors known to influence fish biomass in Hawaii, USA, such as habitat complexity, depth, oceanographic conditions, and benthic composition (Friedlander & Parrish 1998, Friedlander et al. 2003, Friedlander et al. 2007). Here, we re-assess differences in herbivorous fish biomass between fished and unfished regions of the Hawaiian Archipelago with a novel data set and analytical approach to answer 2 questions: (1) How do environmental factors influence herbivorous fish biomass across the Hawaiian Archipelago? and (2) How does incorporating spatial variability of environmental conditions affect estimates of B_{unfished} and depletion in the Main Hawaiian Islands (MHI)?

MATERIALS AND METHODS

Study region

The Hawaiian Archipelago is comprised of 18 islands and atolls that span 2600 km in the central Pacific Ocean. The archipelago is broadly divided into the inhabited MHI and the sparsely inhabited Northwestern Hawaiian Islands (NWHI). The MHI have variable human populations ranging from the lightly populated island of Niihau (170 persons) to the heavily populated island of Oahu (953 207 persons, Table 1). Human populations in the NWHI are limited to small groups of workers at French Frigate Shoals and Midway Atoll and seasonal field camps at other reefs. Despite the geographic isolation of the NWHI, anthropogenic influences are present (Selkoe et al. 2008), though their magnitude is much less compared to the populated MHI. Over the past century, fishing effort in the NWHI, especially for reef fish, has been relatively low (Kittinger et al. 2011), and fishing has been prohibited in the region since 2000. In contrast, fisheries in the MHI have been exploited since AD 1250 with increasing pressure commensurate with a growing population during the last century (Kittinger et al. 2011). Coral reef fisheries in Hawaii exploit multiple species but especially herbivorous fishes such as parrotfishes and surgeon-

fishes (Friedlander & Parrish 1997). While there are multiple regulations governing the harvest of reef fish in Hawaii, such as size restrictions and spatial closures, the difficulty of monitoring fishing effort has resulted in inconsistent fisheries-dependent data, creating a need to explore fishery-independent data (Nadon et al. 2015).

Sampling framework and fish survey method

This study focused on forereef habitat at the 7 largest islands in the MHI and NWHI (Table 1). Between 2010 and 2013, fish and benthic surveys were conducted at 517 forereef sites with data being collected between August and November of each year (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m575p001_supp.pdf). Survey sites were randomly selected from shallower than 30 m, hard bottom habitat at each reef. At each site, divers surveyed fishes using a modified stationary point count (SPC) method (Williams et al. 2011). No surveys in

the MHI were conducted in areas closed to fishing. For the SPC, 2 divers conducted simultaneous counts in adjacent 15 m diameter cylinders extending from the substrate to the limits of vertical visibility. Each SPC consisted of 2 components: a 5 min species enumeration period, in which divers recorded all fish species present in 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 all fishes of each taxon on their list.

Response variables and biomass calculations

Site-level estimates of fish biomass per unit area were used as the core response variables in this study. Because feeding preferences of herbivorous reef fishes are diverse and functional differences have been linked to different aspects of benthic community composition in the Hawaiian Archipelago (Jouffray et al. 2015), we examined spatial biomass patterns of 3 herbivore feeding guilds (scrapers, grazers, and browsers^{§§}) in addition to the aggregate sum of herbivore biomass (Table S1 in Supplement 2 at www.int-res.com/articles/suppl/m575p001_supp.pdf). Scrapers included parrotfish in the *Scarus* and *Chlorurus* genera that feed on the surface of reef substrates providing areas clear of algae important for coral and crustose coralline algae settlement (Mumby 2006). Grazers limit the establishment of macroalgae by intensely feeding on algal turfs and included surgeonfish species from *Acanthurus*, *Ctenochaetus*, and *Zebrasoma* genera (Marshall & Mumby 2015). Browsers feed directly on macroalgae and included surgeonfish from the genus *Naso* and parrotfish from the genus *Calotomus* (Hoey & Bellwood 2010). Additionally, the 3 functional groups vary broadly in their susceptibility to fishing as scrapers and browsers tend to be larger and have lower natural mortality rates compared to grazers, while scrapers are one

Table 1. Study locations, number of surveys per island, and predictor variables. HUM: human population density; COMP: habitat complexity; FOOD: proportion of non-calcified substrate; DEPTH: depth (m); SSTL: lower climatological sea surface temperature (°C). Island means are given for site-level predictor variables (COMP, FOOD, DEPTH) and distributions are plotted in Fig. S4 in Supplement 5. Forereef area constitutes total area of <30 m hard-bottom habitat per island (excluding back-reef and lagoonal zones). These data come from NOAA GIS maps used for survey design and collated from a range of internal and external sources. Human population data per island comes from the 2010 US census (www.census.gov/2010census/). COMP was visually estimated by divers during fish surveys. FOOD was estimated from benthic photos taken at each site. Max DEPTH was recorded at each site. SSTL were obtained from Gove et al. (2013) and represent long-term (1985–2009) averages of oceanic surface waters surrounding islands. MHI: Main Hawaiian Islands; NWHI: Northwestern Hawaiian Islands

| Island | Forereef area (ha) | No. of surveys | HUM | COMP | FOOD | DEPTH | SSTL |
|----------------------|--------------------|----------------|-------|------|------|-------|-------|
| MHI | | | | | | | |
| Hawaii (HAW) | 16840 | 96 | 10.99 | 0.64 | 0.30 | 13.5 | 24.12 |
| Maui (MAI) | 11122 | 56 | 12.99 | 0.60 | 0.22 | 12.2 | 23.85 |
| Lanai (LAN) | 3004 | 35 | 1.03 | 0.55 | 0.20 | 10.7 | 24.10 |
| Molokai (MOL) | 12730 | 40 | 0.58 | 0.51 | 0.24 | 12.0 | 23.89 |
| Oahu (OAH) | 25119 | 44 | 37.95 | 0.33 | 0.15 | 12.9 | 23.87 |
| Niihau (NII) | 9266 | 37 | 0.02 | 0.46 | 0.06 | 14.1 | 23.65 |
| Kauai (KAU) | 18127 | 45 | 3.62 | 0.40 | 0.12 | 13.3 | 23.56 |
| NWHI | | | | | | | |
| French Frigate (FFS) | 8873 | 26 | 0 | 0.53 | 0.50 | 14.7 | 22.78 |
| Maro Reef (MAR) | 25607 | 21 | 0 | 0.62 | 0.57 | 12.6 | 21.73 |
| Laysan (LAY) | 3400 | 20 | 0 | 0.42 | 0.21 | 17.7 | 21.53 |
| Lisianski (LIS) | 30955 | 33 | 0 | 0.89 | 0.64 | 14.6 | 21.33 |
| Pearl & Hermes (PHR) | 8498 | 31 | 0 | 0.71 | 0.32 | 13.0 | 19.69 |
| Midway (MID) | 3294 | 17 | 0 | 0.65 | 0.18 | 15.1 | 19.31 |
| Kure (KUR) | 2438 | 16 | 0 | 0.70 | 0.27 | 13.7 | 18.98 |

^{§§}Throughout the manuscript, readers should consider any reference to 'scrapers' to imply 'scrapers and excavators' and any reference to 'grazers' to imply 'grazers and detritivores'

of the most targeted reef fish in Hawaii (Friedlander & Parrish 1997, Choat & Robertson 2002, Froese & Pauly 2013). Therefore, by analyzing herbivore functional group data separately and in summation, we were able to investigate whether depletion varied between herbivorous fish guilds across the MHI.

Mass of individual fishes was calculated using length to weight conversion parameters taken from published and web-based sources (Kulbicki et al. 2005, Froese & Pauly 2013). Prior to mass calculations, length–length conversions were made when appropriate. Because SPC replicates at each site were not independent and varied (either 2 or 4 reps per site), biomasses were summed by species for each SPC replicate and averaged by site. Site-level species biomasses were then pooled into the 4 response variables (total herbivore, scrapers, grazers, and browsers biomass), based on feeding information taken from FishBase (Froese & Pauly 2013).

Predictor variables

Many ecological and environmental factors have been shown to be associated with differences in reef fish biomass across Hawaii (Grigg 1994, Friedlander et al. 2003, Friedlander & Parrish 1998). The large spatial extent of our study limited our consideration of predictor variables to those for which data were available at a commensurate scale. Using the best available data, we considered 5 factors to explain herbivorous fish biomass across Hawaii: fishing pressure, sea surface temperature (SST), depth, habitat complexity, and food availability. While other factors such as sedimentation rates, wave exposure, and swell gradients are certainly relevant, the lack of high-resolution data precluded the investigation of these variables.

Site scale

We considered 3 site-level predictor variables (depth, habitat complexity, and food availability; Table 1) known to influence reef fish abundance (Friedlander & Parrish 1998, Friedlander et al. 2003). Information on each predictor was collected by divers during each fish survey. Depth (DEPTH) was recorded *in situ* directly from pressure gauges. Habitat complexity (COMP) was measured in 2 ways: In 2010 and 2011 (297 sites), divers estimated complexity on a 5-point scale (1 = very low, to 5 = very high). In 2012 and 2013, divers estimated the maximum ver-

tical relief within their SPC cylinder and the proportion of their cylinder in different relief bins (<0.2, 0.2–0.5, 0.5–1.0, 1.0–1.5, >1.5 m from substrate), and these data were used to generate a mean vertical relief value in each cylinder. In order to analyze fish biomass data associated with the 2 different complexity metrics, we used a data calibration published in Williams et al. (2015). Williams et al. (2015) collected both types of complexity data and generated an equation for predicting mean vertical relief from the 5-point habitat complexity scale. We used their linear regression formula to generate estimates of mean vertical relief at each site surveyed in 2010 and 2011.

The proportion of non-calcified substrate at each site was used as a simple proxy for food availability (FOOD) where high values of non-calcified substrate represented more grazeable substrate. To determine benthic composition, divers took photographs at 1 m intervals along the diameter of each SPC cylinder. Benthic photographs were taken with a Cannon camera attached to a 1 m monopod to ensure a fixed height above the seafloor (image area: roughly 0.15 m²; 0.45 m by 0.34 m). Photos were analyzed to estimate benthic cover by randomly projecting 15 points onto a 5 by 3 grid overlaid on each photo (450 points/site) and identifying the benthos under each point. Taxonomic resolution of benthic organisms varied but produced estimates of the proportion of non-calcified substrate at each site (turf algae and non-calcified fleshy macroalgae).

Island scale

The island-scale predictor variables we considered included both anthropogenic (fishing pressure) and environmental (SST) factors known to influence reef fish abundance (Table 1; Floeter et al. 2005, Williams et al. 2008). Because information on fishing pressure in the MHI is not available, human population density scaled by reef area (HUM) was used as a proxy (Williams et al. 2008, Table 1). Human population data came from the 2010 US census (www.census.gov/2010census). Following Gove et al. (2013), we quantified temperature using the lower climatological mean sea surface temperature (SSTL) at each island. Water temperatures vary seasonally; therefore, SSTL is a good representation of the absolute thermal gradient across the Hawaiian Archipelago. SSTL estimates were calculated from remotely sensed data collected between 1985 and 2009 (Gove et al. 2013).

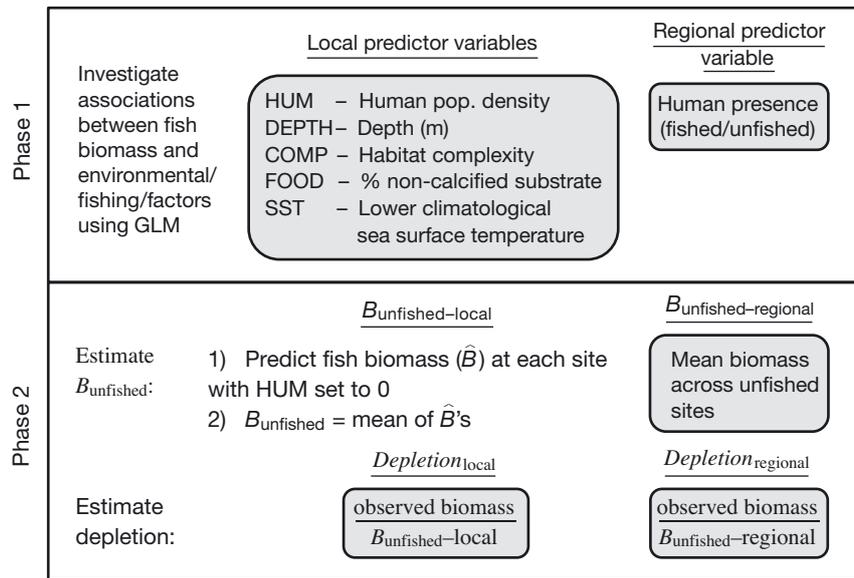


Fig. 1. Conceptual diagram of data analysis

Data analysis

Data analysis proceeded in 2 phases (Fig. 1). In the first phase, we described associations of fishing and local environmental factors with herbivorous fish community biomass. We generated hypotheses for explaining spatial patterns of herbivorous fish biomass from site- and island-scale predictor variables and evaluated the support for each hypothesis using generalized linear models (GLMs). In the second phase, we used model results to estimate B_{unfished} at each island, $B_{\text{unfished-local}}$. Our approach for estimating B_{unfished} is similar to Williams et al. (2015) but differs in 2 main regards. First, we used GLMs rather than generalized additive models (GAMs) because there was no evidence that the relationships we examined required higher-order polynomial models to describe them. Second, we used site-level fish biomass as a response variable rather than island-averages of biomass. This second point is important because a main objective of this study was to describe site-level differences in herbivorous fish biomass and to examine the influence of both within- and across-island variability on estimates of B_{unfished} . Additionally, we estimated an alternative measure of unfished biomass, $B_{\text{unfished-regional}}$. $B_{\text{unfished-regional}}$ was calculated as the mean of fish biomass observations across the unfished NWHI. Thus, $B_{\text{unfished-regional}}$ represented the standard approach used in previous studies for estimating B_{unfished} without accounting for environmental variability (McClanahan et al. 2011, Williams et al. 2011, Edwards et al. 2014, Karr et al. 2015). We then

calculated depletion, the ratio between observed fish biomass at fished locations to B_{unfished} , using both estimates of B_{unfished} and compared how depletion estimates vary when environmental differences are ($B_{\text{unfished-local}}$) and are not ($B_{\text{unfished-regional}}$) controlled for.

Environmental and human associations with herbivore biomass

We generated 11 hypotheses (candidate models) for assessing spatial patterns of herbivorous fish biomass from site- and island-scale predictor variables (Table 2). All hypotheses included human population density and habitat complexity because both fishing and habitat have been shown to influence fish biomass across a wide range of studies (fishing: Newman et al. 2006, Sandin et al. 2008, Williams et al. 2011; habitat: Hixon & Brostoff 1985, Hixon & Beets 1989, Hixon & Beets 1993, Friedlander & Parrish 1998). We included a habitat complexity and food availability interaction based on evidence that the effect of habitat complexity on herbivorous fish biomass can depend on food availability (Mumby et al. 2013). We limited models to 5 terms to prevent overfitting the data and included all combinations of depth, SSTL, food availability, and the habitat complexity–food availability interaction (11 candidate models; Table 2).

We used mixed-effects GLMs to evaluate support for these 11 candidate models of potential influences on site-level herbivorous fish biomass. Human popu-

Table 2. List of 11 candidate sets of fixed-effects used to quantify patterns of fish biomass. All models included a random ISLAND term to account for non-independence of sites within islands. Details on predictor variables are given in Table 1. *K*: number of fixed-effect parameters

| Model | Inferred process | Fixed-effect terms | <i>K</i> |
|-------|--|---------------------------------------|----------|
| M1 | Habitat and fishing | COMP + HUM | 2 |
| M2 | Habitat, temperature, and fishing | COMP + SSTL + HUM | 3 |
| M3 | Habitat, depth, and fishing | COMP + DEPTH + HUM | 3 |
| M4 | Habitat, food availability, and fishing | COMP + FOOD + HUM | 3 |
| M5 | Habitat, food availability, and fishing (interaction) | COMP + FOOD + COMP:FOOD + HUM | 4 |
| M6 | Habitat, temperature, depth, and fishing | COMP + SSTL + DEPTH + HUM | 4 |
| M7 | Habitat, temperature, food availability, and fishing | COMP + SSTL + FOOD + HUM | 4 |
| M8 | Habitat, depth, food availability, and fishing | COMP + DEPTH + FOOD + HUM | 4 |
| M9 | Habitat, temperature, food availability, and fishing (interaction) | COMP + SSTL + FOOD + COMP:FOOD + HUM | 5 |
| M10 | Habitat, depth, food availability, and fishing (interaction) | COMP + DEPTH + FOOD + COMP:FOOD + HUM | 5 |
| M11 | Habitat, temperature, depth, food availability, and fishing | COMP + SSTL + DEPTH + FOOD + HUM | 5 |

lation density, depth, SSTL, and food availability were included as fixed-effects and the nominal variable island was included as a random-effect to account for the non-independence of sites within each island (Table 2).

Exploratory analysis of biomass data indicated scraper and browser categories had an abundance of zeroes (25.5 and 35.4%, respectively). To accommodate this statistical issue, we used a 2-stage modeling approach commonly referred to as delta- (Stefánsson 1996) or hurdle- models (Zuur et al. 2007). In the first stage, we modeled occurrence (presence/absence) using a binomial distribution with the probability of fish occurrence linked to predictor variables via a logit function. In the second stage, we used a Gamma distribution with a log link to model fish biomass conditional on presence as these data were positively skewed. Only the gamma model was needed to analyze total herbivore and grazer categories as all biomass observations were positive in these groups. The independent nature of the binomial and gamma models allows different sets of predictor variables to be investigated. We evaluated all possible combinations of the 5 predictor variables for occurrence (binomial) models including models that did not include human population density as a predictor variable. Thus, candidate occurrence models differed from the 11 candidate conditional biomass (gamma) models which all included human population density. While the negative association of human density with reef fish biomass has been documented across many systems (Newman et al. 2006, 2007, Williams et al. 2011), the relationship between herbivorous fish presence and humans is less clear.

We used Akaike information criterion corrected for small sample sizes (AICc) for model selection and predictions (Burnham & Anderson 2002). We evalu-

ated the relative levels of support for each hypothesis separately for both occurrence and conditional biomass models using AICc. We used model averaging to make biomass predictions. First, we calculated AICc-based relative-importance weights (w_i) that indicated the level of support for each model, given the other models considered and the data. We interpreted models with $w_i > 5\%$ as being 'top models' supported by the data and used these for model averaging for occurrence and conditional biomass predictions.

To describe associations between herbivorous fish biomass and predictor variables, we report effect sizes, estimated as the percent change in model-averaged predictions across the range of predictor variables. For each variable of interest, we predicted fish biomass across the range of that variable's minimum and maximum value, while setting all other predictor variables to their means. Because we were interested in describing the influence of environmental factors on fish biomass without the confounding influence of fishing, human population density was set to 0 for all predictions. In the 'Results' section, we report strong associations as those with a 50% or greater change in the response variable across the range of the predictor variable.

We assessed model assumptions through visual inspection of residuals. To determine if spatial autocorrelation influenced model fits, we tested for a relationship between the Pearson residuals of the models vs. latitude and longitude (non-significant in all cases). We evaluated predictive performance of the models with leave-one-out cross-validation (LOOCV) (Stone 1974). LOOCV involves withholding a single observation from the data set as a validation point and subsequently uses the remaining observations to fit a model and predict a value for the valida-

tion point. LOOCV is repeated until each observation in the data set has been validated. To evaluate the accuracy of predictions for the validation data set, we quantified mean absolute percentage error (MAPE):

$$\text{MAPE} = \frac{1}{n} \sum_{i=1}^n \left| \frac{p_i - o_i}{o_i} \right| \quad (1)$$

where n is the number of validation points, p_i is the predicted value at point i , and o_i is the observed value at point i . Small MAPE values indicate better predictive performance.

Prior to analyses, human population density was square root transformed, the proportion of uncalcified substrate was logit transformed, and collinearity among predictor variables was examined using Pearson correlations and variance inflation factors (VIFs). Collinearity was not problematic as the 2 highest correlation coefficients were between human population density and SSTL ($r = 0.58$), and structural complexity and calcified substrate ($r = 0.38$), and the highest VIF for any of the model combinations examined was low (max. = 1.24). All models were fit in R (R Development Core Team 2015) using the lme4 package (Bates et al. 2015). LOOCV was coded in R by the authors.

Estimates of unfished biomass and herbivore depletion

We estimated unfished biomass for each of the 4 herbivorous fish biomass categories using 2 methods (Fig. 1). The first method accounted for within- and across- island differences in environmental factors and their influence on unfished biomass, producing an estimate of $B_{\text{unfished-local}}$. We calculated $B_{\text{unfished-local}}$ at each island and across the MHI from model-averaged predictions of herbivorous fish biomass. First, occurrence and conditional biomass were predicted at each site based on site-specific environmental covariates with human population density set to 0. Site-level biomass predictions were then calculated as the product of occurrence probabilities and predicted conditional biomasses. Next, site-level biomass predictions were averaged by island or across the MHI to incorporate local variability of environmental conditions into predictions of $B_{\text{unfished-local}}$.

The second method for estimating unfished biomass used mean observed biomasses across the unfished NWHI as an alternative reference point, $B_{\text{unfished-regional}}$. This approach is similar to previous

studies that did not account for environmental influences on estimates of B_{unfished} . Because fishing is prohibited in the NWHI, estimates of B_{unfished} should, theoretically, closely match observed biomass levels. Therefore, we examined how well island predictions of $B_{\text{unfished-local}}$ and estimates of $B_{\text{unfished-regional}}$ matched mean observed biomass at each island in the NWHI as a coarse approximation of model fit (see Supplement 3 at www.int-res.com/articles/suppl/m575p001_supp.pdf).

We defined depletion (D) as the ratio between observed fish biomass at fished locations to expected unfished biomass ($B_{\text{fished}}:B_{\text{unfished}}$; Fig. 1). We calculated depletion at each island, as well as across the MHI, using both $B_{\text{unfished-local}}$ ($D_{\text{unfished-local}}$) and $B_{\text{unfished-regional}}$ ($D_{\text{unfished-regional}}$). Uncertainties in observed mean biomasses, $B_{\text{unfished-local}}$, and depletion were estimated with nonparametric bootstrapping. Data were resampled with replacement 10 000 times. For each bootstrapped sample, mean biomass was recalculated for each island and the NWHI region ($B_{\text{unfished-regional}}$), weighted model averages were used to predict $B_{\text{unfished-local}}$, and depletion was calculated for each island (and MHI) using both $B_{\text{unfished-local}}$ and $B_{\text{unfished-regional}}$. Uncertainties were then calculated from bootstrapped samples using bias-corrected 90th percentile confidence intervals. Note that when observed mean biomass is greater than B_{unfished} , the depletion value will be greater than 1 (see 'Discussion')

To examine potential differences in herbivore depletion estimates when environmental influences on unfished biomass were ($B_{\text{unfished-local}}$) and were not accounted for ($B_{\text{unfished-regional}}$), we calculated relative differences between depletion estimates based on each of the 2 measures of B_{unfished} . Positive differences indicate underestimation of depletion by $B_{\text{unfished-regional}}$, while negative differences indicate overestimation of depletion by $B_{\text{unfished-regional}}$. To assess any statistical significance in depletion estimates, we computed relative depletion differences for each of the 4 herbivorous fish categories on each bootstrapped sample. Significant differences were determined to exist when bias-corrected 90th percentile confidence intervals did not overlap 0.

RESULTS

Occurrence and conditional biomass models indicated acceptable model fit for observational, site-level, coral reef data (Table 3 & Supplement 4 at www.int-res.com/articles/suppl/m575p001_supp.pdf).

Table 3. Model selection results for conditional biomass of the 4 herbivore categories. All models with Akaike information criterion corrected for small sample sizes (AICc) weights > 0.05 are shown. Details on predictor variables are given in Table 1. Details on models are given in Table 2. w_i : AICc relative-importance weight; MAPE: mean absolute percentage error

| Model | Fixed-effect terms | | | | | | Model support & validation | | | |
|-------------------|--------------------|-----|-------|------|-----------|-----|----------------------------|-------|------------|------|
| | COMP | SST | DEPTH | FOOD | COMP:FOOD | HUM | ΔAIC_c | w_i | Adj. R^2 | MAPE |
| Herbivores | | | | | | | | | | |
| M5 | X | | | X | X | X | 0.0 | 0.52 | 0.194 | 30.7 |
| M10 | X | | X | X | X | X | 1.2 | 0.27 | 0.195 | |
| M9 | X | X | | X | X | X | 2.1 | 0.19 | 0.194 | |
| Scrapers | | | | | | | | | | |
| M8 | X | | X | X | | X | 0.0 | 0.80 | 0.277 | 15.5 |
| M4 | X | | | X | | X | 4.1 | 0.11 | 0.265 | |
| M3 | X | | X | | | X | 4.4 | 0.09 | 0.264 | |
| Grazers | | | | | | | | | | |
| M9 | X | X | | X | X | X | 0.0 | 0.77 | 0.109 | 18.9 |
| M5 | X | | | X | X | X | 3.6 | 0.12 | 0.099 | |
| M2 | X | X | | | | X | 5.5 | 0.05 | 0.092 | |
| Browsers | | | | | | | | | | |
| M8 | X | | X | X | | X | 0.0 | 0.49 | 0.286 | 19.5 |
| M5 | X | | | X | X | X | 0.3 | 0.42 | 0.291 | |

Adjusted R^2 values ranged from 0.08 to 0.37 for occurrence models (Supplement 4) while conditional biomass models ranged from 0.092 to 0.291 (Table 3). Herbivores and grazers were present at all sites and, therefore, only conditional abundance models (Gamma GLM) were needed. LOOCV indicated relatively small predictive errors for conditional biomass models with MAPE values as high as 30.7% for predictions of herbivorous fish biomass and as low as 15.5% for scraper biomass (Table 3).

Environmental and human associations with herbivore biomass

Overall, human population density and environmental factors strongly influenced predictions of herbivorous fish biomass (Fig. 2). All 4 herbivore response variables declined with increasing human population density (Fig. 2). The association with human influence was greatest for scraper biomass, with an expected reduction to 10.8% of $B_{unfished}$ at a

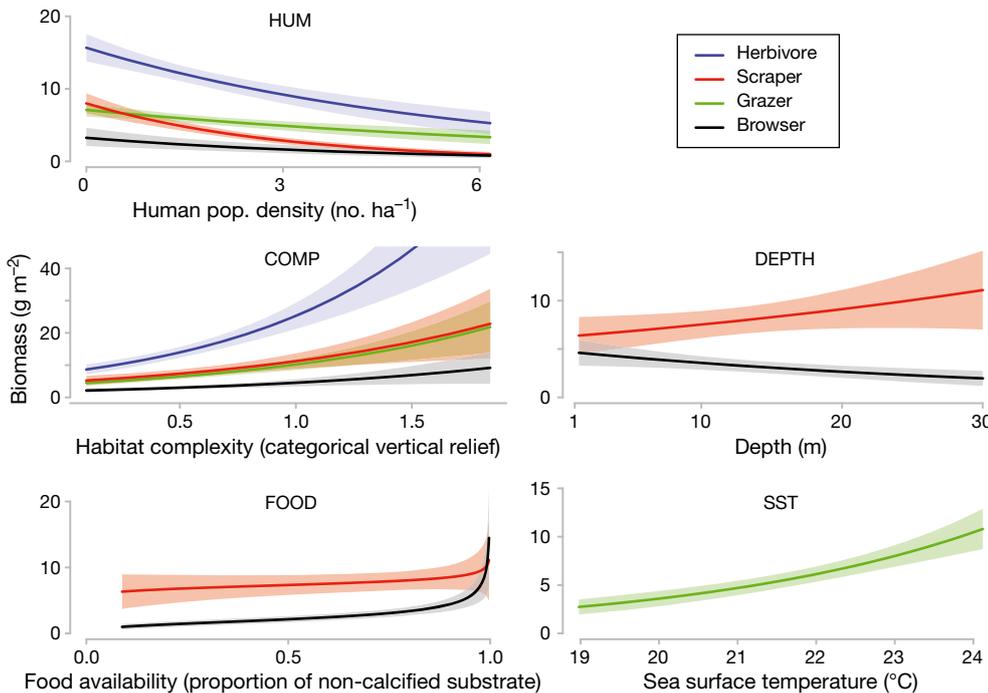


Fig. 2. Predicted relationships for conditional biomass of all 4 herbivore categories (colored lines) across the 5 fixed-effect variables. Shaded regions reflect 90% confidence intervals. For predictions, data values were held at variable means for variables other than the predictor, which was set to values equally spaced between the min. and max. across the Hawaiian Archipelago

human population density equal to that of Oahu, and weakest for grazer biomass, which was only expected to be reduced to 51.7% of B_{unfished} at the same human population density (Fig. 2).

Total biomass of herbivorous fishes demonstrated strong positive associations with habitat complexity (Fig. 2 & Fig. S3 in Supplement 4), with more than 4-fold increases expected across the range of habitat complexity values (Fig. 2). There was support for an interaction between habitat complexity and food availability for total herbivores (Model M5, Table 3). Predictions of total herbivore biomass were low when both food availability and habitat complexity were low, but were disproportionately high when food availability and habitat complexity were high (Fig. 3).

Like total herbivore biomass, grazer biomass was associated with fishing and the interaction between habitat complexity and food availability, in addition to temperature (Model M9, Table 3). Grazer biomass was expected to be low when both food availability and habitat complexity were low, but disproportionately high when food availability and habitat complexity were high (Fig. 3). In addition, grazer biomass was expected to double across the SSTL gradient (Fig. 2).

Predictions of scraper and browser biomass incorporated results from both occurrence and conditional biomass models. Scraper occurrence was strongly and positively associated with habitat complexity, and food availability with limited support for depth, SSTL, and human population density influences (Table S3 & Fig. S2 in Supplement 4). Model selection results for conditional scraper biomass

strongly favored the fishing, habitat complexity, depth, and food availability model (Model M8, Table 3). Scraper biomass was positively associated with depth (Fig. 2).

Browser occurrence was strongly and positively associated with habitat complexity and food availability and negatively associated with depth (Table S3 & Fig. S3 in Supplement 4). However, these predictors had a relatively low adjusted R^2 , indicating they did not provide substantial information about browser presence. Given that at least one individual was observed, our predictors were substantially more informative about how browser abundance. Model selection results for conditional browser biomass showed similar levels of support for the habitat complexity, depth, food availability, and fishing model (M8) and the fishing and habitat complexity-food availability interaction model (M5, Table 3); however, the interaction was weak. Browser biomass had the strongest positive association with food availability (>14-fold increase) and was negatively associated with depth (Fig. 2).

Estimates of unfished biomass and herbivore depletion

Predictions of B_{unfished} that accounted for environmental factors ($B_{\text{unfished-local}}$) illustrated considerable variability across islands in the Hawaiian Archipelago (Fig. 4). Overall, predictions of $B_{\text{unfished-local}}$ for all herbivorous fishes varied by a factor of 2 and were highest at Midway (mean = 24.9 g m⁻², 90% predic-

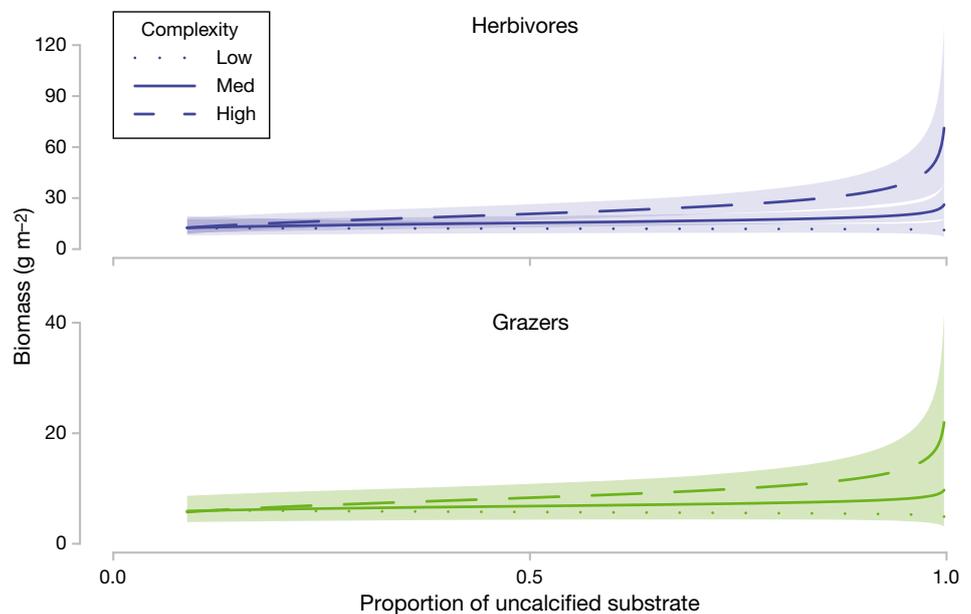


Fig. 3. Predicted biomass relationships for herbivores and grazers (colored lines) based on the habitat complexity \times food availability interaction. Lines represent 3 levels of habitat complexity (low, medium, and high). Shaded regions reflect 90% confidence intervals

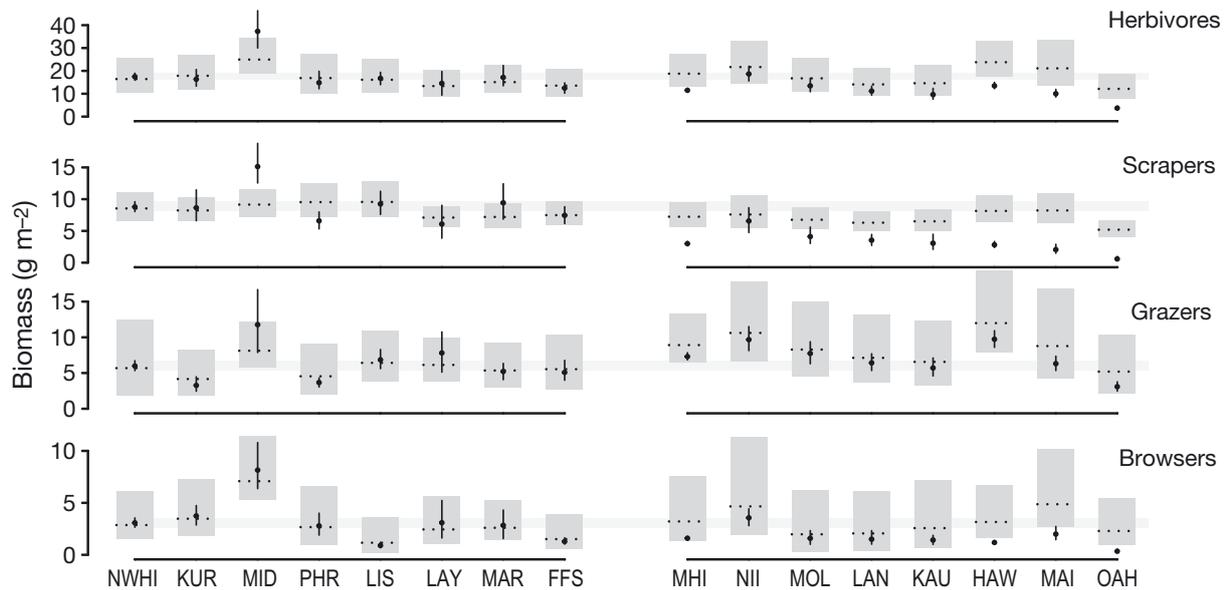


Fig. 4. Variability in unfished biomass (B_{unfished}) estimates and observed mean biomass in the Hawaiian Archipelago for the 4 herbivore categories. Dots and vertical line segments represent observed mean biomass and 90% confidence intervals for each region (Northwestern Hawaiian Islands [NWHI] & Main Hawaiian Islands [MHI]) and island. Note that the NWHI and MHI values represent means across all islands within each of those regions, whereas the island-specific values are means across all sites within each island. Observed biomass in the NWHI was used as an estimate of B_{unfished} ($B_{\text{unfished-regional}}$) and is highlighted by the light grey shading. Dotted horizontal lines represent predictions of $B_{\text{unfished-local}}$; dark grey boxes represent 90% prediction intervals. Islands in the NWHI are sorted from north to south; MHI are sorted from low to high human population density. See Table 1 for full island names

tion interval: 18.7–31.2) and lowest at Oahu (mean = 12.1 g m⁻², 90% prediction interval: 7.8–16.4). Predictions of $B_{\text{unfished-local}}$ for scrapers also varied by a factor of almost 2 and were highest at Lisianski (mean = 9.6 g m⁻², 90% prediction interval: 7.2–12.8) and lowest at Oahu (mean = 5.2 g m⁻², 90% prediction interval: 4.0–6.7). Predictions of $B_{\text{unfished-local}}$ for grazers varied by a factor of almost 3 and were highest at Hawaii (mean = 12.0 g m⁻², 90% prediction interval: 7.8–16.1) and lowest at Kure (mean = 4.2 g m⁻², 90% prediction interval: 1.9–6.4). Predictions of $B_{\text{unfished-local}}$ for browsers were the lowest of all herbivorous fish categories. Browser predictions of $B_{\text{unfished-local}}$ varied by a factor of 4 and were highest at Midway (mean = 7.1 g m⁻², 90% prediction interval: 5.6–11.4) and lowest at LIS (mean = 1.2 g m⁻², 90% prediction interval: 0.2–3.6). Predictions of $B_{\text{unfished-local}}$ were generally lower than predictions of $B_{\text{unfished-regional}}$ for the scraper category and variable for grazer, browser, and total herbivore categories (Fig. 4).

Depletion estimates of herbivorous fish biomass in the MHI varied depending upon which B_{unfished} reference point ($B_{\text{unfished-local}}$ or $B_{\text{unfished-regional}}$) was used. Estimates of depletion based on $B_{\text{unfished-regional}}$ tended to overestimate scraper depletion by up to 40.8%

(Oahu 90% CI: 32.2–48.6) and underestimate grazer depletion (Fig. 5). Depletion patterns for herbivore and browser biomass were less consistent across islands (Fig. 5). Comparisons of mean observed biomasses at islands in the NWHI with predictions of $B_{\text{unfished-local}}$ and estimates of $B_{\text{unfished-regional}}$ indicated that predictions of $B_{\text{unfished-local}}$ were generally closer to mean observed biomass at each island in the NWHI compared to $B_{\text{unfished-regional}}$ (Fig. 4 & Supplement 3). The only major deviations between predictions of $B_{\text{unfished-local}}$ and island mean biomass in the NWHI (major deviations: prediction intervals do not overlap island mean) were at Midway (scrapers and herbivores) and Pearl and Hermes (scrapers). Therefore, depletion estimated based on $B_{\text{unfished-local}}$ were used to describe depletion patterns of herbivorous fish biomass in the MHI.

Overall, scraper biomass was the most depleted and grazer biomass the least depleted in the MHI (Fig. 6). However, spatial depletion patterns varied greatly by island. Scraper biomass depletion was highest on Oahu (mean = 11.3%, 90% CI: 7.5–17.7), and relatively low (<50%) at Kauai, Hawaii, and Maui (Fig. 6). Scraper biomass at the least populated island in the MHI, Niihau, was estimated to be 86.5% of $B_{\text{unfished-local}}$ (90% CI: 66.9%–111.3%).

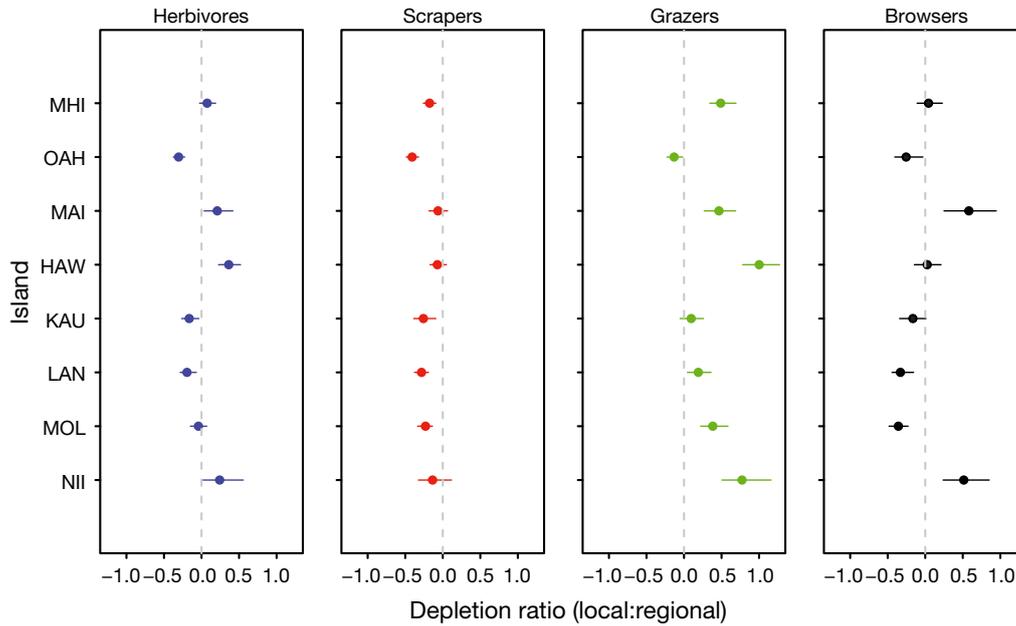


Fig. 5. Relative differences between $D_{\text{unfished-local}}$ and $D_{\text{unfished-regional}}$. Dotted grey vertical line represents no difference between depletion estimates. Negative values indicate an overestimation of depletion by $D_{\text{unfished-regional}}$; positive values indicate underestimation. Depletion estimates presented for each island in the Main Hawaiian Islands (MHI) (rows) and the 4 herbivorous fish categories (columns). As in Fig. 4, the MHI values represent the mean across islands within that region. Segments are 90% confidence intervals. See Table 1 for full island names

Grazer depletion was highest on Oahu, but was only estimated to be at 59.4% of $B_{\text{unfished-local}}$ (90% CI: 47.6–70.3) while grazer biomass at Molokai was estimated at 93.5% of $B_{\text{unfished-local}}$ (90% CI: 76.6%–112.6%).

DISCUSSION

Over the last decade, a growing number of studies have estimated differences in reef fish biomass between fished and unfished areas (McClanahan et

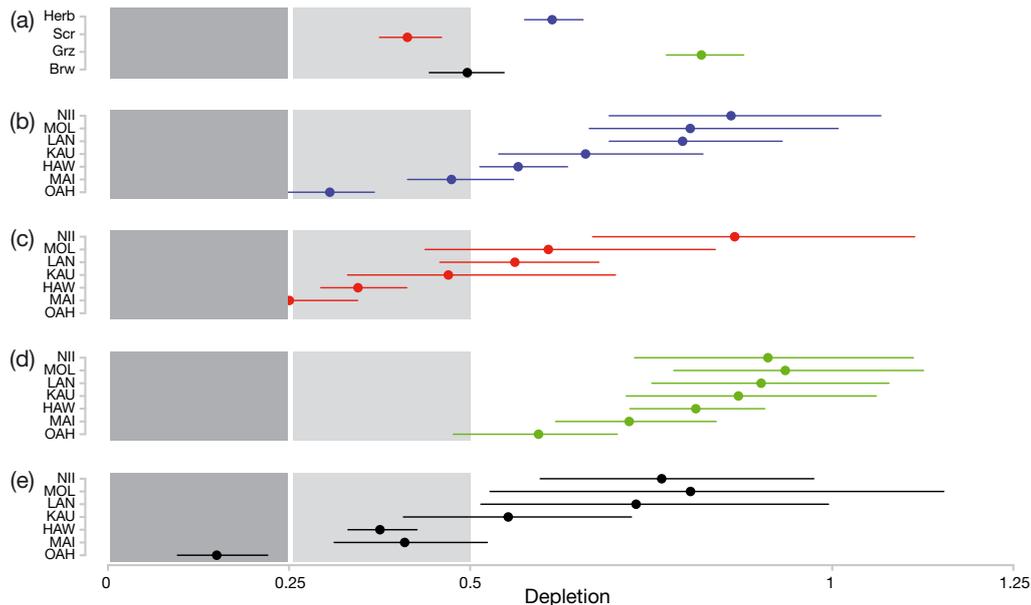


Fig. 6. Depletion estimates (dots) and 90% confidence intervals (segments) based on unfished biomass at each island for the 4 herbivore categories in the Main Hawaiian Islands (MHI) (a) by region and (b–e) by island. Colors correspond to herbivorous fish categories. Colors correspond to herbivorous fish categories: (b) herbivores (Herb, blue), (c) scrapers (Scr, red), (d) grazers (Grz, green), (e) browsers (Brw, black). Islands are sorted from lowest to highest population density. See Table 1 for full island names

al. 2011, Williams et al. 2011, Edwards et al. 2014, Karr et al. 2015). However, only recently have studies begun to account for environmental influences on unfished biomass reference points (Williams et al. 2015). The main findings of this study show that (1) site-level variability of environmental conditions, as well as human population density, are strongly associated with herbivorous fish biomass in the Hawaiian Archipelago, (2) local environmental factors affect island-scale predictions of unfished biomass, (3) ignoring the influence of local environmental factors on herbivorous fishes can result in both over- and under-estimation of biomass depletion, and (4) overall, herbivorous fish biomass across the MHI is above 50% of $B_{\text{unfished-local}}$; however, localized depletion varies both spatially (by island) and by herbivore guild. In sum, these results suggest that failure to account for environmental influences on fish biomass results in strikingly different conclusions about herbivore depletion in coral reef fish communities.

While it is clear that humans alter fish communities on coral reefs (Newman et al. 2006, 2007, Williams et al. 2011), this study demonstrates that local environmental influences can have an equivalent or greater association with fish biomass. In the MHI, when local environmental factors were ignored, depletion of herbivorous fish biomass was exaggerated in some cases and underestimated in others. For scrapers, which are highly prized fisheries targets and perform the key ecological function of creating new calcified substrate on the reef benthos while foraging (Bellwood et al. 2012), biomass depletion was exaggerated by up to 45% when environmental factors were ignored. Specifically, scraper presence and conditional biomass were positively associated with habitat complexity. Benthic habitat in the NWHI was generally more complex than habitat in the MHI, which translated to the NWHI having the potential to support more fish biomass (higher B_{unfished}) compared to the MHI. In contrast to predictions of unfished scraper biomass, predictions of $B_{\text{unfished-local}}$ for grazer biomasses in the MHI were almost always higher than $B_{\text{unfished-regional}}$. Therefore, when $B_{\text{unfished-regional}}$ was used to estimate grazer depletion, depletion was not only underestimated, but observed biomass levels in the MHI were often higher than $B_{\text{unfished-regional}}$. The idea that biomass of lower-trophic level species can exceed unexploited levels is consistent with the idea of prey-release associated with trophic cascades (Boaden & Kingsford 2015). However, during exploratory data analysis, a relationship between grazer biomass and piscivorous fishes across the NWHI was not evident. Furthermore, a trophic release due to re-

duction in predation in the MHI is unlikely for grazers because all fishes in this functional group are targets of either subsistence or aquarium fishing in Hawaii (Friedlander & Parrish 1997, Williams et al. 2008).

An alternative explanation for the patterns of grazer biomass across the archipelago is that environmental conditions in the MHI are more favorable for grazer biomass compared to the NWHI. Previous work has shown colder SSTs can limit the abundance of herbivorous fishes possibly due to decreased feeding and metabolic efficiencies (Floeter et al. 2005). In this study, grazer biomass had a strong positive association with SSTs, and lower climatological mean SSTs were 5°C warmer at the southernmost island of Hawaii compared to the northernmost island, Kure Atoll. For example, biomasses of the yellow tang *Zebрасoma flavescens* were generally higher in the warmer MHI and large acanthurids (*Acanthurus blochii*, *A. dussumieri*, *A. olivaceus*, *A. xanthopterus*) were relatively uncommon at the 3 northern atolls, which are exposed to the coldest water temperatures in the Hawaiian Archipelago (almost a 2°C drop in SSTL compared to the closest island, Lisianski).

Given the strong environmental associations of herbivorous fish community biomass in the Hawaiian Archipelago, depletion estimates that accounted for spatial differences in B_{unfished} provided a more accurate representation of herbivorous fish biomass in the MHI than those that did not. Biomasses of the 4 herbivorous fish categories across much of the MHI were near or above one-half of B_{unfished} estimated, after correcting for environmental influences ($0.5 \times B_{\text{unfished-local}}$). One-half of B_{unfished} is a common reference point for fisheries sustainability based on single-species surplus-production models (Hilborn 2010), suggesting that herbivorous fish in Hawaii may not be as depleted as previously believed (Williams et al. 2011, Edwards et al. 2014). Indeed, this conclusion is consistent with a recent stock assessment of Hawaiian reef fishes (Nadon et al. 2015). Many areas in the MHI are relatively far from human population centers and inaccessible to fishermen without boats (Williams et al. 2008). These factors may contribute to the relatively low estimates of herbivorous fish community depletion across much of the MHI and may translate to these reef areas having higher resilience to shifts in benthic communities (Mumby et al. 2007, Hughes et al. 2010). This is not true, however, on the island of Oahu, where the combination of the highest human population density (highest fishing pressure) and the lowest mean habitat complexity in the MHI (lowest fisheries potential) contributed to Oahu having the most depleted herbivorous fish biomass in the MHI.

A main objective of this study was to evaluate whether incorporating environmental information into estimates of B_{unfished} resulted in more accurate conclusions about the status of herbivorous fish biomass in Hawaii. While comparisons between $B_{\text{unfished-local}}$ and $B_{\text{unfished-regional}}$ overwhelmingly supported the inclusion of environmental data, evaluation of model performance was also critical because our computation of $B_{\text{unfished-local}}$ required extrapolating site-scale biomass predictions to island-scales. Our methodological approach was supported by the relatively low errors for site-level biomass predictions and agreement between predictions of $B_{\text{unfished-local}}$ and observed mean biomass at the unfished islands in the NWHI.

However, our models did suggest some lack of fit, especially at Midway, which had the highest observed biomasses of herbivorous fishes in the study (consistently higher than predictions of $B_{\text{unfished-local}}$). Midway has been subject to the most direct human influences of any island in the NWHI (Kenyon et al. 2010), and thus historical artifacts may be affecting herbivore biomass. Alternatively, environmental factors not considered in our models, such as wave exposure or nutrients levels, could be contributing to higher than expected levels of herbivorous fish biomass. The consistent prediction errors at Midway warrant future efforts that may improve understanding of herbivorous fish responses to human disturbance.

Another valid concern regarding our inferences about exploitation across gradients of human population density is the potential to confound fishing effects with habitat degradation effects. Anthropogenic activities can affect reef fishes directly through exploitation and indirectly through habitat degradation. High human population densities have been linked to increased sedimentation and eutrophication, which can degrade coral reef habitat (Edinger et al. 1998). In the Caribbean, human presence has been associated with the loss of physical reef structure, which can further exacerbate the effects of fishing (Alvarez-Filip et al. 2009). In this study, Oahu, the island with the highest human population density in the MHI, also had the least complex habitat of any island in this study (Fig. S4 in Supplement 5 at www.int-res.com/articles/suppl/m575p001_supp.pdf). However, in general, habitat complexity was not correlated with human population density in the Hawaiian Archipelago. Instead, the lower mean habitat complexities on Oahu and Kauai seem related to island geomorphology and exposure to large wave events (Grigg 1997, Franklin et al. 2013). Furthermore, patterns of reef fish decline

associated with human population density in Hawaii are not consistent with habitat degradation being a causative factor (Williams et al. 2008). Therefore, associations of herbivorous fish biomasses with human population densities in the MHI are probably more strongly related to the influence of fishing as opposed to habitat degradation.

CONCLUSIONS

In summary, spatial patterns of herbivorous fish biomass across the remote and unfished Northwestern Hawaiian Islands add to an emerging recognition that substantial differences in fish biomass can exist, even when fishing is absent (Roberts 2000, Williams et al. 2015). In a broader sense, this study contributes to efforts focused on assessing ecosystem effects of fishing on coral reefs. Recent investigations have shown it is possible to maintain important measures of coral reef ecosystem structure and function when fish biomass exceeds $0.5 \times B_{\text{unfished}}$ (McClanahan et al. 2011, Karr et al. 2015). However, those studies did not account explicitly for factors other than fishing. This work and that of others (Valles & Oxenford 2015) suggest that because fish biomass is sensitive to environmental variability it should be controlled for when assessing ecosystem effects of fishing. Moving forward, the methods used here to estimate depletion patterns of herbivorous fishes, while accounting for environmental variability, could be applied in larger meta-analyses to generate hypotheses about how coral reef ecosystem structure and function changes across natural and anthropogenic gradients.

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