Incorporating fish behavior improves accuracy of species distribution models

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Species distribution models (SDMs) are used to interpret and map fish distributions based on habitat variables and other drivers. Fish behavior has been shown to vary in the presence of divers and is primarily driven by fishing pressure. Diver avoidance behavior or fish wariness may spatially influence counts and other descriptive measures of fish assemblages. Because fish assemblage metrics are response variables for SDMs, measures of fish wariness may be useful as predictors in SDMs of targeted fishes. We used a diver operated stereo-video system to conduct belt-transects and record minimum approach distance (MAD) of targeted reef fishes inside and outside of two marine reserves on the island of O’ahu in the main Hawaiian Islands. By comparing MAD in reserves and fished areas we tested the assumption that it provides a proxy for fishing pressure. We then compared the accuracy of SDMs which include MAD as a predictor with SDMs that do not. MAD showed greater differences between sites than within sites. It was lower inside one reserve compared to the adjacent fished area and did not differ in and outside of the other reserve site which had higher MAD overall. When included as a predictor, MAD greatly improved accuracy of SDMs of targeted fish biomass. In contrast, management status had very low predictive power.

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Abstract

Species distribution models (SDMs) are used to interpret and map fish distributions based on habitat variables and other drivers. Fish behavior has been shown to vary in the presence of divers and is primarily driven by fishing pressure. Diver avoidance behavior or fish wariness may spatially influence counts and other descriptive measures of fish assemblages. Because fish assemblage metrics are response variables for SDMs, measures of fish wariness may be useful as predictors in SDMs of targeted fishes. We used a diver operated stereo-video system to conduct belt-transects and record minimum approach distance (MAD) of targeted reef fishes inside and outside of two marine reserves on the island of O'ahu in the main Hawaiian Islands. By comparing MAD in reserves and fished areas we tested the assumption that it provides a proxy for fishing pressure. We then compared the accuracy of SDMs which include MAD as a predictor with SDMs that do not. MAD showed greater differences between sites than within sites. It was lower inside one reserve compared to the adjacent fished area and did not differ in and outside of the other reserve site which had higher MAD overall. When included as a predictor, MAD greatly improved accuracy of SDMs of targeted fish biomass. In contrast, management status had very low predictive power.

Introduction

A current focus in marine ecology has been to use species distribution models (SDMs) to understand and sometimes predict fish distributions based on habitat drivers. This information can assist with marine spatial planning, including identifying optimal locations for marine reserves (Shucksmith and Kelly 2014, Stamoulis and Delevaux 2015). Fish species respond to their habitat in different ways depending on their life-history strategies, predators, competitors, and food availability (Sale 1998, Boström et al. 2011). Fishing pressure is a primary driver, not only of fish distributions (Jennings and Polunin 1996, Friedlander and DeMartini 2002), but also of fish behavior (Kulbicki 1998). Fish behavior can be substantially altered by the presence of SCUBA divers, depending on fishes' prior experience of divers' activities (i.e. feeding vs spearing) (Cole 1994, Kulbicki 1998, Watson and Harvey 2007). Consequently, it is reasonable to expect that such variability in fish behavior would influence survey counts from underwater visual census (UVC) conducted by observers on SCUBA (Brock 1954) – the most common survey method in shallow water coral reefs. Despite earlier recognition of the potential biases associated with variable responses of targeted fishes to divers (Kulbicki 1998), there have only been a few attempts to quantify the impacts of fishes' diver avoidance behavior on measures of fish assemblages (Dickens et al. 2011, Bozec et al. 2011). Because fish assemblage metrics are response variables for SDMs, including measures of fish behavioral responses to the presence of survey divers may improve the predictive power of SDMs for targeted fishes.

In locations with high fishing pressure, area-based fish survey methods may underestimate fish abundance of species targeted by spear fishers (Kulbicki 1998, Feary et al. 2010). Lindfield et al. (2014) tested the magnitude of avoidance behavior using a diver operated stereo video system (stereo-DOV) to survey fish populations inside and outside of two no-take reserves in Guam using standard open-circuit SCUBA and a closed-circuit rebreather (CCR). CCRs produce no bubbles and, therefore, greatly reduce the disturbance caused by survey divers' presence. They recorded 'minimum approach distance' (MAD – the distance between the diver and the fish at its closest point) for each fish observed on belt transects, finding that fished sites sampled on SCUBA had the greatest average MAD for targeted fish groups. Overall, Lindfield et al. (2014) found that abundance of targeted fishes was 2.6 times greater when surveyed on CCR compared to on SCUBA, demonstrating a dramatic impact of fish behavior on survey estimates. These effects were partially corroborated by Gray et al. (2016) who used a different UVC method and found that biomass of some targeted reef fishes were significantly lower on SCUBA compared to CCR at high fishing pressure locations in the main Hawaiian Islands.

Fishing has obvious and direct effects on targeted fish populations (Jackson et al. 2001). Patterns of fishing pressure are difficult to measure and are rarely mapped (but see Stamoulis et al. 2018)). Diver avoidance behavior of targeted fishes may provide a proxy for spear fishing pressure (Bergseth et al. 2015). Thus, inclusion of diver avoidance behavior in SDMs could have explanatory power beyond correcting underwater survey bias. Fishing pressure directly increases fish wariness and decreases *true* fish biomass, while increased fish wariness may further decrease *observed* fish biomass, due to survey diver avoidance. Thus, including a measure of fish wariness should improve explanatory power and predictive accuracy of SDMs.

In order to test this hypothesis, we used a stereo-DOV to conduct belt-transects and record MAD of targeted reef fishes both inside and outside of two marine reserves on the island of O'ahu in the main Hawaiian Islands. We compare MAD in reserves to fished areas to test the assumption that it provides a proxy for fishing pressure, then compare the accuracy of SDMs including MAD as a predictor with SDMs that do not. The objectives of this study were to 1) evaluate MAD of targeted reef fishes as a proxy for fishing pressure, and 2) determine if including MAD as a predictor in SDMs of targeted reef fish biomass improves model accuracy.

Materials and Methods

Study sites

Surveys were conducted inside and outside of two no-take marine reserves on O'ahu in the Hawaiian Islands (Fig. 1). Pūpūkea is located on the north shore of O'ahu and was originally established in 1983. It was 10 ha when first established and allowed for a range of fishing activities. In 2003 it was expanded to encompass 71 ha and fishing activities were greatly restricted. Surveys of Pūpūkea were conducted during June-October 2016. Hanauma Bay is located on the south-east corner of the island and is the oldest MPA in the state, established in 1967. The entire bay is protected and encompasses 41 ha of marine habitats. Hanauma Bay was surveyed between February and May 2017. Transect locations were randomly selected within management types (reserve and open) on hard-bottom habitats using ArcGIS (Fig. 1).

Field surveys

Pre-determined survey locations were uploaded to GPS units for use in the field. Two divers navigated to waypoints from shore or small boat and used a stereo-DOV to conduct a single 5 x 25 m belt transect on SCUBA (Fig. 2). The transect began on the GPS point and followed the depth contour. Transect length was measured using a 25 m line reel which was secured to the substrate at the beginning of the transect and rolled out as progress was made. Survey time was standardized to 3 min per transect. Field surveys were conducted under Hawai‘i State special activity permit No. 2017-44.

Our stereo-DOV system used two Canon high-definition video cameras mounted 0.7 m apart on a base bar inwardly converged at 7° to provide a standardized field of view. The camera system was built by and purchased from https://www.seagis.com.au/hardware.html. Stereo video imagery was calibrated using the program CAL (SeaGIS), following the procedures outlined in Harvey and Shortis (1998). This allowed for measurements of fish length, distance (range) and angle of the fish from the center of the camera system, and standardization of the area surveyed (Harvey et al. 2001, 2004).

The stereo-DOV system recorded imagery from which we measured the abundance, length, and MAD of all targeted reef fishes encountered within the transect. Fishes located further than 10 m in front or 2.5 m to the left or right of the stereo-DOV system were excluded based on minimum visibility encountered and transect dimensions (Fig. 2). We adopted the ‘targeted’ species classification of a recently published study of fishing effects in MHI, which included species with ≥ 450 kg of annual recreational or commercial harvest between 2000 and 2010, or that were otherwise recognized as important for recreational, subsistence, or cultural fishing (Friedlander et al. 2018, Table S1). Full approval for this research was provided by the Curtin Animal Ethics Committee in accordance with the Australian code for the care and use of animals for scientific purposes (Approval number: AEC_2014_42).

Video analysis

Pairs of videos from the stereo-DOV system were analyzed using the program EventMeasure (SeaGIS). The total length of each targeted reef fish encountered on the transect was measured when the fish was closest to the stereo-DOV and computed by EventMeasure (Harvey et al. 2004). In the case of large schools, a representative subset of 6-10 individuals was measured, and the remaining fishes in the school were allocated to those records based on size. Biomass was calculated from length estimates using the length-mass conversion: $M = a\mathrm{TL}^b$, where parameters a and b are species-specific constants, TL is total length (cm), and M is mass (g). Length-mass fitting parameters were obtained from a comprehensive assessment of length-weight fitting parameters for Hawaiian reef fish species (Froese and Pauly 2017). On transects where targeted species were not recorded, biomass estimates were set to zero.

Fish wariness (MAD)

The shortest distance between the cameras and each targeted reef fish encountered on the transect was identified during the length measurement procedure (see above) and the distance was automatically computed by EventMeasure thus obtaining an accurate measurement of MAD (Harvey et al. 2004). If this was not possible due to the angle of the fish or obstruction of the camera view, another point was recorded and used to calculate MAD for the measured fish (Lindfield et al. 2014). Because MAD represents the minimum distance to targeted fishes, when no targeted fishes were recorded within the maximum measurement range (10 m) of the stereo-DOV, MAD was set to the maximum value of 10 m (Fig. 2).

<u>Data analysis</u>

To test effectiveness of the marine reserves included in this study, a two-way ANOVA was used to compare the effects of management and site on mean targeted fish biomass by transect.

Fish wariness (MAD)

Linear mixed models (LMMs) were used to compare patterns of MAD between sites and management types and assess relationships with fish body length, angle of approach, and water depth. These variables were included as fixed factors in the models, while transect (location) and species were included as random factors. LMMs were developed with the combined data from both sites and for each site separately. MAD values for each individual fish observed were ln(x) transformed to meet assumptions of normality and continuous variables were centered and scaled prior to modeling. A significance test of fixed factors was performed with a type III F-test, a marginal test that asks how much variation a predictor explains after the other predictors are accounted for. Degrees of freedom were estimated using the Kenward-Roger approximation. Then, a linear model was used to compare mean MAD of targeted species by transect among sites and management types with water depth included as a co-variable.

Species distribution models

Boosted regression trees (BRT) were used to develop SDMs of the total biomass of targeted reef fish for each study area. BRT models and spatial predictions were generated in R (R Core Team 2014) using the dismo (Hijmans et al. 2014) and raster (Hijmans 2014) packages. BRT are effective at modeling nonlinearities, discontinuities (threshold effects) and interactions between variables (Breiman 1996, 2001, De'ath and Fabricius 2000). Targeted fish biomass was fourth root transformed prior to modeling. Model fitting and selection was accomplished following the procedures detailed in Elith et al. (2008). To increase parsimony, selected models were then simplified to remove less informative predictor variables (Elith et al. 2008). Simplification generally resulted in models with < 10 predictors. Models with a larger number of predictors generally have higher percent deviance explained, therefore, to allow for comparison, the top eight predictors were retained for all models. Then, the model training dataset was repeatedly sampled with replacement to create 20 bootstrap samples. Using the optimal parameter value combination and simplified set of eight predictor variables, a BRT model was fitted to each bootstrap sample and used to make predictions based on the values of the predictor variables at each transect location. The mean of the bootstrapped predictions was used for interpretation and further analysis.

Habitat variables were those used in (Stamoulis et al. 2018) following a pairwise correlation analysis for the Main Hawaiian Islands. There were 23 total habitat variables of four broad categories: seafloor topography (12), benthic habitat composition (7), geographic (3), and wave energy (1) (Table 1, See (Stamoulis et al. 2018) for further details and predictor generation methods). Four transects in the open area near Hanauma Bay did not have remotely sensed habitat data and were excluded from BRT models.

To determine whether including behavior as a predictor improved model fit and predictive performance, models were developed separately using predictor sets that included and excluded MAD. To establish if model performance increases due to MAD were due solely to accounting for zeros in the response variable, another set of models was developed with a binary variable representing presence of targeted fishes. In addition to the habitat variables described above, management type (reserve/open) was also included as a predictor. In summary, three BRT models were developed separately for each site to explain and predict targeted fish biomass; 1) habitat + management, 2) habitat + management + MAD, and 3) habitat + management + presence of targeted fishes.

Model fit was evaluated using cross-validated percent deviance explained (CV PDE) and cross-validated standard error (CV SE). Predictive performance was assessed by comparing predicted values to observed values for each location. Accuracy of predictions was measured using R^2 and Gaussian rank correlation estimate (GRCE – Boudt et al. 2012), as well as root mean square error (RMSE) and symmetric mean absolute percent error (SMAPE), an alternate to mean absolute percent error that is robust to zero values.

Results

Sampling and reserve effect

Stereo-DOV belt transect surveys were conducted inside the marine reserves and in the adjacent open areas at both Pūpūkea and Hanauma Bay (Table 2). These resulted in a total of 1,486 observations of 35 coral reef fish species targeted by fishers in Hawaiʻi (Table S1). Reserve locations had higher abundances of targeted species such that the majority of observations occurred at locations protected from fishing (Table 2). At Hanauma Bay, 25% of transects had no targeted fishes and at Pūpūkea 13% of transects had no targeted fishes. With few exceptions, these transects were located in the open areas at each study site. Both marine reserves had significantly higher biomass of targeted fishes ($F_{1,120}$=48.9, p<0.001) though the magnitude differed. The ratio of mean targeted fish biomass inside the reserve vs. outside was 4.9 for Hanauma Bay and 1.5 for Pūpūkea.

Fish wariness (MAD) inside versus outside reserves

Reserve sites had lower MAD, though not significant at α=0.05 when data for both sites were combined (Table 3). There was no significant interaction between management and site, though when sites were modeled separately, management was significant at Hanauma Bay ($F_{1,56}$=4.1, p=0.046), though not at Pūpūkea ($F_{1,41}$=0.19, p=0.6). MAD at Pūpūkea was significantly higher overall compared to Hanauma Bay (Table 3, Fig. 3). Fish length, depth, and angle of approach were significantly positively related to MAD. However, when each site was modeled separately, only fish length was significant at Pūpūkea ($F_{1,41}$=25.1, p<0.001). Mean MAD by transect showed a very similar pattern between sites and management types (Table 4, Fig. 4). Depth was not a significant factor at the transect level (Table 4).

Species distribution models

Models that included management, but not behavior explained 57% and 10% of the variability in targeted fish biomass for Hanauma Bay and Pūpūkea, respectively (CV PDE, Table 5). When presence of targeted fishes was included as a predictor, CV PDE increased by 11% for Hanauma Bay and 4% for Pūpūkea (Table 5). For models where MAD was included as a predictor and presence of targeted fishes was not, CV PDE increased by 16% and 22% at Hanauma Bay and Pūpūkea, respectively (Table 5). For these models, MAD accounted for 71% of explained variation at Hanauma Bay and 26% of explained variation at Pūpūkea (Figs. 5 and 6). In contrast, presence of targeted fishes accounted for 57% of explained variation at Hanauma Bay and 0% of explained variation for Pūpūkea. When MAD was included, prediction accuracy increased with larger values of R^2 and GRCE compared to models which did not include MAD (Table 5). Prediction error for all three measures decreased when MAD was added to the models (Table 5). For models incorporating behavior, it explained the greatest amount of variability compared to other predictors (Figs. 5 & 6). In models including management status but not behavior, management was not selected as a final predictor.

Discussion

Management and site differences in fish wariness

MAD was lower inside the Hanauma Bay reserve compared to the adjacent fished area. This is consistent with the hypothesis that MAD is a proxy of fish wariness that increases with fishing pressure. These results correspond to those of Lindfield et al. (2014) who compared the MAD of targeted acanthurids and scarids between reserves and fished areas in Guam, and Goetze et al. (2017) who measured MAD of targeted species before and after harvest events in periodically harvested closures in Fiji. However, MAD did not differ inside the Pūpūkea reserve compared to the adjacent fished area. In addition, MAD was significantly higher on average at Pūpūkea on the north shore of O’ahu, compared to Hanauma Bay on the south shore. A likely explanation is that spearfishing pressure was also higher at Pūpūkea. Surveys were conducted in the summer months when the wave conditions allow for diving/spearfishing and the shoreline at Pūpūkea is very accessible with multiple access points. Spear fishers can swim in from either boundary, or simply enter the reserve directly and illegal spearfishing is a regular occurrence (Stamoulis and

Friedlander 2013). This likely contributes to the lack of difference in MAD at the Pūpūkea reserve compared to adjacent open areas. In contrast, shoreline access to the Hanauma Bay reserve is highly regulated. The reserve is monitored on a daily basis and it is unlikely that any spearfishing (poaching) occurs, with the possible exception of divers crossing the seaward boundary from boats. This likely contributed to the larger relative difference in MAD effect size between reserve and open areas compared to Pūpūkea, as well as the larger relative difference in targeted fish biomass.

Effects of other variables on fish wariness

Fish body length had a positive relationship with MAD as shown in previous studies (Lindfield et al. 2014, Goetze et al. 2017). Optimal fitness theory predicts that as reproductive value increases, risk-taking should decrease (Clark 1994). Previous studies using flight initiation distance (FID) as a measure of fish wariness also showed a positive relationship with body length (Gotanda et al. 2009, Januchowski-Hartley et al. 2011, 2015, Bergseth et al. 2016). Approach angle ranged from 0-25° and had a significant positive relationship with MAD at Hanauma Bay, but not Pūpūkea. This is likely a result of the methodology as opposed to a behavioral response. Fishes measured at a more oblique (higher) angle are farther from the transect and are consequently less likely to be approached closely compared to fishes closer to the transect. In contrast to our results from Hanauma Bay, Goetze et al. (2017) did not find a relationship between MAD and approach angle.

Depth had a positive relationship with MAD. This is contrary to previous findings (Stamoulis et al. 2019) which showed depth to have a negative relationship with FID. This effect is likely context dependent, and the positive influence of depth in this study reflects the low MAD in shallow areas of the marine reserves surveyed in this study. Both Hanauma Bay and Pūpūkea receive a large number of visitors who come to enjoy the abundant marine life. The majority of tourists tend to remain in shallow areas, thus targeted fishes in these marine reserves are likely habituated to non-aggressive human interactions, leading to reduced MAD in shallow areas. In Stamoulis et al. (2019), the marine reserve surveyed has restricted access and does not receive many visitors.

MAD as predictor for species distribution models

Because high fishing pressure is associated with increased wariness and low biomass of targeted species, it is logical to assume maximum MAD where there is minimum recorded biomass. The resulting pattern of MAD in reference to management type is consistent with the results at Hanauma Bay in this study and with the two previous studies that used this metric (Lindfield et al. 2014, Goetze et al. 2017). Including MAD as a predictor for SDMs greatly improved model fits and predictive performance and partial dependence plots indicated a strongly negative relationship between MAD and targeted fish biomass. In contrast, management type was not selected as a final predictor for any models meaning it was a comparatively poor predictor of targeted species biomass. Presence of targeted species accounted for a large portion of explained variability at Hanauma Bay though was not selected as a final predictor at Pūpūkea. For models including behavior, MAD was the best predictor at both sites and explained more variability than presence of targeted species at Hanauma Bay. This suggests that while presence of targeted species can be a good predictor of targeted species biomass in areas with higher variability of targeted species presence, such as Hanauma Bay, MAD is a better predictor even for areas with low variability of targeted species presence, such as Pūpūkea.

When MAD was modeled separately for each site, only fish body length was a significant factor for both sites. Because the response variable for SDMs was targeted fish biomass, which integrates fish length, it was not necessary to correct for length in transect-level estimates of mean MAD. Furthermore, patterns of mean MAD across sites and management types were nearly identical to those shown by models accounting for fish body length and approach angle. Based on these results, mean MAD of targeted species at the transect level appears to be a robust measure of fish wariness when used in SDMs of targeted fish biomass.

It is unclear what portion of the variance explained by MAD in SDMs was due to survey bias from fish behavior and how much from the direct effects of fishing pressure, for which MAD provides a proxy. However, because the direction of these influences on observed targeted fish biomass are the same (negative), it is irrelevant to SDM performance. In order to validate the use of MAD as a proxy for fishing, future research should focus on comparing empirical measures of spearfishing pressure with MAD of targeted species to better quantify this relationship. A drawback of using MAD as a predictor for SDMs is that it is not possible to make predictions to locations for which MAD data is not available. Instead, spatially explicit estimates of fishing pressure could be used directly as a predictor for SDMs (eg. Stamoulis et al. 2018). A better understanding of the relationship of MAD and fishing pressure would help inform this work so that MAD could be used to ground-truth spatial models of fishing pressure.

Another possibility is integrating MAD directly into measures of fish assemblage characteristics used to calibrate SDMs. Distance-based sampling, which is widely used for terrestrial mammals and birds but less so for coral reef fishes (though see Kulbicki 1998, Kulbicki et al. 2010), is one approach that may allow incorporation of MAD. Specifically, in distance sampling, observers record the distance of each organism of interest from the observer at the time of observation, thereby incorporating a measure of behavior (Buckland et al. 2005, Thomas et al. 2006). Creating a detection function, representing the probability of detection as a function of distance from the line, allows for estimation of the proportion of fish missed within the surveyed area, resulting in corrected density estimates (Buckland et al. 2005, Thomas et al. 2006). In this case, detection functions could be generated using data from locations with no fishing pressure, which should correct for altered fish behavior when applied in areas where fishing occurs, thus generating more accurate density estimates for use in SDMs.

Conclusions

In this study, we tested whether using a measure of targeted fish wariness (MAD) as a predictor of targeted fish biomass in SDMs spanning marine reserve boundaries, improved explanatory power and predictive accuracy. Our results show that including mean MAD as a predictor in SDMs greatly improves model performance and accuracy compared to models using reserve status and presence of targeted species. Diver operated stereo-video systems allow for efficient sampling of reef-fish assemblages as well as fish behavior and do not require extensive training, making them useful monitoring tools for managers and communities. Based on the results from this and two previous studies (Lindfield et al. 2014, Goetze et al. 2017), MAD appears to be a useful proxy for fishing pressure. In order to fully validate MAD as a proxy for fishing, future research should focus on comparing empirical measures of spearfishing effort with MAD of targeted species. In addition, research should seek to improve spatially explicit estimates of fishing pressure, for which MAD could provide a valuable reference, to extend SDM predictions to un-sampled areas.

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References

Bergseth, B. J., G. R. Russ, and J. E. Cinner. 2015. Measuring and monitoring compliance in no-take marine reserves. Fish and Fisheries 16:240–258.

Bergseth, B. J., D. H. Williamson, A. J. Frisch, and G. R. Russ. 2016. Protected areas preserve natural behaviour of a targeted fish species on coral reefs. Biological Conservation 198:202–209.

Boström, C., S. Pittman, C. Simenstad, and R. Kneib. 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Marine Ecology Progress Series 427:191–217.

Boudt, K., J. Cornelissen, and C. Croux. 2012. The Gaussian rank correlation estimator: robustness properties. Statistics and Computing 22:471–483.

Bozec, Y.-M., M. Kulbicki, F. Laloë, G. Mou-Tham, and D. Gascuel. 2011. Factors affecting the detection distances of reef fish: implications for visual counts. Marine Biology 158:969–981.

Breiman, L. 1996. Bagging predictors. Machine Learning 24:123–140.

Breiman, L. 2001. Statistical modeling: The two cultures (with comments and a rejoinder by the author). Statistical Science 16:199–231.

Brock, V. E. 1954. A preliminary report on a method of estimating reef fish populations. The Journal of Wildlife Management 18:297–308.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 2005. Distance Sampling. Page Encyclopedia of Biostatistics. John Wiley & Sons, Ltd.

Clark, C. W. 1994. Antipredator behavior and the asset-protection principle. Behavioral Ecology 5:159–170.

Cole, R. G. 1994. Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in Northeastern New Zealand. Biological Conservation 70:93–99.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

Dickens, L. C., C. H. R. Goatley, J. K. Tanner, and D. R. Bellwood. 2011. Quantifying Relative Diver Effects in Underwater Visual Censuses. PLoS ONE 6:e18965.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Feary, D. A., J. E. Cinner, N. a. J. Graham, and F. A. Januchowski-Hartley. 2010. Effects of customary marine closures on fish behavior, spear-fishing success, and underwater visual surveys. Conservation Biology 25:341–349.

Friedlander, A. M., and E. E. DeMartini. 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., M. K. Donovan, K. A. Stamoulis, I. D. Williams, E. K. Brown, E. J. Conklin, E. E. DeMartini, K. S. Rodgers, R. T. Sparks, and W. J. Walsh. 2018. Human-induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries. Aquatic Conservation: Marine and Freshwater Ecosystems 28:146–157.

Froese, R., and D. Pauly. 2017. FishBase. Online database. www.fishbase.org.

Goetze, J. S., F. A. Januchowski-Hartley, J. Claudet, T. J. Langlois, S. K. Wilson, and S. D. Jupiter. 2017. Fish wariness is a more sensitive indicator to changes in fishing pressure than abundance, length or biomass. Ecological Applications 27:1178–1189.

Gotanda, K. M., K. Turgeon, and D. L. Kramer. 2009. Body size and reserve protection affect flight initiation distance in parrotfishes. Behavioral Ecology and Sociobiology 63:1563–1572.

Gray, A. E., I. D. Williams, K. A. Stamoulis, R. C. Boland, K. C. Lino, B. B. Hauk, J. C. Leonard, J. J. Rooney, J. M. Asher, K. H. L. Jr, and R. K. Kosaki. 2016. Comparison of reef fish survey data gathered by open and closed circuit SCUBA divers reveals differences in areas with higher fishing pressure. PLOS ONE 11:e0167724.

Harvey, E., D. Fletcher, and M. Shortis. 2001. A comparison of the precision and accuracy of estimates of reef-fish lengths determined visually by divers with estimates produced by a stereo-video system. Fishery Bulletin 99:63–71.

Harvey, E., D. Fletcher, M. R. Shortis, and G. A. Kendrick. 2004. A comparison of underwater visual distance estimates made by scuba divers and a stereo-video system: implications for underwater visual census of reef fish abundance. Marine and freshwater research 55:573–580.

Harvey, E. S., and M. R. Shortis. 1998. Calibration stability of an underwater stereo-video system: Implications for measurement accuracy and precision. Marine Technology Society Journal 32:3–17.

Hijmans, R. J. 2014. Raster: Geographic data analysis and modeling. http://CRAN.R-project.org/package=raster.

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2014. dismo: Species distribution modeling. http://CRAN.R-project.org/package=dismo.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637.

Januchowski-Hartley, F. A., N. A. J. Graham, J. E. Cinner, and G. R. Russ. 2015. Local fishing influences coral reef fish behavior inside protected areas of the Indo-Pacific. Biological Conservation 182:8–12.

Januchowski-Hartley, F., J. Cinner, N. Graham, T. Morove, and D. Feary. 2011. Fear of fishers: Human predation explains behavioral changes in coral reef fishes. PLoS One 6:e22761.

Jennings, S., and N. V. C. Polunin. 1996. Effects of Fishing Effort and Catch Rate Upon the Structure and Biomass of Fijian Reef Fish Communities. Journal of Applied Ecology 33:400–412.

Kulbicki, M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. Journal of Experimental Marine Biology and Ecology 222:11–30.

Kulbicki, M., N. Cornuet, L. Vigliola, L. Wantiez, G. Moutham, and P. Chabanet. 2010. Counting coral reef fishes: Interaction between fish life-history traits and transect design. Journal of Experimental Marine Biology and Ecology 387:15–23.

Lindfield, S. J., E. S. Harvey, J. L. McIlwain, and A. R. Halford. 2014. Silent fish surveys: bubble-free diving highlights inaccuracies associated with SCUBA-based surveys in heavily fished areas. Methods in Ecology and Evolution 5:1061–1069.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sale, P. F. 1998. Appropriate spatial scales for studies of reef-fish ecology. Australian Journal of Ecology 23:202–208.

Shucksmith, R. J., and C. Kelly. 2014. Data collection and mapping – Principles, processes and application in marine spatial planning. Marine Policy 50, Part A:27–33.

Stamoulis, K. A., and J. M. S. Delevaux. 2015. Data requirements and tools to operationalize marine spatial planning in the United States. Ocean & Coastal Management 116:214–223.

Stamoulis, K. A., J. M. S. Delevaux, I. D. Williams, M. Poti, J. Lecky, B. Costa, M. S. Kendall, S. J. Pittman, M. K. Donovan, L. M. Wedding, and A. M. Friedlander. 2018. Seascape models reveal places to focus coastal fisheries management. Ecological Applications 28:910–925.

Stamoulis, K. A., and A. M. Friedlander. 2013. A seascape approach to investigating fish spillover across a marine protected area boundary in Hawai‘i. Fisheries Research 144:2–14.

Stamoulis, K. A., E. S. Harvey, A. M. Friedlander, I. D. Williams, K. C. Weng, C. Wiggins, G. W. Wagner, and E. J. Conklin. 2019. Flight behavior of targeted fishes depends on variables other than fishing. Ecological Indicators 96:579–590.

Thomas, L., S. T. Buckland, K. P. Burnham, D. R. Anderson, J. L. Laake, D. L. Borchers, and S. Strindberg. 2006. Distance Sampling. Page Encyclopedia of Environmetrics. John Wiley & Sons, Ltd.

Watson, D. L., and E. S. Harvey. 2007. Behaviour of temperate and sub-tropical reef fishes towards a stationary SCUBA diver. Marine and Freshwater Behaviour and Physiology 40:85–103.

Figure Legends

Figure 1: Survey locations at a) Pūpūkea and b) Hanauma Bay.

Figure 2: Transect dimensions and measurement range of the stereo-DOV and measures of MAD in areas with low and high fishing pressure.

Figure 3: Fixed effects from LMM model of MAD for both sites combined.
Confidence intervals are from profile likelihoods. All continuous variables were scaled and centered previous to modeling. PUP = Pūpūkea, HAN = Hanauma Bay.

Figure 4: Management x Site effect for linear model of mean MAD by transect.
Confidence intervals are from profile likelihoods. PUP = Pūpūkea, HAN = Hanauma Bay.

Figure 5: Partial dependence plots for Hanauma Bay BRT model of targeted fish biomass including targeted fish behavior – MAD.

Figure 6: Partial dependence plots for Pūpūkea BRT model including targeted fish behavior – MAD.

Figure 1

Survey locations at a) Pūpūkea and b) Hanauma Bay.

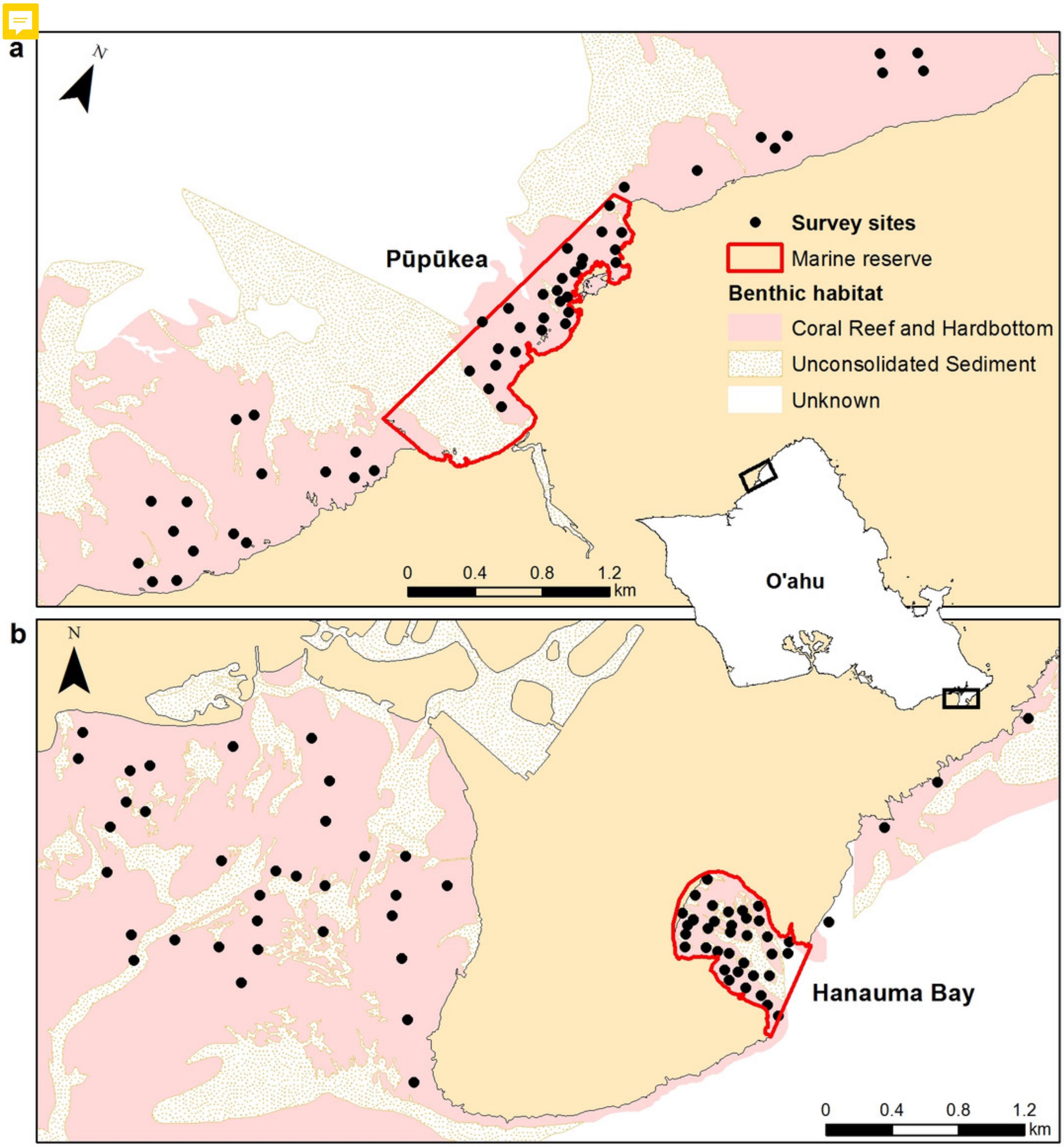

Figure 2

Transect dimensions and measurement range of the stereo-DOV and measures of MAD in areas with low and high fishing pressure.

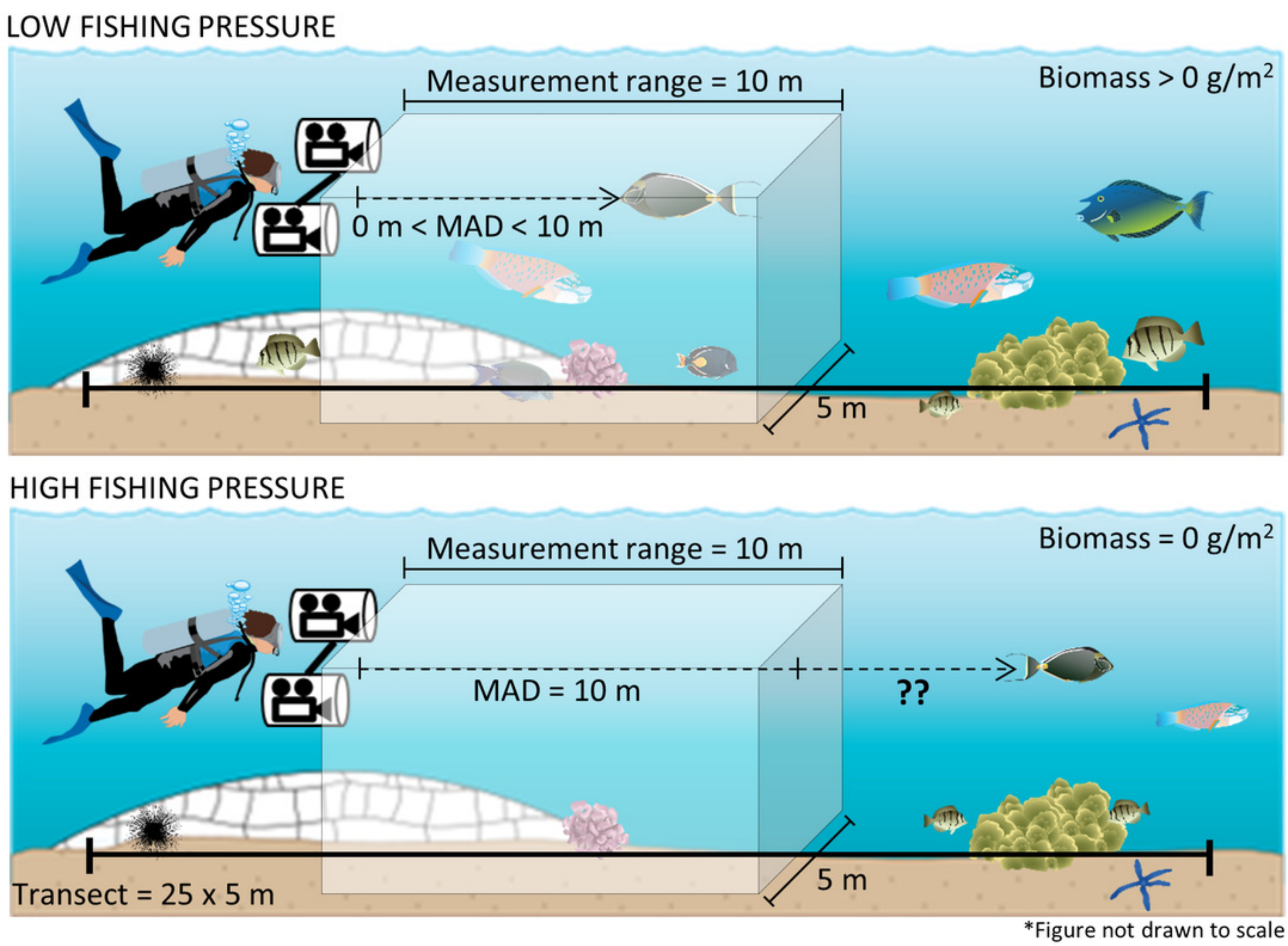

Figure 3

Fixed effects from LMM model of MAD for both sites combined.

Confidence intervals are from profile likelihoods. All continuous variables were scaled and centered previous to modeling. PUP = Pūpūkea, HAN = Hanauma Bay.

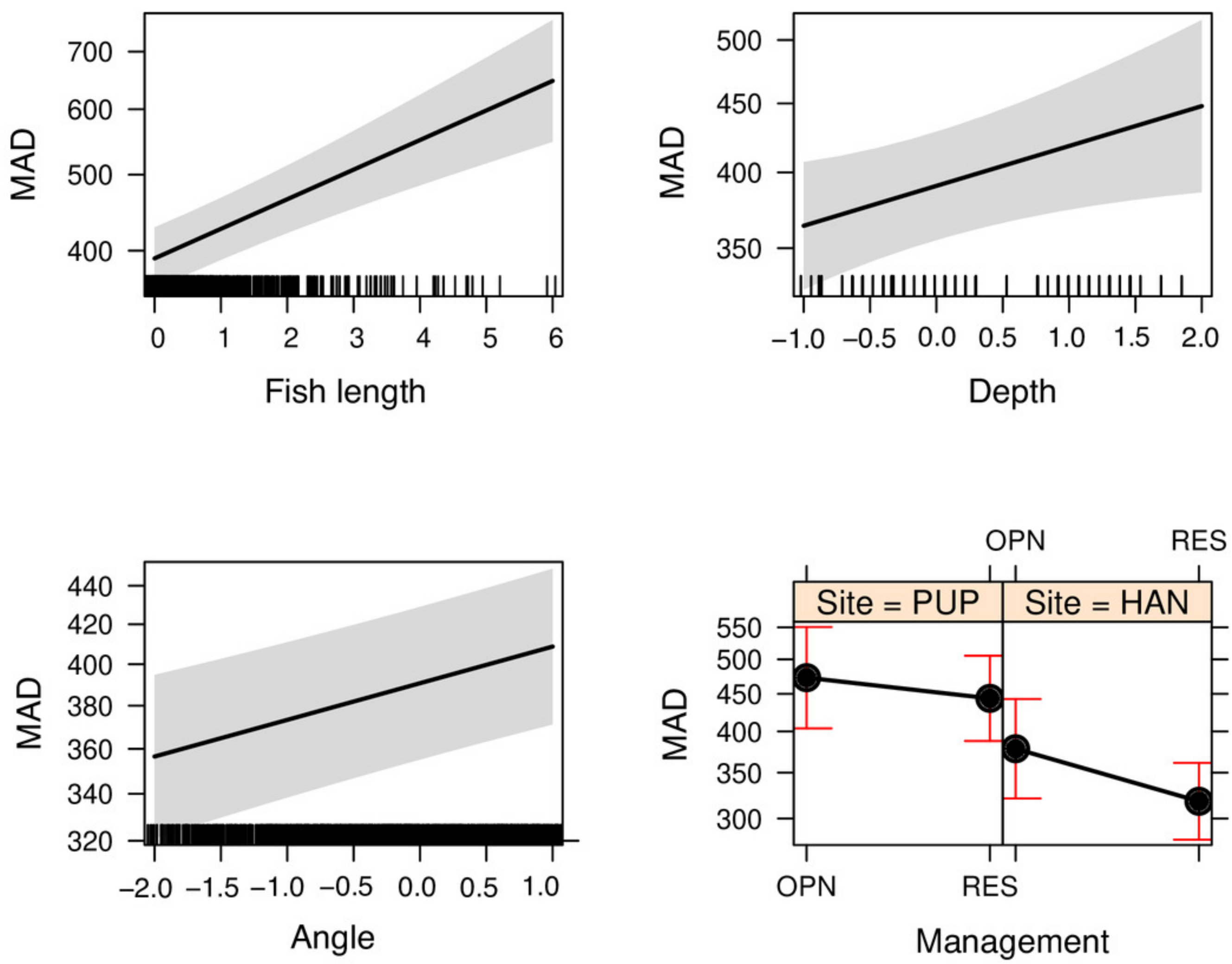

Figure 4

Management x Site effect for linear model of mean MAD by transect.

Confidence intervals are from profile likelihoods. PUP = Pūpūkea, HAN = Hanauma Bay.

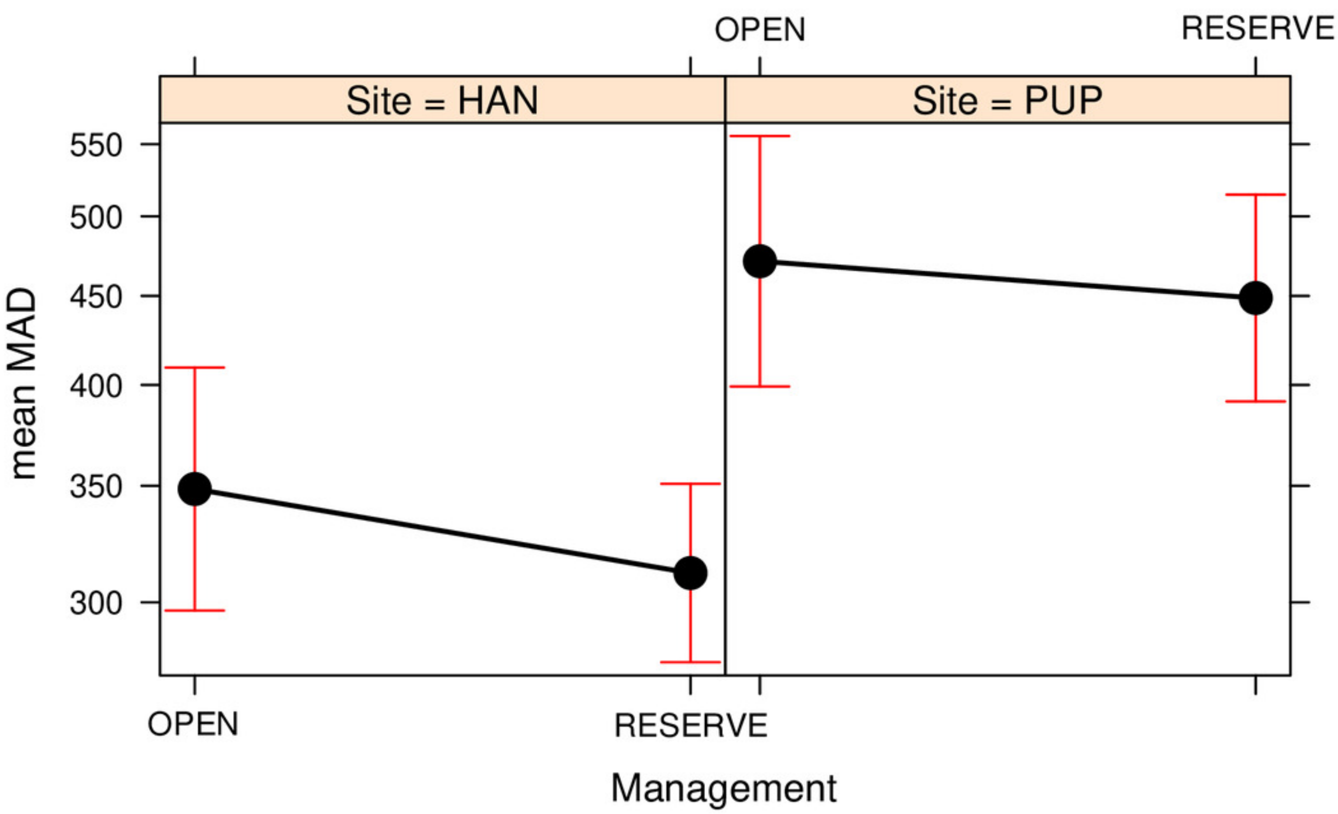

Figure 5

Partial dependence plots for Hanauma Bay BRT model of targeted fish biomass including targeted fish behavior – MAD.

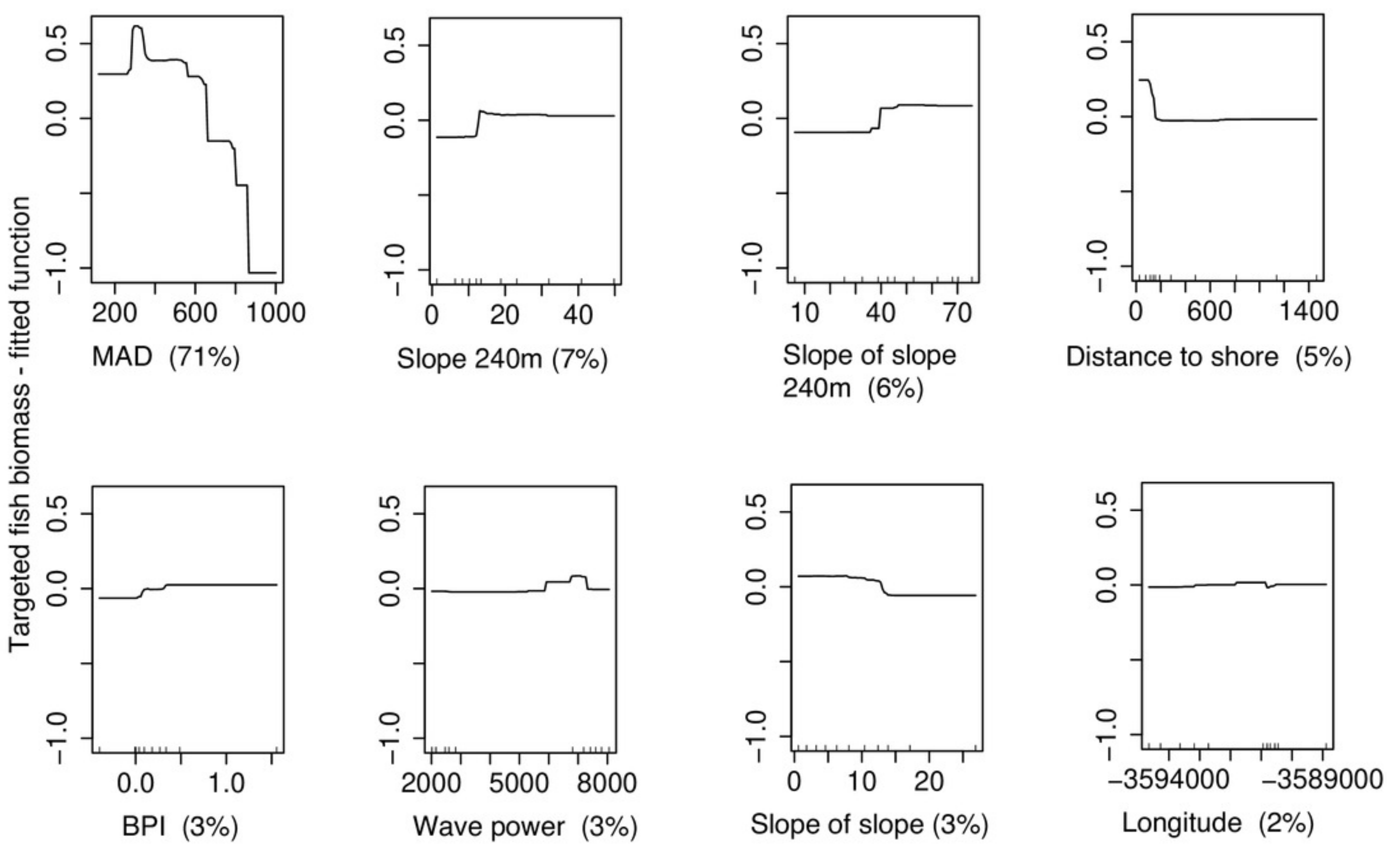

Figure 6

Partial dependence plots for Pūpūkea BRT model of targeted fish biomass including targeted fish behavior – MAD.

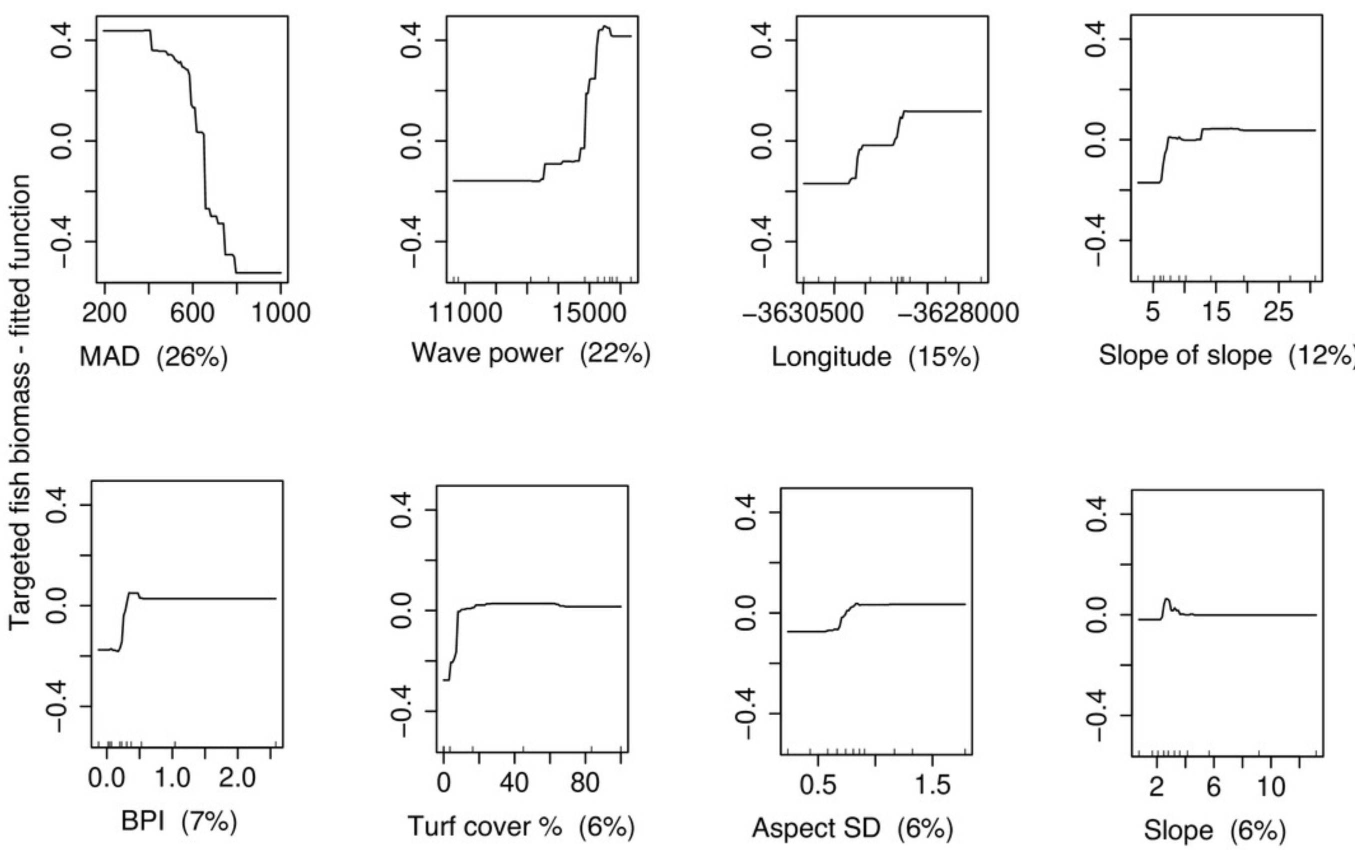

Table 1(on next page)

Habitat predictors used in SDMs.

Number of individual datasets of each type indicated in parentheses.

Table 1:

Habitat predictors used in SDMs.

Number of individual datasets of each type indicated in parentheses.

Predictor dataset types	**Datasets**	**Description**
Seafloor topography (12)	Depth, Slope, Slope of slope, Aspect, Planar and profile curvature, BPI	Seafloor topography metrics derived from bathymetry including depth, slope, structural complexity, exposure, curvature, and bathymetric position index (BPI). Slope, slope of slope, and BPI were calculated at two scales.
Benthic habitat composition (7)	Percent cover of CCA, Macroalgae, Turf, and Soft bottom, Proximity index, Shannons diversity index	Percent benthic cover of major cover types, seascape fragmentation/patch isolation, habitat diversity.
Geographic (3)	Latitude, Longitude, Distance to shore	Geographic location and distance from shore.
Oceanographic (1)	Wave Power	Wave height x wave period.

Table 2(on next page)

(on next page)

Transect and sample numbers of targeted fishes by site and management.

Table 2:

Transect and sample numbers of targeted fishes by site and management.

Site	Management	Transects	Fishes recorded
Pūpūkea	Reserve	25	475
	Open	27	272
Hanauma Bay	Reserve	35	572
	Open	37	167
	Total:	124	1,486

Table 3(on next page)

Linear mixed model results for MAD combining both sites.

Table 3:

LMM results for MAD combining both sites.

	Sum Sq	Mean Sq	DF	Den DF	F value	P value	
Management	0.42	0.42	1	96.8	3.2	0.08	
Site	2.36	2.36	1	105.7	18.0	<0.001	***
Fish length	4.68	4.68	1	897.0	35.7	<0.001	***
Depth	0.71	0.71	1	97.3	5.4	0.02	*
Angle	3.06	3.06	1	1417.4	23.3	<0.001	***
Mgmt x Site	0.08	0.08	1	95.4	0.6	0.44	

Table 4(on next page)

Linear model results of mean MAD by transect.

Table 4:

LM results of mean MAD by transect.

	DF	Sum Sq	Mean Sq	F value	P value	
Management	1	0.16	0.16	1.3	0.26	
Site	1	3.00	3.00	24.3	<0.001	***
Depth	1	0.22	0.22	1.8	0.19	
Mgmt:Site	1	0.02	0.02	0.2	0.67	
Residuals	94	11.62	0.12			

Table 5(on next page)

BRT model evaluation comparison for models including management (Mgmt), management and presence of resource species (Pres) and management and behavior (MAD).

Accuracy metrics include cross validated percent deviance explained (CV PDE), r-squared (R^2), and gaussian rank correlation estimate (GRCE). Error metrics include cross-validated standard error (CV SE), root mean square error (RMSE) and symmetric mean absolute percent error (SMAPE).

Table 5:

BRT model evaluation comparison for models including management (Mgmt), management and presence of resource species (Pres) and management and behavior (MAD).

Accuracy metrics include cross validated percent deviance explained (CV PDE), r-squared (R^2), and gaussian rank correlation estimate (GRCE). Error metrics include cross-validated standard error (CV SE), root mean square error (RMSE) and symmetric mean absolute percent error (SMAPE).

	Hanauma Bay			Pūpūkea		
	Mgmt	Mgmt + Pres	Mgmt + MAD	Mgmt	Mgmt + Pres	Mgmt + MAD
Accuracy						
CV PDE	56.8	67.5	72.5	10.4	14.8	32.6
R^2	0.37	0.43	0.58	0.27	0.42	0.57
GRCE	0.81	0.83	0.87	0.67	0.75	0.81
Error						
CV SE	7.6	6.7	5.7	19.4	12.7	10.0
RMSE	26.6	27.2	25.1	40.7	36.9	30.7
SMAPE	1.02	0.94	0.91	1.03	1.01	0.95