



Anthropogenic and environmental drivers of *Acanthurus achilles* presence in Hawai'i

Rachel B. Layko^{1,2}, Mary K. Donovan^{3,4,*}

¹School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, AZ 85281, USA

²Center for Global Discovery and Conservation Science, Arizona State University, Hilo, HI 96720, USA

³Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kāne'ohe, HI 96744, USA

⁴Hawai'i Monitoring and Reporting Collaborative (HIMARC), Kāne'ohe, HI 96744, USA

ABSTRACT: Despite the ecological and social importance of reef fishes, data on their populations, habitat use, and other drivers are often scarce, which creates challenges for effective management. These challenges are particularly acute for rare or at-risk species such as *Acanthurus achilles*, a reef fish with a documented population decline in recent years in Hawai'i, USA. We used a data set of *in situ* fish surveys from across the main Hawaiian Islands combined from multiple survey programs to quantify *A. achilles* presence and absence and applied generalized linear mixed-effects models to examine the relationships between presence of (1) all individuals, (2) juveniles, and (3) adults with 27 spatially continuous environmental and anthropogenic drivers to understand the main drivers of presence. Using the modeled relationships between presence and all drivers, we predicted the probability of *A. achilles* presence at a 100 m scale within the 30 m depth contour of the main Hawaiian Islands. Environmental drivers, especially habitat drivers such as depth and rugosity, emerged as significant drivers of *A. achilles* presence, while anthropogenic drivers like land-based pollution and fishing had fewer significant relationships with *A. achilles* presence. The predicted probability of presence varied both between islands as well as within islands, with the highest probability of presence around Kaho'olawe and Hawai'i and the lowest around O'ahu. Our modeling approach and high-resolution spatial predictions provide empirical evidence of the importance of environmental drivers in explaining *A. achilles* presence and identify preferred habitat at relevant scales for fisheries management.

KEY WORDS: Reef fish · Fisheries management · Human impacts · Species distribution models

1. INTRODUCTION

Coral reef fisheries provide livelihoods and crucial nutrition sources for millions of people (Cinner 2014, Golden et al. 2016) while also being closely tied to people's identities, lifestyles, and cultures (Cinner 2014, Kittinger et al. 2015, Grafeld et al. 2017). Despite their importance, our understanding and management of reef fisheries is limited by a lack of data. In particular, we lack data on fish biology, fisheries catch and effort, and other drivers of fish populations (Sadovy 2005, Costello et al. 2012, Zeller et al. 2015). A number of factors make it difficult to quantify reef

fishery dynamics, including the large geographic areas the fisheries span and the dispersed nature of the fisheries, which often involve many species and the use of multiple gear types (Pauly & Zeller 2014, McCoy et al. 2018). The current reporting systems that do exist are often not comprehensive, and catch is either under-reported or unreported altogether, especially in Pacific jurisdictions such as Hawai'i, USA (Zeller et al. 2008, Pauly & Zeller 2014). These challenges in reporting are especially problematic for non-commercial catch, which can make up a large proportion of a reef fishery; one study found that non-commercial reef fisheries in Hawai'i made up an

*Corresponding author: mdoono@hawaii.edu

average of 84% of total reef catch during the study period of 2004–2013 (McCoy et al. 2018).

When fisheries data are poor or incomplete, tools like species distribution models can be used to supplement data gaps and inform management (Young & Carr 2015, Oyafuso et al. 2017). Species distribution models evaluate the relationships between a species and drivers that influence its presence or abundance, and how these patterns manifest spatially. This approach can be used to provide insights on the distribution of rare species (Raxworthy et al. 2003, Guisan et al. 2006, Pearson et al. 2007) and to contextualize the relative influence of specific drivers, such as the role of fishing versus biophysical conditions (Donovan et al. 2023, Zuercher et al. 2023). Originally used for detecting species–environment relationships, species distribution models are now widely used for conservation planning (Guisan & Zimmermann 2000) and are especially powerful tools for data-poor fisheries given that they can be based on data sources that are either dependent on fisheries or independent from fisheries. These models are also effective tools for decision-makers and managers, because they can be used to predict biodiversity patterns based on available environmental data (Mellin et al. 2010) and to prioritize favorable areas for management (Villero et al. 2017, Sofaer et al. 2019).

In this study, we used a species distribution modeling approach to examine drivers of *Acanthurus achilles*, a rare and little-studied species of surgeonfish (Family: Acanthuridae) known in Hawai'i as pāku'iku'i. *A. achilles* inhabits Pacific reef ecosystems in Polynesia and Micronesia (Randall 2007), where this herbivorous reef fish species feeds on filamentous and leafy algae (Randall 2007). While few studies have been conducted on the basic biology and life history of *A. achilles* (T. B. Grabowski et al. unpubl.), observations described by Randall (2007) note that *A. achilles* is a territorial species that prefers shallow, wave-exposed rocky shores or coral reefs where its algal food source is abundant (Randall 2007). *A. achilles* is a culturally and ecologically important species in Hawai'i and both juveniles and adults are harvested (Titcomb 1972, Walsh et al. 2019).

Over the past 20 yr, monitoring data from the West Hawai'i Aquarium Project (WHAP) collected along the west coast of the island of Hawai'i have found that *A. achilles* populations and recruitment are in decline (Walsh et al. 2019). Juvenile *A. achilles* were previously targeted for aquaria before the closure of the aquarium fishery in 2017. Despite the closure of aquarium take and other spatial fishing restrictions, *A. achilles* population declines have persisted (Walsh et al. 2019). In response, the State of Hawai'i Division

of Aquatic Resources (DAR) temporarily closed *A. achilles* fishing in West Hawai'i in December 2022 for 2 yr to allow for studies on population status and trends and to identify suitable management strategies (West Hawai'i Pāku'iku'i Replenishment 2022). Our understanding of *A. achilles* in Hawai'i is limited due to poor data availability. In part, this may be because the areas that are regularly monitored by WHAP are limited in spatial scale and habitat diversity and may not be representative of the preferred habitat of *A. achilles* (Walsh 2014). Data collection for nearshore fisheries in Hawai'i is also limited, as no comprehensive data are collected on nearshore fishery production (McCoy et al. 2018), and fishing licenses are not currently required for non-commercial fishing.

While population declines of *A. achilles* have been recorded, the relationships between anthropogenic and environmental drivers and species presence are not well understood. Therefore, we examined *in situ* fish surveys combined from multiple sources alongside anthropogenic and environmental drivers to parse out the influence of environmental variability and human drivers on the presence of a declining and rarely studied species. This study addressed 2 overarching research objectives: (1) to identify which environmental and anthropogenic drivers are related to *A. achilles* presence, and (2) to determine which nearshore areas in Hawai'i are the most likely to support *A. achilles* populations. We predicted the probability of *A. achilles* presence to vary according to habitat characteristics, including a preference for high-energy, shallow, hard-bottom habitat (Randall 2007, Walsh et al. 2019). Further, we hypothesized that there would be negative relationships between anthropogenic drivers, including fishing, and *A. achilles* presence. Previous studies on other species from the genus *Acanthurus* in the Caribbean found differences in habitat distribution between juveniles and adults (Lawson et al. 1999); therefore, we also hypothesized that drivers of *A. achilles* presence would vary between adults and juveniles. By identifying the most important drivers of *A. achilles* presence and therefore areas of most suitable habitat, we aim to inform management decisions to improve outcomes for this declining species currently under consideration for adaptive management.

2. MATERIALS AND METHODS

We followed previously established methodology for using *in situ* fish surveys combined with environmental and anthropogenic driver data to examine the relationships between *Acanthurus achilles* presence

and drivers across the main Hawaiian Islands (Donovan et al. 2023).

The Hawaiian Islands are a chain of volcanic islands that span 2500 km in the Pacific Ocean and comprise

one of the most isolated archipelagos in the world. The study area included nearshore waters in the main Hawaiian Islands, 8 islands located at the southeastern extent of the larger archipelago (Fig. 1). The coral

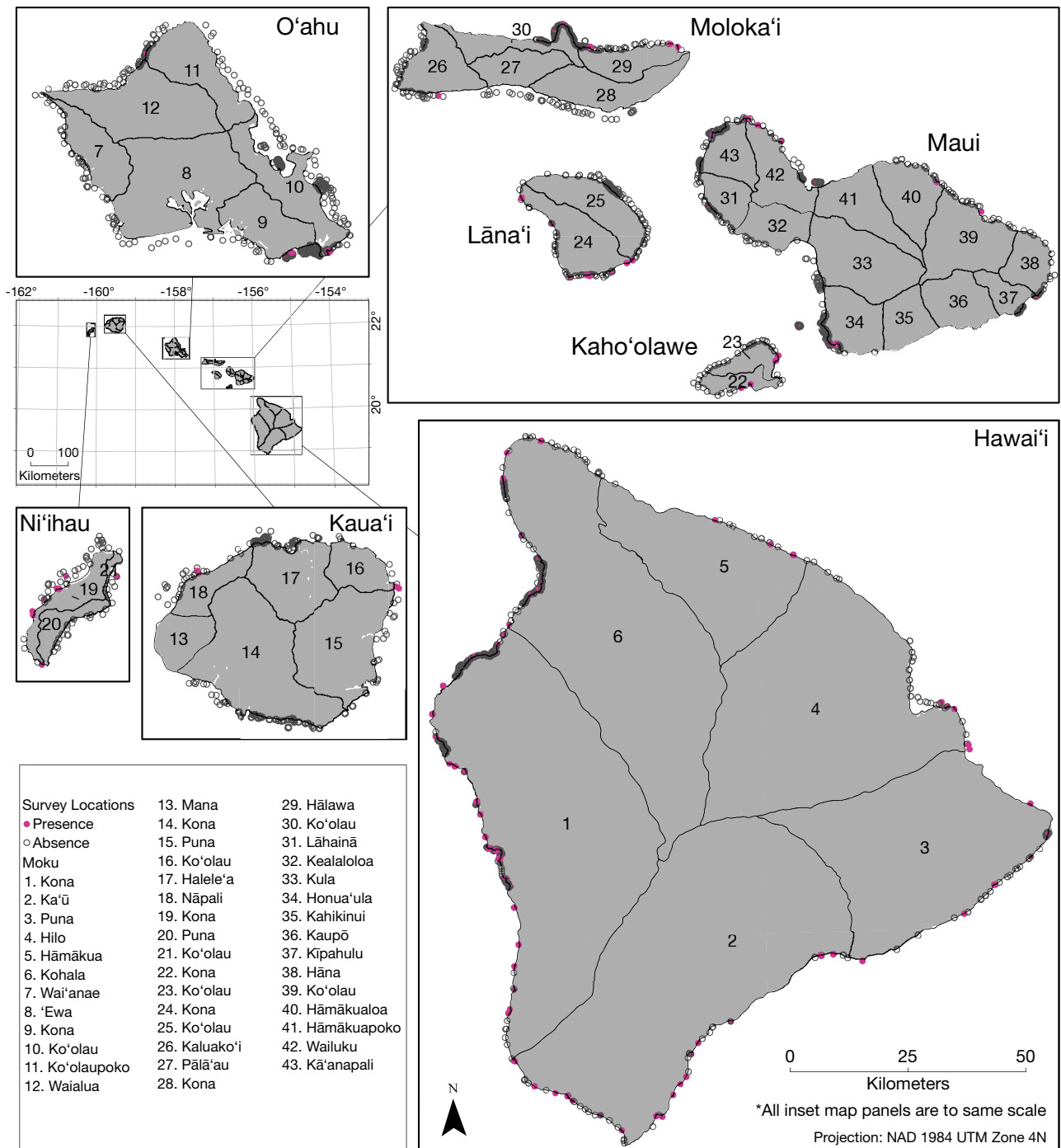


Fig. 1. Main Hawaiian Islands, displaying the location of surveys included in this analysis. Locations of *Acanthurus achilles* presence are shown as pink circles, and survey locations where no *A. achilles* were recorded are indicated by open circles. Black lines on land are moku boundaries, delineations used in traditional forms of resource management in Hawai'i, with numbers that correspond to moku names in the legend

communities of this archipelago are shaped by large swells and strong trade winds (Dollar 1982, Grigg 1983). Analysis was limited to hard-bottom habitat types, namely coral, pavement, and boulder habitats, that were up to 30 m in depth, as this is the depth limit of routine surveys.

Data on *A. achilles* presence and absence were collected from surveys compiled by the Hawai'i Monitoring and Reporting Collaborative (HIMARC) (Donovan et al. 2023). The HIMARC database consists of data collected by 7 different partner organizations; the data are standardized to create a spatially robust data set of nearshore fish counts within 0–30 m depth. Fish surveys were conducted predominately using belt transect methods (20 × 4, 25 × 4, or 25 × 5 m), with one data provider that also conducted 15 m diameter stationary point counts (Donovan et al. 2023). This analysis included 4775 surveys distributed across the 8 main Hawaiian Islands. Surveys were conducted between 2004 and 2014, which represents a time period before a major bleaching episode in Hawai'i in 2014–2015 that caused widespread coral mortality (Kramer et al. 2016) and is aligned with the timeframe of driver data sets (described in Section 2.1) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m740p161_supp.pdf). A focus on this timeframe also allows for understanding relationships between environmental and anthropogenic stressors related to *A. achilles* presence aside from coral bleaching, which is important because *A. achilles* populations were already declining prior to the major bleaching event in 2015 (Walsh et al. 2019).

2.1. Environmental and anthropogenic drivers of fish presence

We relied on existing driver data sets compiled by Lecky (2016), Wedding et al. (2018), and Donovan et al. (2023) (Table S1). We included 27 environmental and anthropogenic drivers in the model to account for gradients in local conditions across 4 groups: (1) land-based pollution, (2) fishing, (3) physical oceanography, and (4) habitat. The set of drivers used here was determined by Donovan et al. (2023) after assessing a larger set of variables and selecting the subset representative of the hypothesized drivers of reef fishes, with no driver pairs correlated above Spearman's ρ of 0.7. The final set of drivers was scaled to a common spatial extent and resolution of 100 m (Donovan et al. 2023) (Table S1). Land-based pollution includes drivers like golf course runoff, agriculture runoff, and habitat modification. Fishing drivers include both commercial

and non-commercial fishing, as well as different gear types including line, net, and spear. Physical oceanography includes drivers such as temperature, light, and productivity. Habitat drivers include habitat type (coral, pavement, boulder habitats), as well as depth and rugosity. See Table S1 for a full list of drivers and data sources. Before inclusion in the model, all continuous drivers were standardized to a zero mean and unit standard deviation to allow for comparisons across drivers with different units.

A generalized linear mixed effect model (GLMM) was used to examine the relationships between *A. achilles* presence and absence and the 27 environmental and anthropogenic drivers in the main Hawaiian Islands. We chose to investigate *A. achilles* presence rather than abundance due to the relative rareness of the species that makes abundance measures difficult to capture. Presence–absence data were used to model probability of presence using a generalized linear model with a binomial distribution and a logit link with the 'lme4' package in R (version 4.2.2) (Bates et al. 2015, R Core Team 2022). Additionally, 3 random intercepts were included to address spatial and temporal variation: survey year (to address temporal variation), data set ID (to address variation associated with the multiple data sets with different collection methods included in the HIMARC database), and moku (a cultural and ecological land division unit in the main Hawaiian Islands, to address spatial variation) (Donovan et al. 2023).

Because we hypothesized that the drivers of presence would vary by life history stage, we ran 3 models: (1) a full model with any observation of *A. achilles* defined as present, (2) a model with adult individuals greater than 15 cm in length as present, and (3) a model with juvenile individuals less than 15 cm as present. The 15 cm length cutoff was designed to select for individuals that have not yet reached sexual maturity and was based on life history data from T. B. Grabowski et al. (unpubl.) that estimated length of young of the year (YOY). We did not account for seasonality of recruitment in our juvenile model given evidence from a life history study suggesting that *A. achilles* in Hawai'i are continuous spawners (T. B. Grabowski et al. unpubl.).

For each of the 3 models, we included all drivers as fixed effects and the 3 random intercepts. For all 3 models, Y is 1 when *A. achilles* is present at location i and 0 otherwise. The model structure is as follows:

$$\text{Logit}(q_{iynd}) = \beta_0 + \bar{\mathbf{X}}_i \times \bar{\boldsymbol{\beta}} + \alpha_y + \gamma_m + \rho_d + \varepsilon_i \quad (1)$$

$$Y_i \sim \text{Bernoulli}(q_{iynd})$$

where β_0 is an intercept term, $\bar{\beta}$ are fixed effects, and \bar{X} is a matrix containing predictor data. ϵ_i is a normally distributed error term. We also included 3 random intercepts α for year (y), ρ for dataset (d), and γ for moku (m). Drivers were considered statistically significant if their coefficient p-value was less than 0.05. Model assumptions were validated by visually inspecting the residuals and conducting outlier and overdispersion tests (Hartig 2022). Pseudo R-squared values were obtained to assess model fit (Bartón 2023). We also assessed the predictive capabilities of the model by (1) comparing the deviance to a null model (intercept-only with no predictors but retaining the random effects), and (2) calculating classification error rate of the model predictions using probability cut-offs of 0.5, 0.7, and 0.9.

2.2. Spatial variation in the probability of drivers' influence on fish presence

To examine the spatial variability of *A. achilles* presence, the modeled relationships were used to predict the probability of presence across the entire study extent. This approach allowed us to estimate the predicted probability of *A. achilles* presence as a continuous raster, with values for all areas regardless of the availability of survey data. We predicted the median probability of *A. achilles* presence per pixel and constructed 95% prediction intervals considering only the fixed effects from the GLMM (Knowles et al. 2023). Pixels were classified as hard or soft bottom, and only those pixels classified as hard bottom were included in the analysis (Donovan et al. 2023). The output is a 100 m square grid of predicted probabilities of *A. achilles* presence for the study extent. Density plots of the predicted probability of presence were created to compare patterns at 2 spatial scales: between islands and between moku. Probability values were highly skewed toward 0, so the probabilities were log-transformed into logged odds, which is symmetric around 0, for interpretation.

3. RESULTS

3.1. Environmental and anthropogenic drivers of fish presence

We found more numerous significant relationships between environmental drivers and *Acanthurus achilles* presence and fewer significant relationships between anthropogenic drivers and *A. achilles* presence (Fig. 2),

which was consistent across all 3 models (all individuals, adults only, and juveniles only). The amount of variability explained by the drivers was consistent across the 3 models (Table S2), with pseudo- R^2 values equal to 0.42, 0.46, and 0.44 for the full, adult, and juvenile models, respectively. Additional variability was explained by the random effects with conditional R^2 values equal to 0.62, 0.55, and 0.66, respectively. Generally, the predictors were informative compared to a null model, with lower deviance explained across all models (Table S2), and classification error rate was greater than 90% across all models and all probability cutoffs (Table S2).

Significant relationships were most frequent between the physical oceanography drivers and *A. achilles* presence (Fig. 2). Three of the drivers had significant positive relationships with *A. achilles* presence across the 3 models: wave anomaly maximum (full: $\beta = 0.853$, $p \leq 0.001$, adult: $\beta = 0.880$, $p \leq 0.001$, juvenile: $\beta = 0.777$, $p \leq 0.001$), sea surface temperature (SST) long-term mean (full: $\beta = 1.015$, $p \leq 0.001$, adult: $\beta = 0.520$, $p = 0.02$, juvenile: $\beta = 1.244$, $p \leq 0.001$), and chlorophyll *a* (chl *a*) anomaly frequency (full: $\beta = 0.651$, $p \leq 0.001$, adult: $\beta = 0.737$, $p \leq 0.001$, juvenile: $\beta = 0.658$, $p \leq 0.001$). Of these drivers, SST long-term mean had the highest magnitude of effect, followed by wave anomaly maximum, and then chl *a* anomaly frequency. While relationships were mostly similar across the 3 models with respect to the physical oceanography drivers, there were several differences. Wave anomaly frequency had a significant positive relationship with *A. achilles* presence only in the full model ($\beta = 0.430$, $p = 0.003$). Chl *a* long-term mean had a significant negative relationship with *A. achilles* presence in both the adult and juvenile models (adult: $\beta = -0.904$, $p = 0.006$, juvenile: $\beta = -1.153$, $p = 0.001$), but not in the full model. Additionally, the juvenile model had several differences from the other models, including a significant negative relationship between SST standard deviation and juvenile *A. achilles* presence ($\beta = -0.486$, $p = 0.005$) and a positive significant relationship with chl *a* anomaly maximum and juvenile *A. achilles* presence ($\beta = -0.427$, $p = 0.036$).

Of the habitat variables considered, we found that depth and rugosity were significant across all 3 models (Fig. 2). Rugosity had a positive effect in all 3 models with *A. achilles* presence (full: $\beta = 0.532$, $p \leq 0.001$, adult: $\beta = 0.698$, $p \leq 0.001$, juvenile: $\beta = 0.353$, $p \leq 0.001$). Depth had a negative relationship with *A. achilles* presence in all 3 models (full: $\beta = -0.529$, $p \leq 0.001$, adult: $\beta = -0.817$, $p \leq 0.001$, juvenile: $\beta = -0.266$, $p = 0.021$). No significant relationships were identified for boulder habitat, while pavement habitat

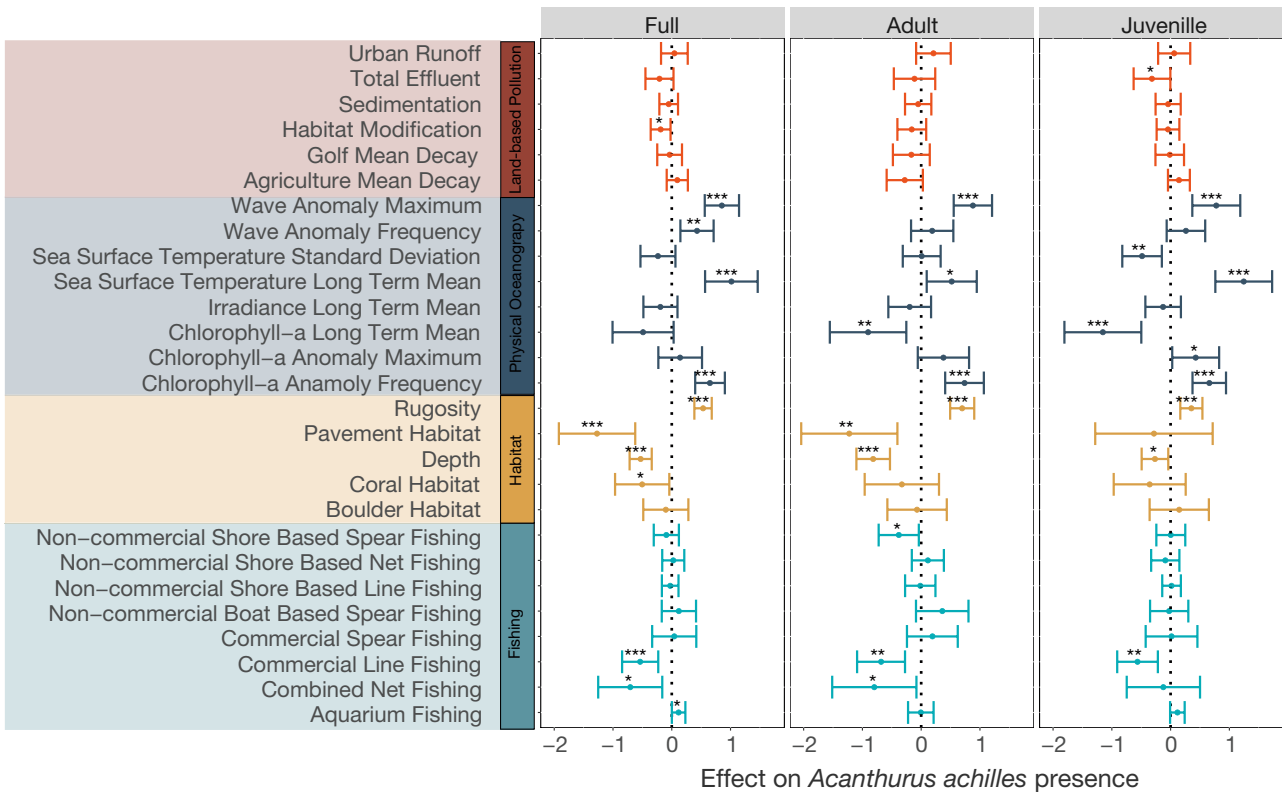


Fig. 2. Influence of drivers on *Acanthurus achilles* presence are represented by the coefficients (denoted as points) and bounded by 95% confidence intervals for each of the 3 models (panels). The x-axis represents the change in the log-odds probability of *Acanthurus achilles* presence. Drivers with confidence intervals that do not intersect the x-axis are significant and their corresponding p-values are indicated accordingly: ***p ≤ 0.001; **p ≤ 0.01; *p ≤ 0.05. Drivers with confidence intervals that intersect the x-axis are not significant

had a significant negative relationship in the full and adult models (full: $\beta = -1.272$, $p \leq 0.001$, adult: $\beta = -1.223$, $p = 0.003$), and coral habitat had a significant negative relationship only in the full model ($\beta = -0.503$, $p = 0.032$) (Fig. 2).

Anthropogenic drivers contributed less to the overall variation explained by the model (Fig. 2) compared to the oceanographic and habitat drivers. Overall, land-based pollution drivers largely did not have significant relationships with the probability of *A. achilles* presence. There were 2 exceptions: in the full model, habitat modification had a significant negative relationship with the probability of *A. achilles* presence ($\beta = -0.190$, $p = 0.028$) and in the juvenile model, total effluent was found to have a significant negative relationship ($\beta = -0.317$, $p = 0.047$).

Responses to fishing drivers were predominantly not significant or they were negative (Fig. 2). Commercial line fishing had a significant negative relationship with probability of presence in all 3 models (full: $\beta = -0.537$, $p = 0.001$, adult: $\beta = -0.683$, $p = 0.001$, juvenile: $\beta = -0.563$, $p = 0.001$). Combined net fishing had a significant negative effect in both the full

and adult models (full: $\beta = -0.707$, $p = 0.011$, adult: $\beta = -0.798$, $p = 0.029$), but not in the juvenile model. Additionally, non-commercial shore-based spearfishing had a significant negative relationship with the probability of *A. achilles* presence in the adult model ($\beta = -0.382$, $p = 0.028$). The only exception to these patterns was aquarium fishing, which had a significantly positive relationship with *A. achilles* presence in the full model ($\beta = 0.116$, $p = 0.047$).

3.2. Spatial variation in drivers' influence on fish presence

The predicted probability of *A. achilles* presence varied between and within islands (Fig. 3). While there was variation between moku on the same island, the probability of presence at the moku scale generally followed similar patterns (Fig. S1). As spatial patterns were similar across models, we focused on the full model results (results for the adult and juvenile models are shown in Figs. S2 & S3). The predicted probabilities over the study extent ranged from 0.000

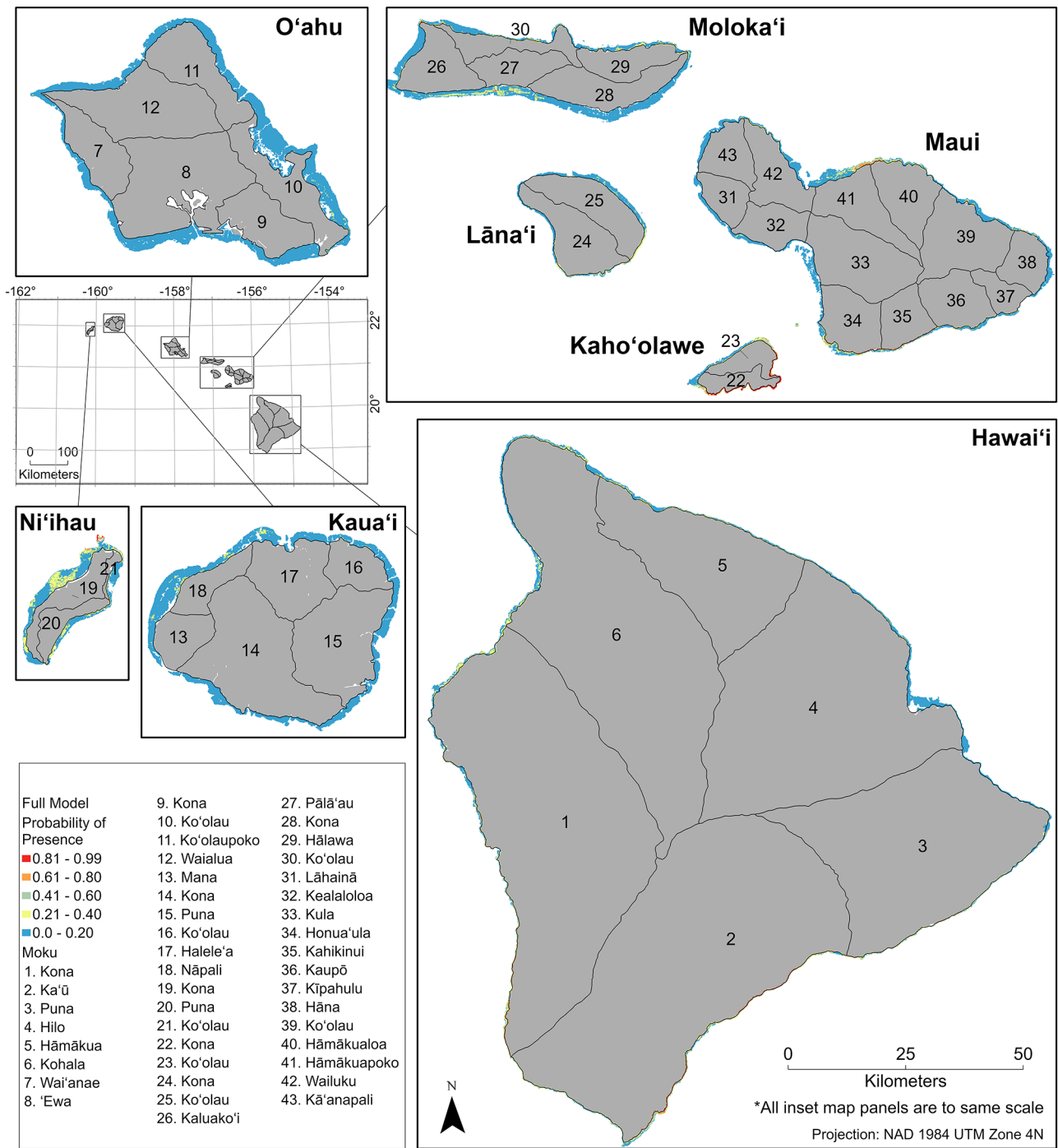


Fig. 3. Predicted probability of *Acanthurus achilles* presence based on the model with 27 drivers for all individuals (full model) for the entire study extent. Areas in blue and yellow indicate lower probability of presence, and areas in red and orange indicate higher probabilities of presence. Black lines on land are moku boundaries, delineations used in traditional forms of resource management in Hawai'i, with numbers that correspond to moku names in the legend

to 0.968, with a median of 0.032 and a mean of 0.111. By island, Kaho'olawe had the greatest mean probability of *A. achilles* presence, followed by Hawai'i and then Ni'ihau. O'ahu had the lowest probability of presence and Kaua'i had the second lowest (Fig. 4).

Broadly, the spatial predictions showed most areas to have a low predicted probability of *A. achilles* presence (Fig. 4). Areas of higher probability of presence were found in shallower areas and formed bands of higher predicted probability that wrapped around the

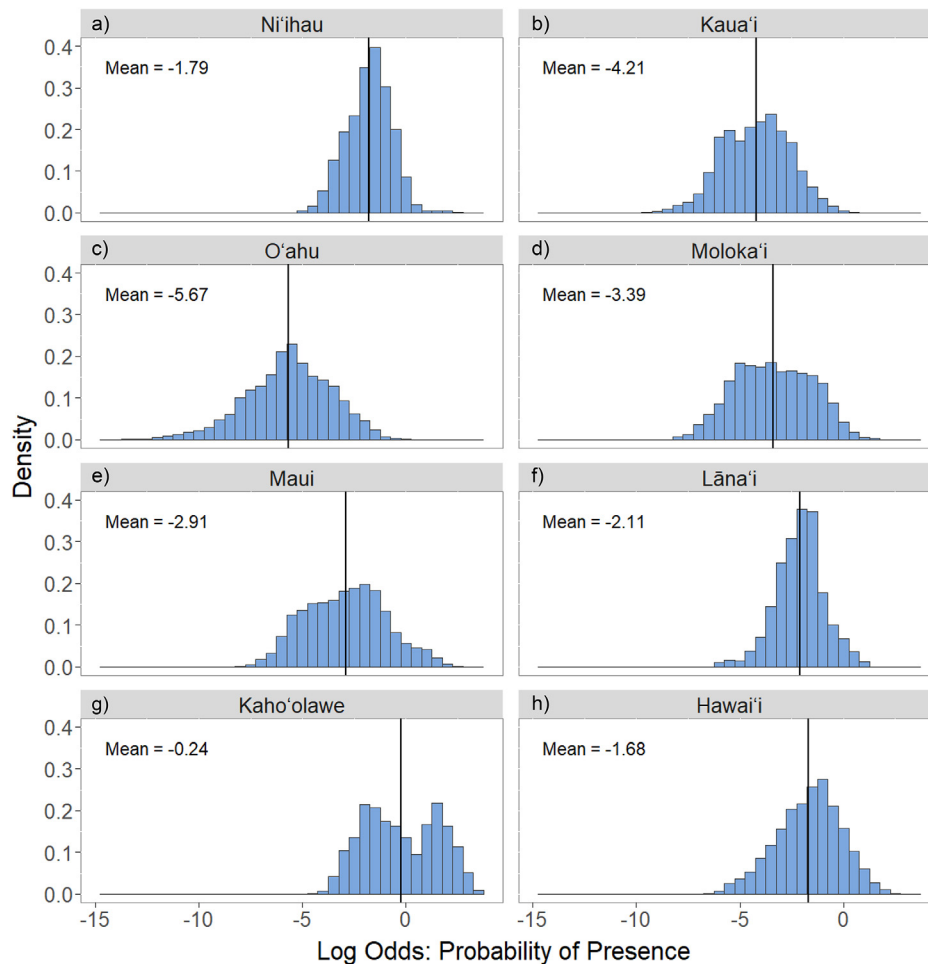


Fig. 4. Density of predicted log odds probability of *Acanthurus achilles* presence based on all pixels within the study extent for each island (a–h) roughly ordered from northwest to southeast (Fig. 1). The x-axis is the log odds probability of *A. achilles* presence and the y-axis is the density for each of the bins on the x-axis. The black vertical line represents the mean value of the log odds probability of presence and is labeled in the upper left corner of each plot

shorelines. In some areas, where the 30 m depth contour extends farther from shore, there were clusters of pixels with higher probability of presence that appeared in patch-like aggregations, particularly around Ni'ihau. Although Ni'ihau was not predicted to support areas of the highest probability of presence, the nearshore area had several larger patches with probabilities ranging from 20 to 40%. The southern and eastern sides of Kaho'olawe had the most continuous areas of high probability of presence, with most pixels classified as greater than 60% probability of presence. There were also large stretches of high predicted probability of presence in and around several bays on the southeastern side of Hawai'i, including Honomalo Bay and Okoe Bay, and on the southwestern side of the island spanning from Honu'apo Bay at the northern end to just shy of the southernmost point of Hawai'i Island. On Maui, several areas had high pre-

dicted probability of presence, including along the northern shore between Ku'au and Pauwela Point and along the southwestern point of the island. Uncertainty in the predicted probability of presence varied throughout the study extent and was largest at moderate probabilities, and while some areas had low positive probabilities of presence, the prediction often overlapped zero (Fig. 5).

4. DISCUSSION

We found that environmental variation was especially relevant for determining *Acanthurus achilles* presence in Hawai'i, indicating the importance of considering natural variation in the management of this species. Of the environmental drivers, the habitat drivers — most notably depth and rugosity — had sig-

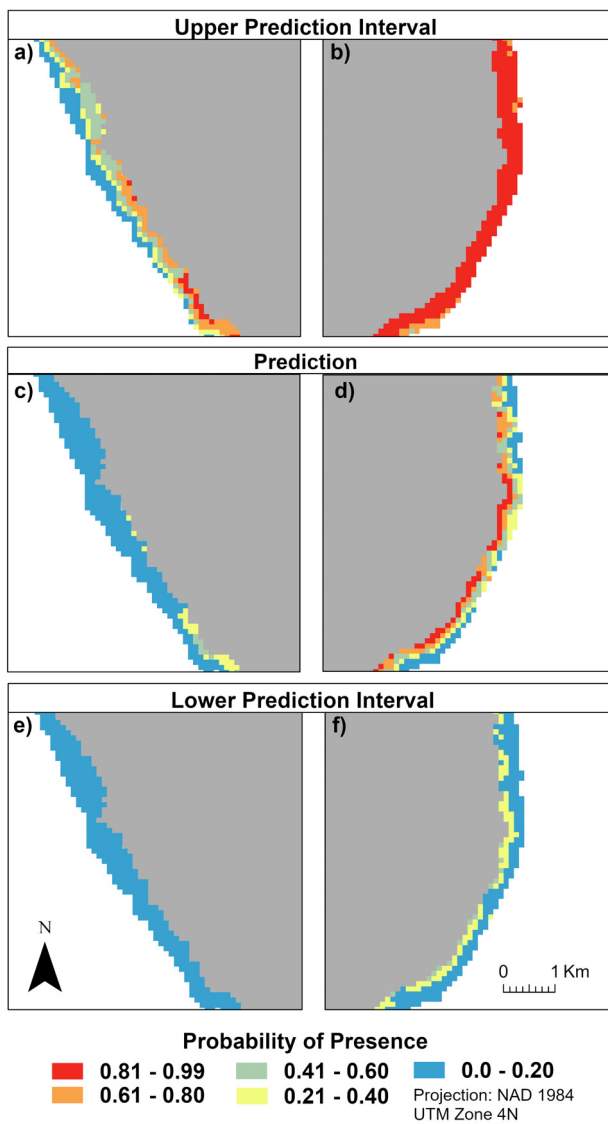


Fig. 5. Predicted probability of presence for 2 areas, one with (a,c,e) low predicted probability and one with (b,d,f) high predicted probabilities of presence. Panels (c) and (d) show the predicted probability of presence of *Acanthurus achilles*. Panels (a) and (b) show the upper bound of the 95% prediction interval, and panels (e) and (f) show the lower bound of the 95% prediction interval. Areas are anonymized so that the high-resolution spatial predictions can be displayed while still protecting the identity of the mapped locations and this sensitive fishery. All map panels are displayed at the same spatial scale

nificant and consistent trends across juveniles, adults, and all individuals combined, indicating the important role of these drivers in influencing *A. achilles* distribution. We also found that *A. achilles* are more likely to be found in warm and productive waters, indicated by the positive relationships with mean SST and chl *a* anomaly frequency. Fewer of the anthropo-

genic drivers we analyzed had significant relationships with *A. achilles* presence, and those that did were often weaker than other drivers and not significant across all 3 models. Our spatial predictions revealed wide variation in the probability of *A. achilles* presence across the main Hawaiian Islands and lesser variation between moku of the same island. The results underscore a need to explicitly consider environmental drivers in fisheries management approaches for *A. achilles*.

Natural gradients in biophysical drivers play important roles in coral reef ecosystems, for example, by shaping benthic regimes on reefs (Gove et al. 2015, Jouffray et al. 2019) and by constraining herbivorous fish populations (Cheal et al. 2012, Williams et al. 2015, Heenan et al. 2016). Therefore, our results, which underscore strong relationships between environmental drivers and *A. achilles* presence, are consistent with the broad understanding of reef system functioning and, more specifically, the role of environmental variability. We found that the probability of *A. achilles* presence was higher in more rugose areas, which is consistent with the positive relationship between rugosity and fish biomass that is well established in the literature (Caley & St John 1996, Friedlander & Parrish 1998, Gratwicke & Speight 2005). Further, *A. achilles* presence was positively associated with shallow areas with high wave energy which aligns with previous observations of *A. achilles* in high wave energy nearshore environments (Randall 2007) and with studies on other grazer surgeonfish species in multiple oceans (Bouchon-Navaro & Harmelin-Vivien 1981, Lewis & Wainwright 1985, Cheal et al. 2012), including in Hawai'i (Friedlander & Parrish 1998). Field and lab experiments have also demonstrated that wave energy shapes habitat use in coral reef fish, including Acanthuridae species, through species morphology and swimming performance (Fulton et al. 2005, Bejarano et al. 2017), as well as the productivity and availability of food sources (Oakley-Cogan et al. 2020). Time series data indicate that herbivore populations can be limited by food even in areas with moderate to high levels of fishing (Hawkins et al. 2006, Adam et al. 2011, Gilmour et al. 2013). Further, there is evidence of an interaction between habitat complexity and food availability, with herbivore biomass being disproportionately high when both food availability and habitat complexity were high (Helyer & Samhuri 2017). Given this context, alongside our results of a preference for complex, high wave energy habitats, food availability could be playing a significant role in determining the distribution of *A. achilles*. Although beyond the scope

of our models, patterns in dispersal and connectivity play important roles in species distribution in Hawai'i at multiple spatial scales (Christie et al. 2010, Toonen et al. 2011, Wren et al. 2016). The archipelago is not a single well-mixed community and is separated by several distinct multi-species barriers to dispersal formed in part by distance and ocean currents (Toonen et al. 2011). Additionally, marine protected areas or other types of spatial management can influence populations through dispersal (Christie et al. 2010). While we did not have the ability to evaluate the role of these forces in our analysis, we acknowledge the role of ocean currents and connectivity in determining locations of *A. achilles* presence.

We did not find strong evidence of a preferred habitat type across the categories we analyzed — pavement, coral, and boulder, which were compared against areas where habitat type is unknown. Locations were assigned to the 'unknown' category due to areas of low data quality or high uncertainty in the assigned habitat type and made up a small portion of the survey locations (904 of the total 4775). While the adult and full models found that the probability of presence was lower for pavement habitat, the juvenile model did not share the same patterns. There are several potential explanations for the limited significant relationships found between *A. achilles* and different habitat classes. First, it is possible that the spatial resolution of the habitat data (100 m pixels) did not capture relevant patterns of *A. achilles* habitat use. Scale is an important consideration in the detection of ecological relationships, and changes in the spatial resolution of habitat data can alter the detection of relationships between fish and habitat variables (Kendall et al. 2011). Further, reef fish species differ in their scales of movements and habitat usage (Meyer et al. 2010), an important consideration when designing studies that are at relevant spatial scales to reef fish (Sale 1998). In this study, we scaled the driver layers from their native spatial resolution to a consistent 100 m pixel scale. This standardization required downscaling of some of the driver layers, while other layers had to be upscaled, including the habitat raster, for making spatial predictions. However, we assigned habitat classes to the survey locations using the native resolution (60 m) habitat layer, but perhaps that resolution still does not capture fine-scale habitat differences and/or natural barriers between habitat types, which can play a role in reef fish species' home range and movement patterns (Meyer et al. 2010). Another layer of complexity is that ecologically relevant scales may differ between habitat types; a study on another species of acanthurid found that territory size in

uncolonized pavement was 4 times larger than that in reef crest habitat (Semmens et al. 2005). A second explanation for the habitat results is that our models captured habitat variation within other drivers that had significant relationships with *A. achilles* presence, including depth, rugosity, wave energy, and productivity drivers. A third possible explanation is that *A. achilles* are not selective in their habitat use. Surgeonfish play important roles as active mobile trophic links, and studies indicate that the capacity of surgeonfish to link reef and non-reef habitats may be higher than other reef fish families (Sambrook et al. 2019, Tebbett et al. 2022). Future analysis of habitat type could be improved by combining new data sources to delineate unknown habitat areas, by considering non-reef habitats in a broader seascape approach, and by evaluating the influence of habitat at different spatial resolutions.

We found a greater influence of environmental drivers as compared to anthropogenic drivers, possibly because the influence of anthropogenic drivers may be harder to detect given the rarity of *A. achilles* presence. Another possibility is that the influence of anthropogenic drivers was overwhelmed by the environmental drivers, and as our model did not include interactions, we were not able to capture this influence which previous studies have identified in Hawai'i (Williams et al. 2008, Helyer & Samhoury 2017). Of relevance to management for this species, most of the fishing drivers included in this analysis had non-significant relationships with *A. achilles* presence. The exceptions to this pattern were commercial line fishing, which had a significant negative relationship across all 3 models, and combined net fishing, which had a significant negative relationship in the adult and full models. These results should be interpreted cautiously, as they represent broad trends in fishing for all reef species and do not specifically focus on the *A. achilles* fishery. The prediction layers we used were based on island-wide totals (McCoy et al. 2018) that were then spatially dispersed in near-shore areas using different methods specific to the fishery (commercial, non-commercial) and gear type (Lecky 2016, Wedding et al. 2018). These layers represent our best understanding of the highly diverse and spatially dispersed non-commercial fisheries of Hawai'i of all reef fishes. The other significant relationship that emerged from the fishing drivers was a positive relationship between aquarium fishing and *A. achilles* presence in the full model. While no species-specific data are available for the food fishery, we know that *A. achilles* was the fourth most collected aquarium species prior to the statewide closure

of all aquarium fishing in 2018, although commercial aquarium landings had declined in the previous 2 decades prior to the aquarium fishery closure (Walsh et al. 2019), and non-commercial estimates of reef fish landings in West Hawai'i were estimated to be 3 times the amount of landings by the aquarium fishery (Walsh 2014). As *A. achilles* are a prized aquarium species, we would expect that aquarium fishers would target areas with high numbers of *A. achilles* and thus aquarium fishing and preferred *A. achilles* habitats would have similar spatial distributions. Further, the magnitude of the relationship was small relative to other drivers and not significant when adults and juveniles were investigated separately, so overall evidence of a relationship is weak. Nonetheless, this is a correlative study, and given that cause and effect cannot be established, and that the direction of this relationship is counter to the expectation that fishing can reduce population sizes, this finding does not indicate that aquarium fishing increases *A. achilles* presence.

We found wide variation in the probability of *A. achilles* between islands, demonstrated by the stark differences between the island of O'ahu, which had the lowest predicted probabilities of presence, and Kaho'olawe, which had the highest predicted probabilities of presence. O'ahu and Kaho'olawe represent opposite extremes of human population across Hawai'i. O'ahu is the most densely populated island, with a population density more than 5 times higher than Maui, the next most densely populated island (United States Census Bureau 2020), and contemporarily, Kaho'olawe is uninhabited. Previous studies have established that resource fish biomass in the main Hawaiian Islands varies with population density and found Kaho'olawe to have the highest biomass and densely populated O'ahu to have the lowest (Friedlander et al. 2018). While population density provides a good lens of comparison between these 2 islands, and our results follow similar patterns, these differences are also likely related to the environmental variation that differs between the 2 islands, given the dominance of those factors in our models. We found one of the largest contiguous patches of very high predicted probabilities of *A. achilles* presence along the southern coast of Kaho'olawe. The patterns of high predicted probability in this area align with the patterns of underlying driver layers which show high rugosity and high chl *a* anomaly frequency in this area, both of which were strong drivers in the model. In contrast, nearshore areas around O'ahu had the lowest predicted probabilities of *A. achilles* and were characterized by low rugosity, areas of modified habitat, and large swaths of pavement habitat, all

of which had negative relationships with *A. achilles* presence.

We found that drivers influencing the presence of all individuals and juveniles and adults were generally consistent. In some cases, we only detected the influence of a given driver in the model of all individuals, likely owing to statistical power from a larger proportion of observations with the species present. While the spatial predictions from the adults and juveniles followed similar patterns of locations with higher predicted probabilities of presence, the adult model predicted higher probabilities in presence with (1) respect to the geographic extent (more pixels with higher probabilities) as well as (2) higher individual probabilities (predicted value in a given pixel) in those areas, as compared to the juvenile model. Very little is known about the habitat use and geographic distribution of juvenile *A. achilles*, and our results do not add much to this lack of knowledge except that the underlying drivers are generally similar to those of adults.

Species distribution models are important tools to support decision-making and resource management but are often subject to multiple forms of uncertainty that limit their practical use (Rocchini et al. 2011). Uncertainty can stem from multiple sources, including the selection of variables, the spatial and temporal scales of the underlying data, and the statistical algorithm used (Wiens et al. 2009). Reporting the spatial distribution of uncertainty, alongside the estimated values from species distribution models, supports the utility of results for informing management because it helps users understand the overall quality of the model and can inform field application of model results (Guisan & Zimmermann 2000). However, despite the importance of presenting uncertainty, a review of marine-based species distribution models found that 94% of studies did not report uncertainty from data deficiencies and model parameters (Robinson et al. 2017). In our study, we analyzed and displayed uncertainty levels around our spatial predictions to highlight their strengths and limitations. The uncertainty levels of the predicted values are lowest around either limit of our predictions, 0 and 1, and the highest uncertainty values correspond with areas that have predicted probabilities of presence of around 0.50. Given that the data set we analyzed includes many more observed absences than presences, we anticipated having a higher degree of certainty in predicting areas with a high probability of presence. We included the prediction intervals on our maps to make the uncertainty around our predicted probability explicit and to indicate areas where mapped

values are the most reliable, which is important for decision-makers in considering the management of this sensitive fishery.

Our study is not an investigation of trends over time and cannot conclude which drivers are causing the observed population declines noted by Walsh (2014) and Walsh et al. (2019); however, we provide valuable insights on the characteristics of important habitat for this species. Our work contextualizes past observed declines by emphasizing the strong role of environmental variability in the presence of *A. achilles*. By combining these insights with time-series of drivers, future work could identify where population declines may or may not be related to human stressors. The combined database of underwater surveys from HIMARC provides a spatially and temporally robust fishery-independent database that made it possible to study this data-poor species. Concerns about the ability of monitoring protocols to capture *A. achilles* presence at shallow depths have been reported (Walsh et al. 2019), but we found *A. achilles* presence was well represented across depths by the in-water dive surveys used in this analysis (Fig. S4). A caveat of the driver layers is that they span 2004–2014, prior to several major bleaching events in Hawai'i that occurred in 2014, 2015, and 2019. These major bleaching events were highly site-specific and altered the reef community structure (Bahr et al. 2017, Winston et al. 2022). Including data following these bleaching events would contribute to additional understanding of how climate drivers are influencing habitat distribution of *A. achilles*. Finally, the data format provided by some data providers constrained our identification of YOY, which we used to distinguish between juvenile and adult individuals. Life history analyses suggest that YOY might reach 13.8 ± 1.1 cm fork length (mean \pm SE) (T. B. Grabowski et al. unpubl.), but because some data providers record individual length using bins of values (e.g. 12–15 cm), we were constrained by those bins and thus defined juveniles as ≤ 15 cm and adult individuals as > 15 cm.

5. CONCLUSION

We combined a robust set of presence and absence data with a suite of anthropogenic and environmental drivers to parse out the influence of different drivers on the probability of *Acanthurus achilles* presence and map how these driver relationships contributed to the spatial variation in patterns of predicted probability. Environmental drivers emerged as important in explaining patterns of *A. achilles* presence at the

statewide scale. While minimizing human stressors remains important, these findings highlight the importance of considering the role of ecosystem variability in species distributions, especially in the consideration of different management approaches. Preferred habitat for *A. achilles* includes areas that are warm and shallow with high rugosity, high energy, and high productivity. Spatial patterns of predicted presence vary between and within islands, which underscores the importance of local variation. Local fisheries management should consider these differences when evaluating interventions. Employing a species distribution modeling approach augments our understanding of data-poor fisheries to make informed management decisions, an especially imperative task given the importance of reef fish ecologically and socially and the multitude of threats that they face.

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