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Kisei R. Tanaka[1], Andrea L. Schmidt[1,2], Tye L. Kindinger[1], Jonathan L. Whitney[1], and Jennifer C. Samson[1]

[1] Pacific Islands Fisheries Science Center
National Marine Fisheries Service
1845 Wasp Boulevard
Honolulu, Hawaii 96818

[2] Cooperative Institute for Marine and Atmospheric Research
University of Hawaii
1000 Pope Road
Honolulu, Hawaii 96822

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Executive Summary

The Magnuson-Stevens Fishery Conservation and Management Act of 1996 directs regional fishery management councils and the National Marine Fisheries Service (NMFS) to identify and describe “essential fish habitat (EFH)” for all federally managed species to ensure conservation and sustainable management of living marine resources. This report summarizes the statistically-derived density patterns of *Aprion virescens* in shallow coastal waters of the main Hawaiian Islands (MHIs) from 2010 to 2019. A spatiotemporal modeling technique was used to predict changes in the species’ localized density (spatially resolved number of individual estimates per 100 m^2) in relation to environmental variables. *A. virescens* densities varied between 0 and 7.27 individuals per 100 m^2, while several hotspots coinciding with increased density were detected. Changes in *A. virescens* densities over time were best explained by the combination of static (depth) and a dynamic surface oceanographic condition (monthly surface wind speed variability). The geographic center of *A. virescens* density was observed between O‘ahu and Moloka‘i. The observed annual centroids shift was not reflective of a uniform shift in densities but localized changes in density across the MHI shallow waters. Overall, these findings indicate that a spatiotemporal model that can estimate local trends improved the interpretation of species distribution change. The results indicate shallow-water habitats in the MHIs are likely essential for *A. virescens*. The analysis identified existing challenges in determining habitat-use patterns and emphasized the further need for additional systematic sampling to refine the species’ distribution patterns within habitats.

Introduction

The Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens Act) of 1996 requires the identification and delineation of essential fish habitat (EFH), defined as *"those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity"* for all species under federal fishery management plans (AN ACT 1996; Waldeck and Buck 2001). Under the EFH definition, necessary habitat includes physical, chemical, and biological attributes that support the complete life cycle of a designated species (e.g., egg, larval, juvenile, adult, and spawning adult). The Magnuson-Stevens Act also stipulates that Fisheries Management Plans (FMPs) must *"(1) identify and describe EFH, (2) minimize to the extent practicable adverse effects from fishing on EFH and its ability to support fishery ecosystems, and (3) identify other actions to encourage conservation and enhancement of EFH*" [16 U.S.C. § 1853(a)(7)]. The biogeography of living marine resources (LMRs) is complex and can vary across space and time (e.g., Álvarez-Noriega et al., 2020). Without environmentally informed EFH delineations, resource managers will be unable to promote a sustainable fishery and healthy marine and freshwater ecosystems. It is, therefore, crucial to (1) develop approaches to monitor and quantity local species-habitat associations, and (2) understand and describe the species' spatial and temporal variations to incorporate EFH into fisheries management decisions.

Aprion virescens (common name 'green jobfish'; Hawaiian name 'uku') is a reef-associated snapper most often seen at depths of 0–180 m in tropical coastal Indo-Pacific regions (Froese and Pauly 2010; Nadon et al. 2020; Franklin 2021; O'Malley et al. 2021). *A. virescens* is commercially important throughout its geographic range and is often captured using baited handlines and surface trolling lures (Haight et al. 1993; Kelley and Ikehara 2006; Ayers 2022). In Hawaii, they are a principal species comprising the deep-slope bottom fish resource across the Hawaiian Archipelago, with a recent annual commercial harvest of 42 t in 2019 (HDAR, 2019). In shallower depths, *A. virescens* are a popular target for spearfishing in the main Hawaiian Islands and elsewhere. A recent benchmark analysis of *A. virescens* habitat completed by Nadon et al., (2020) found that the Greater Maui (Maui, Moloka'i, Lāna'i, and Kaho'olawe islands) contained a large portion of the specie's habitat (58%), followed by Hawaii (23%), O'ahu (11%), and Kaua'i- Ni'ihau (8%) (Nadon et al. 2020).

The EFH for *A. virescens* is broadly designated from the shoreline to offshore down to 240 meters deep (PIRO, 2020), with level 1 EFH projections available (i.e., species' presence/absence; Franklin 2021). The need to unify coastal land management with fishery management was reinforced by the EFH provisions in the reauthorization of the 1996 Magnuson-Stevens Act (AN ACT 1996). Coastal development and nearshore fishing activities in Hawaii may affect multiple aspects of *A. virescens* ecology (Friedlander et al. 2006). At the same time, there are few empirical studies quantifying the species' density (EFH level 2 criterion) in the shallow waters (0–30 m) (e.g., Meyer et al., 2007). Informed fisheries management decisions will likely depend on EFH relevant information, such as whether a target species exhibits an allometric relationship between distribution area and stock biomass. Data gaps hamper ongoing work to define the species' nearshore EFH. More information is needed on the species' habitat utilizations from offshore to nearshore to refine the species' EFH designations in the main

Hawaiian Islands (MHI), a goal identified as a research priority by the Western and Central Pacific Fisheries Commission (WPRFMC, 2021).

Under the Magnuson-Stevens Act, the Western Pacific Regional Fishery Management Council (WPFMC) has identified a need for a model-based approach in predicting the distribution of Management Unit Species (MUS) based on multiple habitat-related variables to designate essential fish habitat (EFH) and habitat areas of particular concern (HAPC) for all species included in the Fishery Ecosystem Plans (WPRFMC, 2021). This is particularly crucial and timely in data-poor Pacific regions where shifts in baseline environmental conditions are occurring at an accelerated rate. To this end, we developed a statistical EFH level-2 modeling framework employing a combination of *in-situ A. virescens* density data enhanced by various gridded satellite products to estimate the species' abundance in shallow MHI waters. This is the first study to use a large, fishery-independent database as a source of data for analysis and prediction of the habitat distribution of *A. virescens* along the nearshore coastal area in the MHI region. The results of this study provide information on the spatial distribution of *A. virescens*, which fisheries managers can use to distinguish the species' EFH and apply enhanced management strategies.

Material and Methods

Environmentally enhanced *Aprion virescens* in situ density data

The study domain encompasses the shallow (0–30 m) waters around the main Hawaiian Islands. The *in-situ* fishery-independent density observations for *A. virescens* were collected through the National Coral Reef Monitoring Program (NCRMP). The fishery-independent survey was based on a stratified random sampling design using the paired-diver stationary point count (SPC) method (Ayotte et al. 2015; Heenan et al. 2017; McCoy et al. 2019) (NCEI Accession 0162472, 0157591, 0210958, 0157589, 0157590, 0211063, 0210958) and collected during daylight hours. This survey occurred from April to December, but primarily from June to October. The SPC diver-based sampling method records fish species, size, and abundance in paired 15-m diameter survey cylinders (353 m^2) extending from the seafloor to the surface. The divers deploy a marked transect line across the main axis of the cylinders and use this line as a frame of reference to estimate the extent of the cylinders. These surveys provide site-level density and biomass records across a range of fish species and trophic groups. We used a portion of the survey data collected from 8 islands across the MHI region over 10 years (2010, 2012−2013, 2015−2016, 2019) at 2968 survey sites (Figure 1). The detailed description of this specific survey can be found in McCoy et al., (2019).

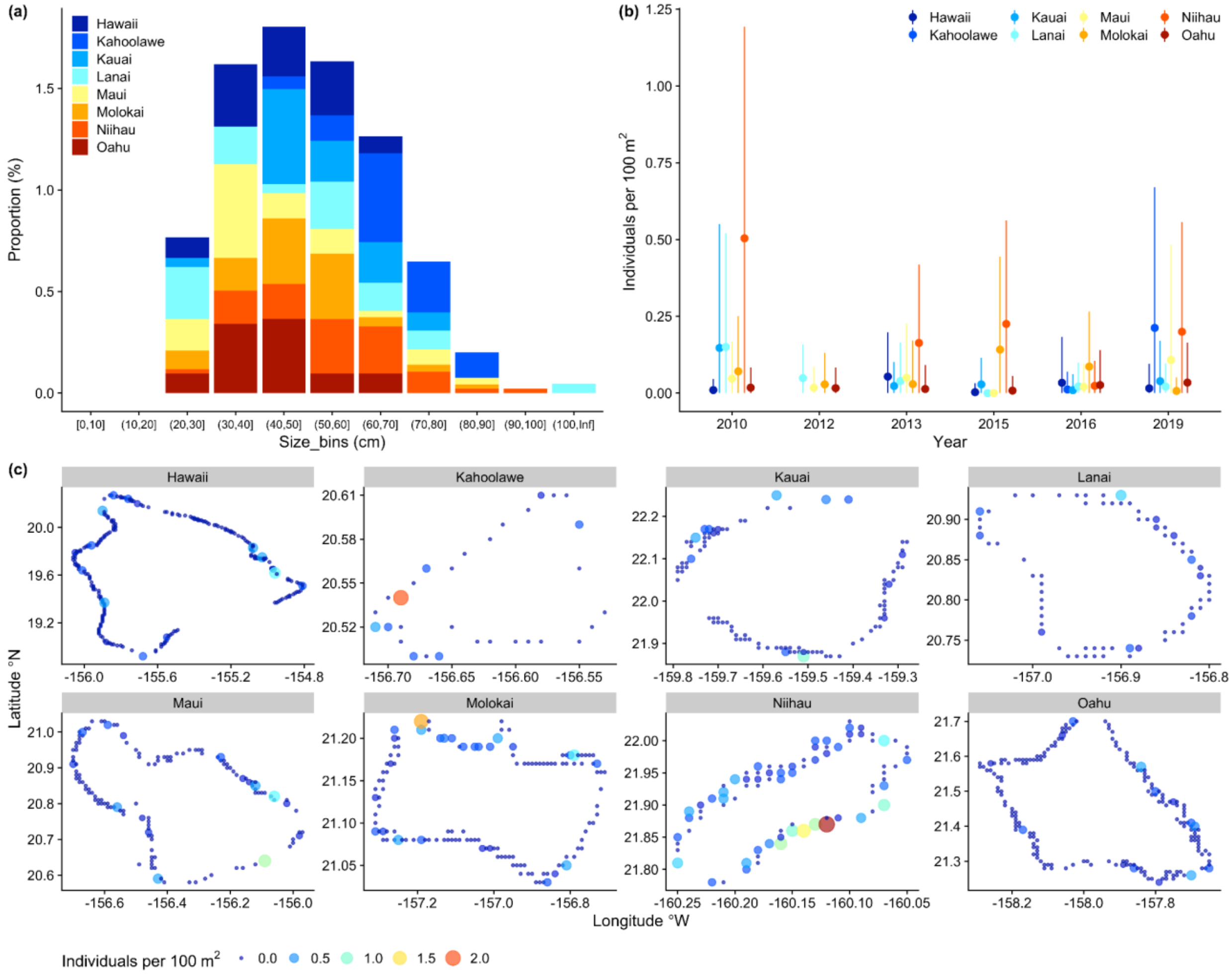

Figure 1. Fishery-independent (a) size compositions, (b) temporal trends, and (c) spatial distributions of Aprion virescens *density observations in the shallow main Hawaiian Islands waters (0−30 m) for the 2010−2019 period. Data were provided by from the National Coral Reef Monitoring Program.*[1]

Relevant environmental variables that are associated with the density distribution of *A. virescens* were included in the analysis: depth, sea surface temperature (SST), surface chlorophyll-*a* concentration (Chl _a), and surface wind speed (SWS) (Figure 2 & Table 1). Temporally corresponding SST, Chl_a, and SWS values at each surveyed location were obtained for every time-stamped and georeferenced NCRMP survey record (n=2968) using the Environmental Data Summary (EDS: Tanaka & Oliver 2021). The resolution of the environmental data was coarser than the expected accuracy of most survey site locations (<5 km), so horizontal positions were matched to the nearest available gridded data within 0.1°. Gridded SST data was gathered from the NOAA Daily Global 5km Geo-Polar Blended Sea Surface Temperature Analysis (v1.0;), which provided daily SST with a resolution of 0.05°. Daily surface Chl_a concentrations were averaged using two Chlorophyll-a datasets (Aqua MODIS v.2018.0 and ESA OC CCI v5.0; both at ~0.05° resolution; PML, 2020; Shanmugam, 2011)(Shanmugam 2011; Plymouth Marine

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[1] www.coris.noaa.gov/monitoring/

Laboratory 2020). The Daily Advanced Scatterometer (ASCAT) Surface Wind Fields Level 3 data set was used to derive daily sea surface wind speed with a resolution of 0.25° (Kako et al. 2011). A gridded bathymetric dataset (~0.0008° resolution) from the NOAA Coastal Relief Model, 3 arc second, Vol. 10 (NGDC, 2005), was used to estimate the depth at each horizontal position. For every dated NCRMP survey record, we used EDS to calculate each environmental variable's mean, standard deviation, 5th quantile, and 95th quantile values over the past one month from the corresponding survey date.

Table 1. Description of environmental variables included in Aprion virescens *density modeling effort. CRM: Coastal Relief Model, AquaMODIS: Aqua Moderate Resolution Imaging Spectroradiometer, ESA OCCCI: European Space Agency Ocean Colour Climate Change Initiative, ASCAT: Advanced Scatterometer.*

Data set	**Description**	**Temporal range**	**Spatial scale (°)**	**Sources**	**Unit**
Bathymetry_CRM	Ocean depth	n/a	0.0008	Coastwatch	m
Chlorophyll A AquaMODIS	Sea-surface chlorophyll concentration	8day	0.04	Oceanwatch	mg m^{-3}
Chlorophyll A ESA OCCCI	Sea-surface chlorophyll concentration	8day	0.04	Oceanwatch	mg m^{-3}
ASCAT Level 3	Sea-surface wind speed	Daily	0.25	Oceanwatch	m s^{-1}
NOAA Geo-Polar Blended SST Analysis	Sea-surface temperature	Daily	0.05	Oceanwatch	°C

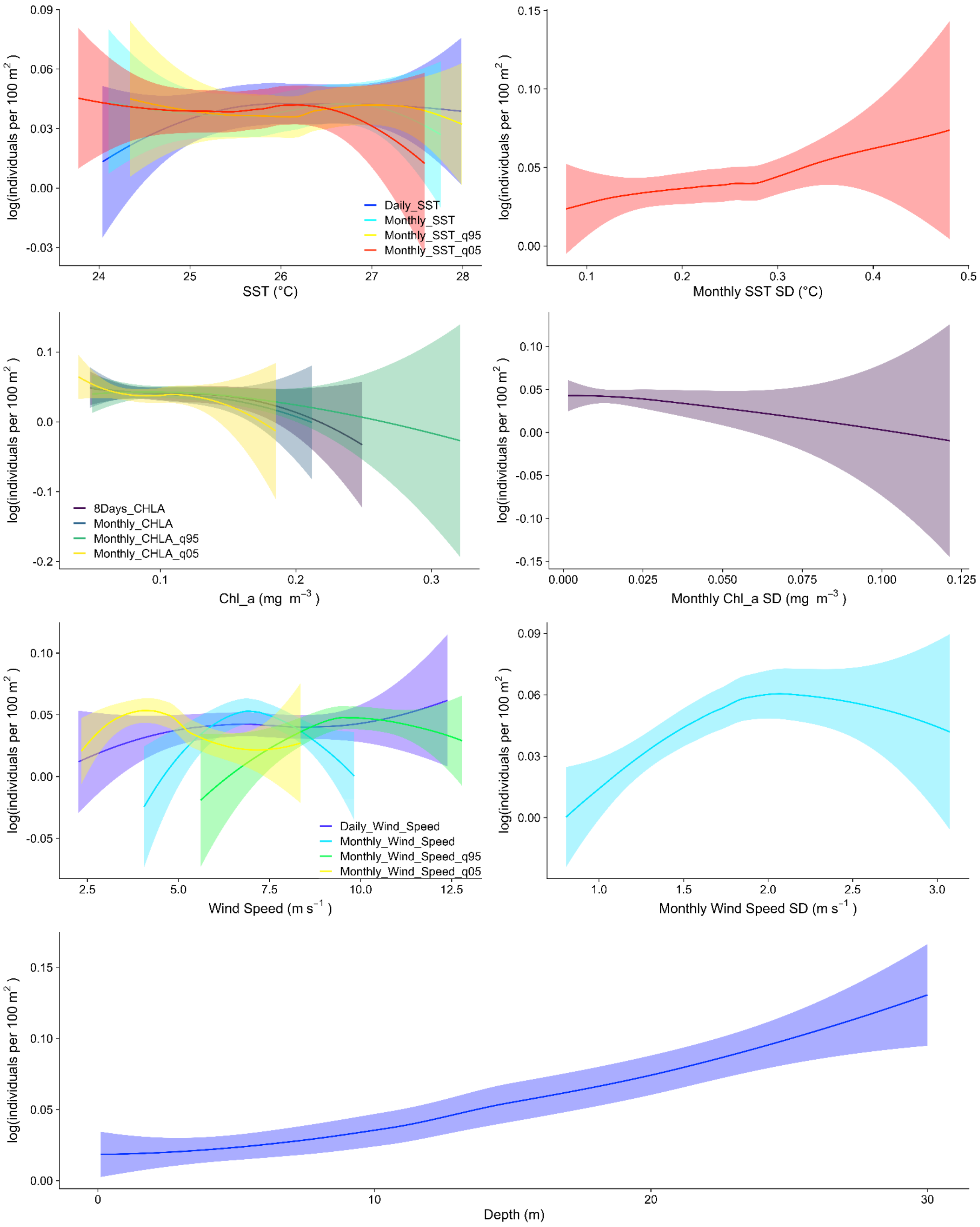

Figure 2. Differences in relative Aprion virescens *density (y-axis) at temporally-summarized environmental gradients in shallow main Hawaiian Islands waters (0–30 m). Solid line is a local polynomial regression fitting smoothing using a span of 1. Shaded area is 95% intervals.*

Spatiotemporal modeling of changes in *Aprion virescens* density

We estimated localized changes in the distribution of *A. virescens* density in relation to dynamic environmental variables using a spatiotemporal model. Spatiotemporal models are becoming increasingly popular in ecology. The approach incorporates a spatially explicit temporal trend (i.e., local trend) alongside spatial (temporally constant) and spatiotemporal (time-varying) components, thereby imposing correlation across space and time in the estimates of target response variables. Using this approach, *A. virescens* density is modeled as a function of 'fixed' effects resulting from explicit habitat variables and random effects as a product of unobserved or 'latent' spatiotemporal effects using Gaussian Markov random fields. Accounting for spatial autocorrelation between spatially referenced observations proximate in both space and time can derive biogeographical signals for evaluating the species' habitat preference in shallow water.

We applied a statistical mixed-modeling approach (generalized additive mixed-effect model; GAMM) that accounts for spatial autocorrelation between spatially referenced observations and effects of environmental drivers. While *A. virescens* is large (up to 112 cm total length), long-lived (up ~30 years old), and reaches sexual maturity at age 4 (Nadon et al. 2020), we modeled the density of all size bins and year class combined as the species exhibits low density across the MHI (mean 0.05, max 2.26 individuals per 100 m^2), we chose density over biomass as it is more relevant to the species' stock assessment (Nadon et al., 2020).

We used the R *sdmTMB* package (Barnett et al. 2021; Anderson et al. 2022) to fit a full spatiotemporally explicit GAMM with a local trend to estimate size-aggregated *A. virescens* density through space and time. The sdmTMB package provides a flexible mixed modeling framework that incorporates an automatic differentiation platform, which fits models by finding the minimum log likelihood based on nlminb optimization routine (Kristensen 2014). We included both spatial and spatiotemporal components. Sampling year was included as a factor (estimating a separate mean per year) to account for annual fluctuations in density. Environmental variables used to predict *A. virescens* density (e.g., depth and temperature) are often correlated. Variance inflation factors (VIFs) were therefore calculated, and variables with VIF value > 3 were removed to minimize collinearity (Table 1; Tanaka et al., 2017; Zuur et al., 2007). The full models were fitted with the VIF-filtered covariates (fixed year effects and five environmental covariates). We used thin plate regression splines with fixed basis dimensions to allow for a smooth relationship between some predictors and the response variable. *A. virescens* density data contained zero and continuous positive values. Therefore we used a Tweedie distribution model with a log link. This setting has been shown to perform well with zero-inflated data (Tweedie 1984; Tanaka et al. 2018; Barnett et al. 2021). The full model can be written as follows:

$$y_{s,t} \sim Tweedie(\mu_{s,t}, \rho, \Phi), 1 < \rho < 2,$$

$$\mu_{s,t} = exp\left(\alpha_t + \sum_{k=1}^{n_k} f_k(x_k) + \omega_s + \epsilon_{s,t} + \zeta_s t\right),$$

$$\omega \sim MVNormal\left(0, \sum\nolimits_{\omega}\right),$$

$$\epsilon_t \sim MVNormal\left(0, \sum\nolimits_{\varepsilon}\right),$$

$$\zeta \sim MVNormal\left(0, \sum\nolimits_{\zeta}\right),$$

Equation 1.

where $y_{s,t}$ is *A. virescens* density (individuals per 100 m^2) at location s and time t, μ is the mean *A. virescens* density at location *s* and time *t*, ρ is the Tweedie power parameter that varies between 1 and 2, and φ is the dispersion parameter. The α_t is estimated independently for each year (i.e., independent means for each year). The f_k is a spline smooth function for environmental covariate x_k. ω_s and $\epsilon_{s,t}$ are spatial and spatiotemporal random effects, respectively, derived from Gaussian Markov random fields (Cressie and Wikle 2015) with respective covariance matrices $\sum_{\varepsilon}$ and $\sum_{\omega}$. The $\zeta_s t$ are the spatially varying coefficients that capture local trends through time (i.e., 2010–2019), also derived from Gaussian Markov random fields. Time, t (i.e., year), is incorporated after multiplying with ζ_s and centered by its mean value. All random fields incorporate covariance matrices constrained by anisotropic Matérn covariance functions with independent scales but share the same κ parameters controlling the decay rate of spatial correlation as a function of distance (Thorson 2019; Wikle et al. 2019). Using the INLA package, the continuous random fields with triangulated mesh were prepared with vertices at 500 kt (Figure A2). The random fields account for spatial and temporal autocorrelation between sampling events and estimate unmeasured components of *A. virescens* habitat suitability (i.e., relative density), allowing that suitability to change through time. The models estimate a spatiotemporal random field that controls for remaining correlated spatial correlation processes each year that are not accounted for by the fixed effects. This random field follows a stationary autoregressive (AR1) process with a first-order correlation. Conventional diagnostic plots (quantile-quantile plot) and spatial patterns in residuals were examined to analyze model fits (Figure A3).

Identification of shallow water Aprion *virescens* density hotspots using local trends

We predicted *A. virescens* density at each grid location defined by NOAA CRM bathymetry data (originally at 3 arc seconds, ~90 m but aggregated to .01 decimal degrees) to develop a smooth surface of density estimates across the study domain. Predictions of the density of *A. virescens* were based on all fixed and random effects for each year. To investigate annual variability in the spatial distribution of *A. virescens*, we generated maps of mean predicted density (individuals per 100 m^2) from 2010 to 2019. We use the mean predicted density and localized linear trends over time as a benchmark for describing how *A. virescens* density distributions change. To provide a metric for comparing annual differences in the distribution of abundance, we estimated the center of gravity (COG) from predicted densities y for each location s and time t;

$$COG_t = \frac{\sum y_{st} L_s}{\sum Y_{st}}$$

Equation 2

where L_s is the y coordinate Y_{st} of location s. The COG is an important ecological indicator that describes the average latitudinal and longitudinal centers of the population (Tanaka et al. 2018; Friedland et al. 2021). All analyses were performed in the R programming environment.[2]

Results

Model Fit and Selection

Candidate predictors with VIF values > 3 were omitted before fitting a GAMM (Table 1). Stepwise backward selection using chi-square statistical tests and Akaike's information criteria (AIC) was used to reduce a post-VIF full model to a parsimonious model with lowest AIC and only significant variables (Tanaka et al. 2018). The inclusion of depth and monthly surface wind variability as predictors yield the parsimonious model identified by the AIC-based model selection procedure (Table 2). The addition of monthly surface wind variability showed a substantial decrease in AIC from the post-VIF full model (ΔAIC 7, Table 2) therefore included in the parsimonious model. Based on AIC and inspection of residuals (Figure A3a), the rest of the results will focus on analyzing the parsimonious model. The cross-validation result suggested that the final model can predict that the model performance was close to being ideal (1:1 slope; Figure A3b); however, variability in model accuracy increased at higher density (Figure A3b).

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[2] ver. 4.0.1.; R Core Team, 2021; <www.r-project.org>.
Reproducible R scripts and data can be found in github.com/krtanaka/pifsc_efh.

Table 2. The formula for Aprion virescens *density includes full and parsimonious models after covariate selection. SST: Sea Surface Temperature, ChlA: Chlorophyll_A, SWS: Surface Wind Speed. Knots are set at 5 for all continuous predator variables. VIF: Variance Inflation Factor. Covariates with VIF > 3 are shown in bold.*

Level	**Predictors**	**AIC**
Pre-VIF global model	Year + s(depth) + s(daily_SST) + s(**8day_ChlA**) + s(daily_SWS) + s(**monthly_mean_SST**) + s(**monthly_mean_ChlA**) + s(monthly_mean_SWS) + s(**monthly_95th_quantile_SST**) + s(**monthly_5th_quantile_SST**) + s(**monthly_95th_quantile_ChlA**) + s(monthly_5th_quantile_ChlA) + s(**monthly_95th_quantile_SWS**) + s(**monthly_5th_quantile_SWS**) + s(monthly_SST_SD) + s(monthly_ChlA_SD) + s(monthly_SWS_SD)	n/a
Post-VIF full model	Year + s(depth) + s(daily_SST) + s(daily_SWS) + s(monthly_mean_SWS) + s(monthly_5th_quantile_ChlA) + s(monthly_SST_SD) + s(monthly_ChlA_SD) + s(monthly_SWS_SD)	682.3
Parsimonious model	Year + s(depth) + s(monthly_SWS_SD)	675.4

Spatiotemporal dynamics of *Aprion virescens* density distributions in shallow waters

Response curves for *A. virescens* density as a function of depth and monthly surface wind variability (SD) were linear and dome-shaped, respectively, with higher density were predicted at deeper and higher wind speed variability (Figure 3). The predicted *A. virescens* density varied from 0 to 7.27 individuals per 100 m^2 from 2010 to 2019, where the lowest mean density was found in O‘ahu ($\mu = 0.02$, $\sigma = 1.2*10^{-4}$), and the highest was from Ni‘ihau and Kaua‘i islands ($\mu = 0.1$, $\sigma = 7.9*10^{-4}$) (Table 3 & Figure 4a). The highest mean predicted density was found in the Ni‘ihau−Kaua‘i region, while O‘ahu was characterized with the lowest predicted density. Predictions from the parsimonious model show fine-scale spatial structures in rates of changes of *A. virescens* density across the MHI region (Figure 4b). An increase in density was most pronounced in the southwest corners of Ni‘ihau and Kaua‘i, while overall decreasing trends were found across the MHI region (Figure A4). Note that these density distributions extend deeper than 30 m, and findings from these analyses only describe the dynamics of density distribution within the MHI survey domain of 0−30 m.

From 2010 to 2019, mean *A. virescens* density varied between 0.02 and 0.15 individuals per 100 m^2 while linear trends varied from -0.065 (O‘ahu) to 0.041 year-1 (Ni‘ihau−Kaua‘i) (Figure 5a). No significant trends were found over time in any sub-regional groups (Figure 5a). The geographic center of *A. virescens* density showed moderate interannual variability between O‘ahu and Moloka‘i, where the largest COG shift occurred between 2015 and 2016 (Figure 5b). The observed shift over time in the COG is not reflective of a uniform shift in densities, but likely reflects localized changes in density in MHI islands (e.g., Maui and Hawai‘i).

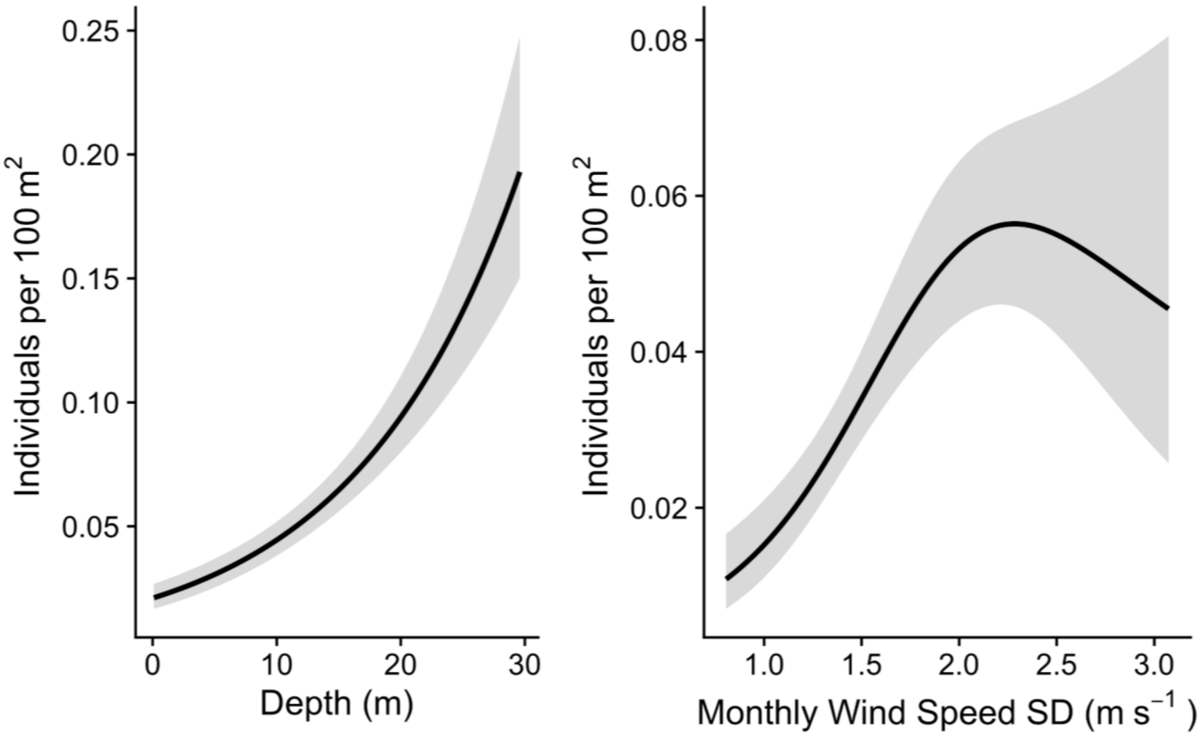

Figure 3. Plots describing the partial effect of significant univariate environmental variables in the best-fitting generalized additive mixed models for Aprion virescens *density in the MHI shallow waters, with 95% confidence intervals for the fitted line.*

Table 3. Summary of predicted Aprion virescens *density (individuals per 100 m^2) modeling efforts in the MHI shallow waters, 2010–2019.*

Islands	**Max**	**Mean**	**SE**
Ni‘ihau–Kaua‘i	3.6	0.1	0.000791
O‘ahu	1.01	0.02	0.000122
Moloka‘i–Maui–Lāna‘i–Kaho‘olawe	7.27	0.06	0.000346
Hawai‘i	2.11	0.04	0.000355

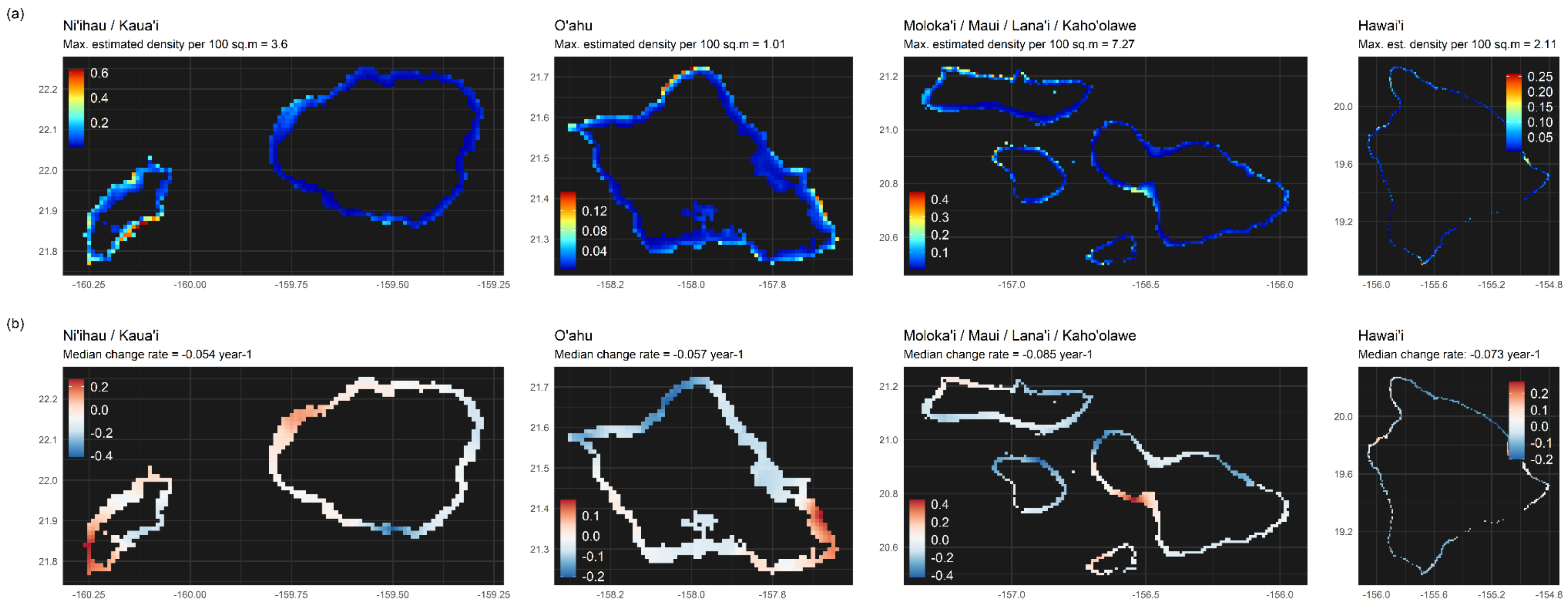

Figure 4. Model predicted spatial and temporal patterns of Aprion virescens *density across the main Hawaiian Islands; (a) spatial distribution of mean density (individuals per 100 m^2) over 2010–2019, (b) predicted local trend (slope coefficient of log density) over 2010–2019. All predictions were made across a 0.01 decimal degree grid to 30-m depth.*

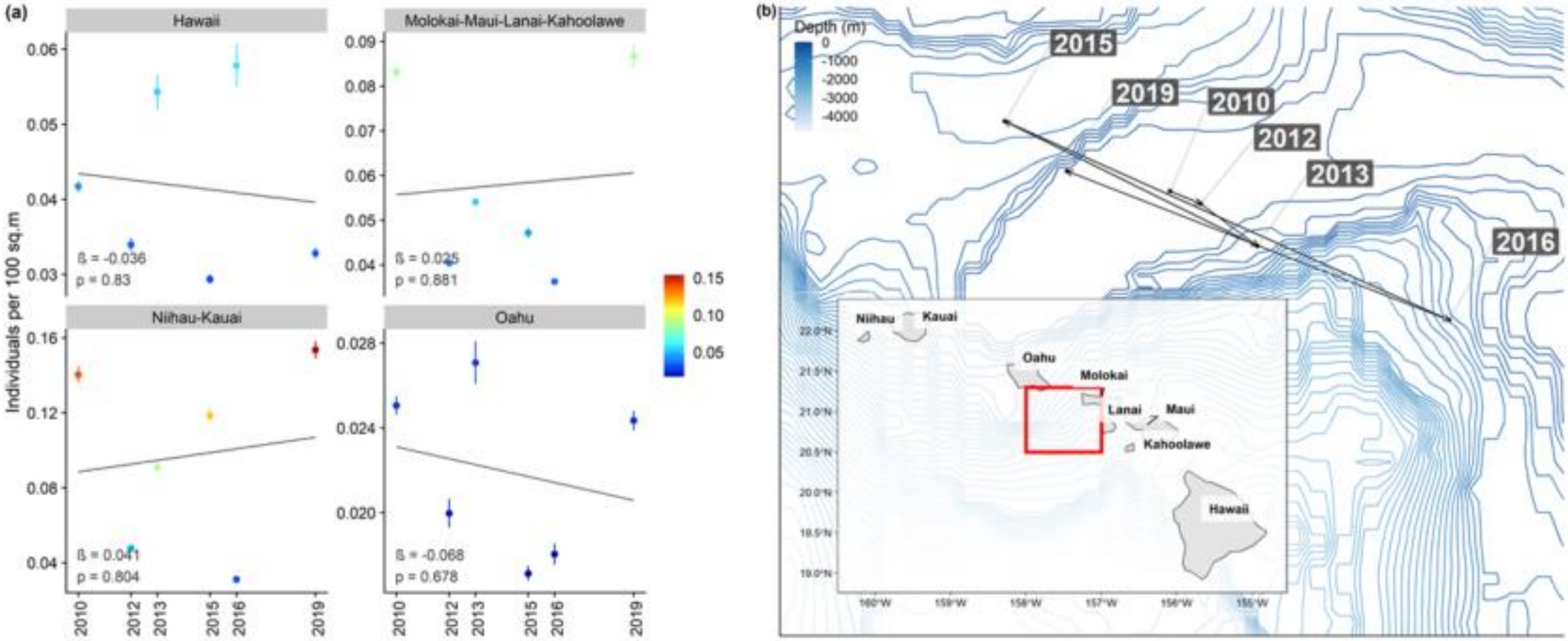

Figure 5. Interannual changes in Aprion virescens density estimates from 2010 and 2019: (a) temporal trends with 95% confidence intervals, (b) changes in center of gravity (COG), where arrows represent the direction of change in annual centroids.

Discussion

Few studies have characterized *A. virescens* EFH (Meyer et al. 2007; Franklin 2021). In the MHI, the species is considered a habitat generalist and displays wide distribution coupled with various habitat ranges, including shallow-water reefs, insular shelves, and deep-water slopes between 20 m and 180 m (O'Malley et al. 2021). The predicted abundance estimates were coherent with those obtained in previous studies in the MHI (e.g., Franklin, 2021; Nadon et al., 2020). A recent analysis of *A. virescens* habitat found that the Maui Nui complex hosts a large portion of the species' habitat in the MHI, where our density modeling also showed higher density in Niʻihau, Molokaʻi, and Maui (max = 7.27, μ = 0.06, σ = 0.000346; Figure 4a). While we found generally low *A. virescens* density (< 0.05 individuals per 100 m^2) across the shallow MHI waters, the density COGs were found near Penguin Bank (-11.42°N 175.5°W; Figure 5b), implying that the species density in shallow waters was predicted across the study domain. The density modeling of *A. virescens* revealed a significant linear positive relationship with depth and a tendency for *A. virescens* density to be highest toward deeper waters (Figure 3). This finding agrees with a recent EFH level 1 (presence-absence) analysis conducted at a larger spatial scale (Franklin 2021). The conventional model selection indicates that common oceanographic variables such as chlorophyll-*a* concentration (Chl-*a*) and sea surface temperature (SST) were less useful or statistically unrelated. The mixed additive modeling approach revealed a quantified additive influence of dynamic and static environmental covariates. Higher *A. virescens* density was more likely to be observed in deeper waters when surface wind variability over the past month is high (Figure 3). However, the predicted patterns in *A. virescens* density found in this study does not necessarily imply an overall population ecology at the regional level (i.e., species whole distribution range across MHI), and the density-environment relationship found in this study should be treated with caution as individuals from unsampled areas (areas with depth > 30 m) were not incorporated in our density modeling. For example, the deeper depth ranges of Penguin Bank are considered the species' core habitats (25% interquartile range of predicted occurrence), but were outside of this study's spatial scope (Franklin 2021).

Federal and state agencies are tasked with conducting population and habitat assessments for living marine resources (LMR) using the best available data and models. We used spatiotemporal modeling of geographically comprehensive fishery-independent data to derive the first-ever model-based density estimates of a bottom-fish MUS across the MHI shallow waters. Spatiotemporal models that reflect LMR distributions, such as those used here, can be harnessed to understand large-scale patterns and processes that drive LMR habitat use (Brodie et al. 2020; Evans et al. 2021). This information may be used to enhance indices of relative abundance that serve as proxies for the CPUE, which is commonly used as the index in stock assessment modeling and in determining stock abundance status (Thorson et al. 2015; Cao et al. 2017). Our study also establishes a way to account for uneven sampling effort and incorporate habitat condition information, including oceanographic indices as demonstrated here, into a target species density estimate. Local environmental variables, such as SST and Chl-*a* considered in this study, were often unavailable to capture complex associations between environment and ecological process due to original survey designs and time lags in species responses coupled with the non-linear intrinsic nature of population dynamics (Hallett et al. 2004). This approach includes temporarily summarized habitat conditions as additional covariates to explain variation in groundfish spatiotemporal density (Tanaka and Oliver 2021). The methodology developed in this study is applicable to other regions where commercially important fish span areas monitored by multiple scientific surveys. This type of information is critical in developing informed management strategies such as marine spatial planning (Evans et al. 2021). This study presents the first step towards incorporating the physical and climate variables that lead to the development of dynamic EFH analysis, with the ultimate goal of delineating EFH across the MHI region.

However, as with any modeling exercise, some caution should be exercised when interpreting the results. The analysis was restricted to fishery-independent data to provide statistically comparable density estimates in shallow-water areas. Existing diver and camera surveys providing information on species abundance in this region have large temporal gaps, meaning that these data may not accurately represent the target species' ecology. For example, the NCRMP survey covers a broad spatial range but lacks seasonality data, as it only covers a fraction of the surveyed year. *A. virescens* exhibits a strong seasonality characterized by the summer spawning season (Everson et al. 1989) and winter-summer migrations (Meyer et al. 2007). Furthermore, the NCRMP sampling design targets hard-bottom and reef-associated fishes (McCoy et al. 2019), while *A. virescens* is known to utilize soft bottom, low rugosity habitat, and the transition between the two (Whitney, *per.comm),* meaning that NCRMP surveys likely provide an incomplete understanding of the species' affinity for seasonally-dependent habitats. In addition, as our focus was on size and sex aggregated *A. virescens* density changes, phenological differences between life stages, such as shifts in habitat preferences between juvenile and adult stages (Tanaka et al. 2018), were not addressed. Current work on habitat preferences of early life stages is limited and most *A. virescens* larvae sampling sites occur in the water-column and do not overlap with those covered by NCRMP surveys. The smallest individual *A. virescens* detected in NCRMP visual surveys was 22 cm (Whitney, *per. comm*), and therefore the underlying data set does not characterize juvenile stages. For early life stages, previous definitions of *A. virescens* EFH assumed that larval depth was limited to the lower limit of the adult habitat (WPRFMC, 2011). Analyses of depth integrated ichthyoplankton tows taken offshore of Oahu in 1985−1986 suggest a maximum depth of 40 m for larvae between 2 and 6.5 mm in length (Schmidt, *per. comm;* Boehlert & Mundy, 1996). Habitat preferences and distribution patterns for early life stages, particularly larger larvae and pelagic juveniles remains unknown as individuals these sizes (~3−9 cm) are absent from collections or available survey data. This knowledge gap limits our understanding of the pelagic and benthic habitats used during the first year after hatching. Studies on juvenile *A. virescens* benthic habitat preferences are also extremely limited. A single juvenile has been found in a flat hard-bottom area with *Halimeda sp.* stands (Parrish 1989). In a separate study focused on adults, the single sexually immature individual in the study appeared to have high residency at the site in question (Filous et al. 2017). Future research should focus on (1) understanding habitat use of early life stages (<9 cm) especially surveys of larvae in nearshore water column and juveniles transitioning from pelagic to benthic habitat; (2) quantifying environmental effects on the species' relevant life cycle phases and (3) improving links between response variables' spatial and temporal scales with environmental predictors. These factors would likely improve the utility of EFH model outputs and may result in an improved understanding of environmental variables driving *A. virescens* distribution throughout their life cycle.

Currently, there is a lack of information on the influence of environmental variables or abiotic factors (e.g., depth, temperature, oxygen) on the spatiotemporal distribution of MUS. Diverse information sets are necessary to manage EFH and protected areas involving multispecies fisheries. The previous review panel's recommendations included increasing efforts to monitor and record various *in situ* environmental variables (e.g., bottom water temperature and salinity) in fishery-independent surveys. Calibrating historical data and coordinating future data collection efforts to fully understand and manage changing density and shifting distribution of fish species can serve as platforms to synthesize the ecology of these MUS.

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Appendix A

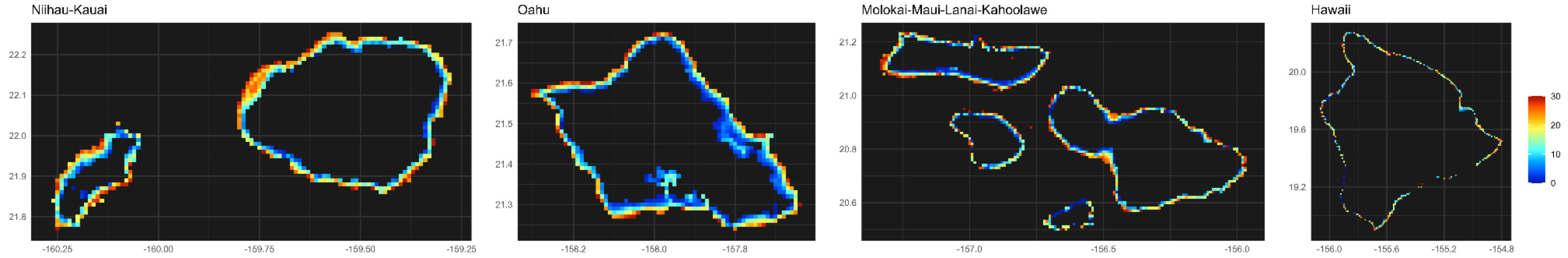

Figure A 1. Bathymetric profiles of Aprion virescens *density model domain within the main Hawaiian Islands. Bathymetric data were drawn from NOAA Coastal Relief Model, 3 arc second, Vol. 10.*

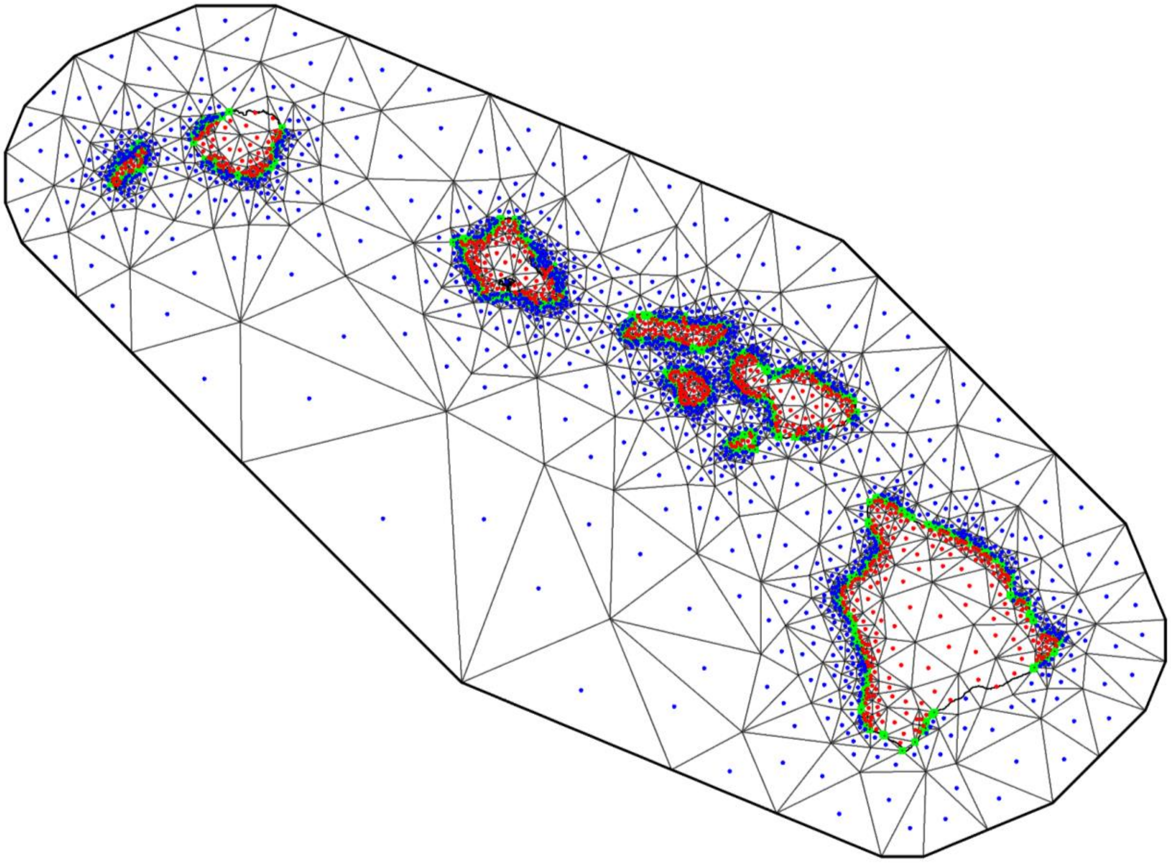

Figure A 2. Triangulated mesh covering the main Hawaiian Islands region prepared with vertices at 500 kt using the R INLA package. Axis units are in km based on UTM Zone 4 projection. Polygons with blue points represent spatial domains considered for spatial autocorrelations in the spatiotemporal generalized linear mixed model calibration process. Polygons with green dots represent land masses and were not included in the spatial autocorrelations in the spatiotemporal generalized linear mixed model calibration process.

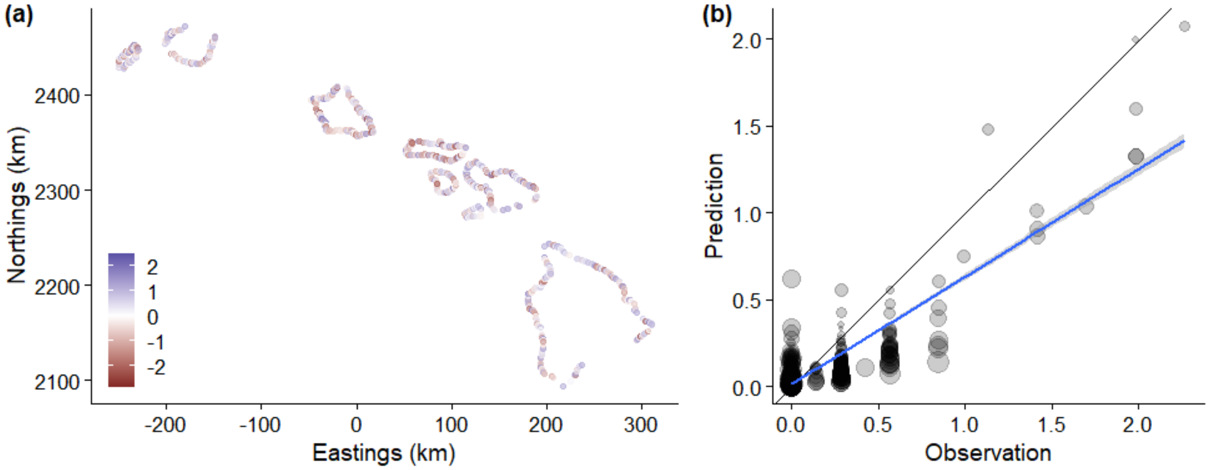

Figure A 3. (a) Graphical summary of model residuals for the season-, stage-, and sex-aggregated Aprion virescens *generalized additive mixed modelling effort, and (b) observed versus predicted plots complemented by linear regression lines. The solid line represents the 1:1 line and an ideal model performance.*

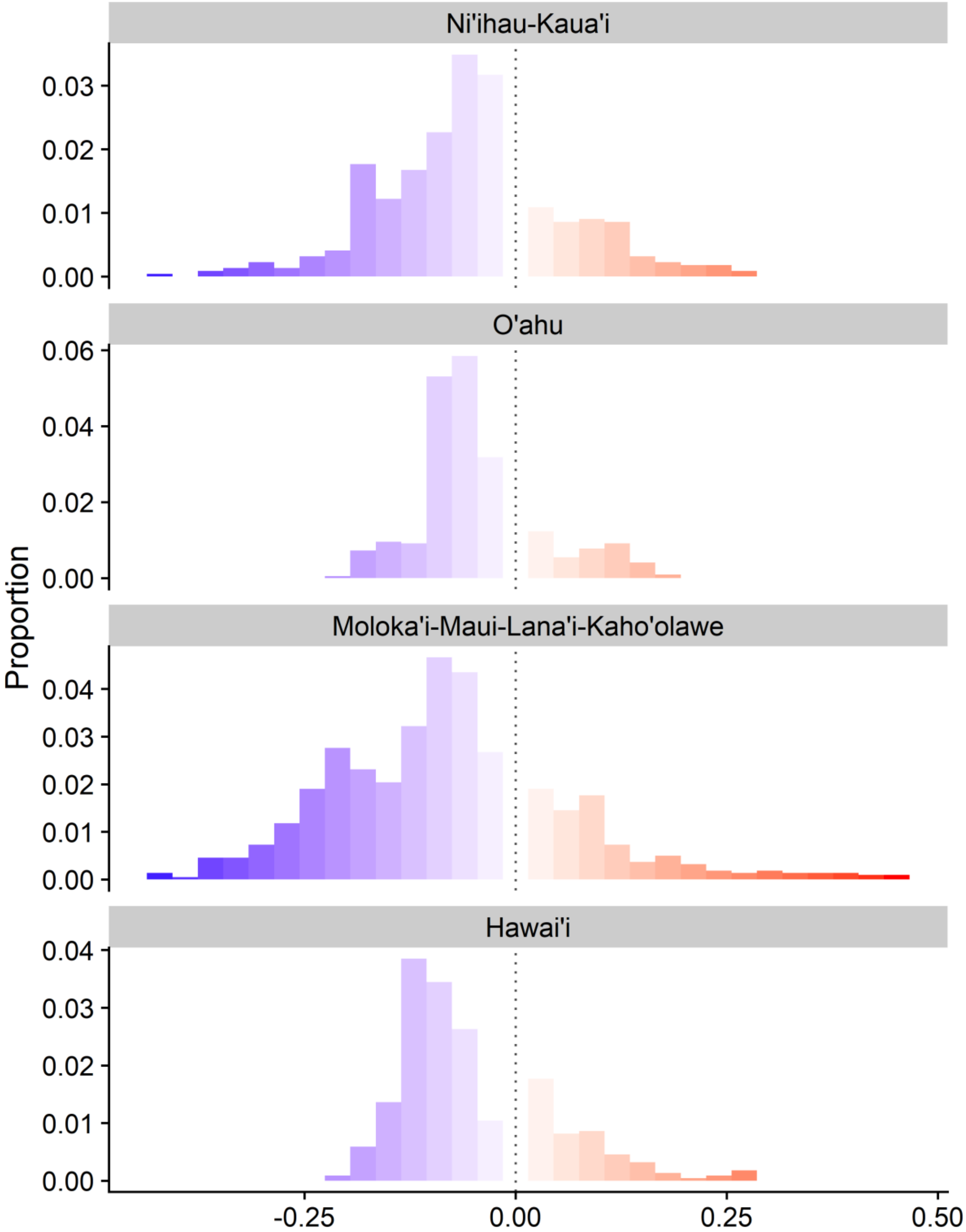

Figure A 4. Spatially aggregated changes in Aprion virescens *log density (2010−2019) within selected regional groups.*

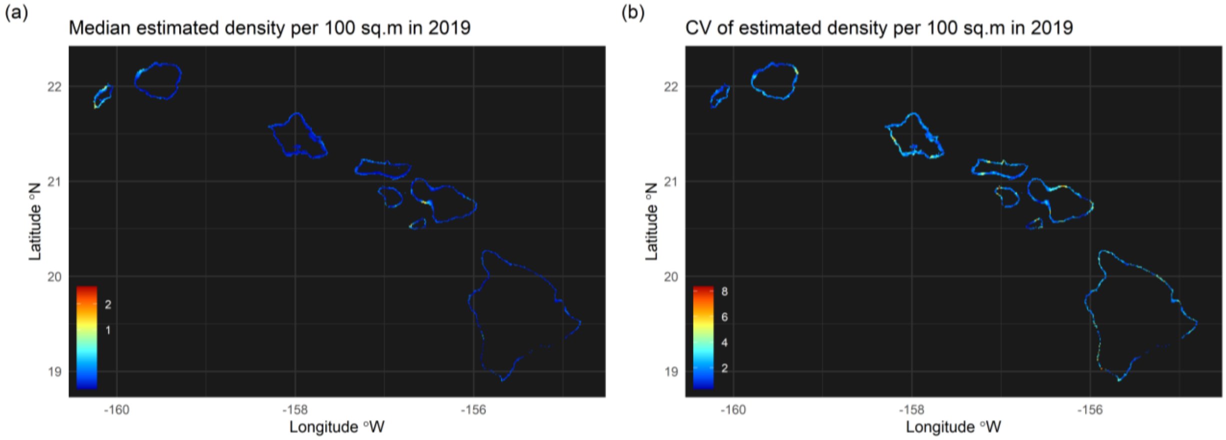

Figure A 5. Spatial variability of median Aprion virescens *density and associated uncertainty in 2019. The high coefficient of variation (CV) value mean high uncertainty of modeling results.*