Modelling Critically Endangered marine species: Bias-corrected citizen science data inform habitat suitability for the angelshark (Squatina squatina)

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AUTHORSHIP **Nicola Noviello***

School of Biological Sciences, University of Bristol.

Christopher McGonigle

School of Geography and Environmental Sciences, Ulster University.

David M P Jacoby

Institute of Zoology, Zoological Society of London.

Eva K M Meyers

Zoological Research Museum Alexander Koenig (ZMFK).

David Jiménez Alvarado

Grupo en Biodiversidad y Conservación, IU-ECOAQUA, Universidad de Las Palmas de Gran Canaria.

Joanna Barker

Conservation and Policy Department, Zoological Society of London.

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*CORRESPONDING AUTHOR: Nicola Noviello

EMAIL ADDRESS: nicolanoviello@outlook.com

ABSTRACT

1.

As an increasingly important resource in ecological research, citizen scientists have proven dynamic and cost-effective in the supply of data for use within habitat suitability models. With predictions critical to the provision of effective conservation measures in cryptic marine species, this study delivers baseline ecological data for the Critically Endangered angelshark (*Squatina squatina*), exploring (1) seasonal, sex-differentiated distributions (2) environmental distribution predictors, and (3) examining bias-corrected, imperfect citizen science data for use in coastal habitat suitability models with cryptic species.

2.

Citizen science presence data, comprising over 60,000 hours of sampling effort, was used alongside carefully selected open-source predictor variables, with MAXENT generating seasonal male and female habitat suitability models for angelsharks in the Canary Islands. A biased prior method was used, alongside two model validation measures to ensure reliability.

3.

Citizen science data used within MAXENT suggest that angelshark habitat suitability is low in coastal areas during warmer months, with fewer occurrences despite negligible change in sampling effort. The prime importance of bathymetry may indicate the importance depth for reproductive activity and possible diel vertical migration, while aspect may act as a proxy for sheltered habitats away from open ocean. Substrate as a predictor of female habitats in spring and summer could imply soft sediment is sought for birthing areas; assisting in the identification of areas critical to reproductive activity, and thus locations which may benefit from spatial protections.

4.

Using model outputs to inform Recovery Plan development and ecotourism are identified as plausible safeguards of population recovery, while the comparison of biased

and bias-corrected models highlights some variance between methodologies, with bias-corrected models producing greater areas of habitat suitability. Accordingly, an adaptive framework is provided for the implementation of citizen science data within the modelling of cryptic, coastal species' distribution.

KEYWORDS

bias file, citizen science, coastal, distribution, threatened species, habitat suitability model.

1. INTRODUCTION

The provision of spatial protection may help the recovery of threatened species, contingent on their life history. By identifying and prioritizing critical habitats and migratory patterns, the pressures exerted by anthropogenic stressors can be mitigated and conservation efforts refocused to target the overarching protection needed for the recovery of species (Stirling et al., 2016). Yet, the challenges associated with the protection of data deficient and rare species can be prohibitive; with efforts and costs further increasing for cryptic or nocturnal species, and those inaccessible to scientific monitoring (Huveneers et al., 2009; Stratmann, Barrett & Floyd, 2016). Citizen science may provide a viable solution to these challenges, with opportunistic data collection able to contribute valuable information on distribution and abundance, where traditional methods are either not feasible, or not resourced under existing monitoring programmes (Tiago, Pereira & Capinha, 2017).

The use of citizen science data has already proven instrumental to policy changes relating to the distribution of rare and threatened species (see Hyder et al., 2015), and is predicted to become ever more important in future decision-making. Enhancing public participation and engagement throughout the marine spatial planning process, citizen science provides a viable and efficient method of coastal data collection where full scientific monitoring may be unfeasible, whilst delivering community benefits and cost-effective use of research funding (Hyder et al., 2015; Jarvis et al., 2015, see examples: Bradsworth et al., 2017; Coxen et al., 2017; Tiago, Pereira & Capinha, 2017) .With over 27 million scuba diver certifications issued globally since 1967 (PADI, 2019), the public represents a huge, untapped resource for marine citizen science initiatives which, when effectively managed, may contribute important data to inform research and monitoring initiatives for rare and invasive species, climate change, marine protected areas, and fish conservation (Arin & Kramer, 2002; Ditton et al., 2002; Rudd & Tupper, 2002). For example, the Seasearch initiative (www.seasearch.co.uk), a citizen science project gathering data on marine species and habitats in the UK and Ireland, has been used by government bodies to promote Marine Conservation Zones and identify priority species for conservation (Seasearch, 2013; see Hyder et al., 2015), corroborating the value of non-specialist data collectors.

Yet, despite the provision of many advantages, the use of citizen science is not without its limitations; data quality has proven a major constraint, particularly regarding imperfect detection, a pertinent concern for cryptic, nocturnal species like the angelshark (*Squatina squatina*) (Mengersen et al., 2017; Dwyer et al., 2019). Likewise, dive-specific limitations can include weather conditions, dive-site, depth, accessibility, turbidity and avoidance of areas such as pollution points (Reddy & Dávalos, 2003; Schmeller et al., 2009; Botts, Erasmus & Alexander, 2011; Hassall, 2012).

On the contrary, a critical assumption of presence-only distribution modelling is that data are derived from systematic random sampling, with a complete lack of bias (Phillips et al., 2009; Kramer-Schadt et al., 2013). This is very rarely the case yet can be of amplified concern with citizen science datasets, where imperfect geographic sampling can yield model predictions with increased instances of over or under-predicting habitat suitability (Kramer-Schadt et al., 2013). Thus, Habitat Suitability Model (HSM) specific studies have advocated the use of bias files to represent relative sampling intensity across the study area. Although never able to fully counteract biases created during data collection, this method has produced better corrections than alternative measures, whilst enhancing predictive performance, particularly in presence-only models with limited data (Elith et al., 2011).

With suspected declines of ≥80% within three generations, the angelshark is listed as Critically Endangered on the IUCN Red List of threatened species (Morey et al., 2019). The Canary Islands have been identified as a unique stronghold for angelsharks (Barker et al., 2016; Jiménez-Alvarado et al., 2020), but here the species is under threat from accidental bycatch (Barker et al., 2016), with habitat degradation, pollution and human disturbance identified as other potential threats in the Canary Islands. Hence, baseline ecological data for the angelshark is urgently required for ensuring appropriate conservation and management actions (Barker et al., 2016). With an understanding of species distribution critical to this, HSMs have become integral in expanding our knowledge of data-poor and cryptic species (Huveneers et al., 2009; Aguirre-Gutiérrez et al., 2013; Araujo et al., 2017; Meyers et al., 2017), whilst providing critical justification for marine protected area planning, material for fisheries interactions and as a visual tool, accessible to scientists and non-specialists alike (Young & Carr, 2015). Moreover, greater knowledge of angelshark habitat requirements and movements can inform future management decisions in the Canary Islands, following the inclusion of angelsharks on the Spanish Endangered Species List as in "in danger of extinction" - the highest category of protection.

Found in coastal marine waters, including estuaries and brackish waters, the historic range for angelshark extends from northern Scotland and southern Scandinavia to Western Sahara and Canary Islands, including the Mediterranean Sea and Sea of Marmara (Compagno, 1984; OSPAR Commission, 2010; Lawson et al., 2020). Seasonal migrations are thought to take place within its northern ranges, with individuals moving north as water temperatures rise in the summer months (OSPAR Commission, 2010); though Ellis et al. (2021) also highlight seasonal inshore-offshore migrations occurring within the *Squatinidae* family. Dorsoventrally flattened and demersal, Angelsharks typically inhabit areas of soft, benthic sediment at depths of 0.3m to 150m (OSPAR Commission, 2010; Meyers et al., 2017; Morey et al., 2019). Sexual dimorphism in the angelshark is largely defined by size, with such differences generally associated with behavioural divergence, and varying degrees of sexual segregation, as has widely been observed within shark populations (Springer, 1967; Ruckstuhl & Neuhaus, 2002; Safi, König & Kerth, 2007; van Toor, Jaberg & Safi, 2011; Munroe, Simpfendorfer & Heupel, 2014).

There already exists evidence of spatial sex-divergence within the *Squatina* genus, with indications that the angelshark may also display segregation in space by sex (Bridge, Mackay & Newton, 1998; Awruch et al., 2008; Meyers et al., 2017). Therefore, if fishing pressure is high in areas key to, for instance, feeding or mating aggregations, or where subsections of the population reside (e.g., gravid or birthing females and neonates) there is a potential for higher rates of decline within those demographics. Thus, the verification of sexual segregation in angelsharks could inform conservation strategies by highlighting areas of differential exploitation and disturbance between the sexes (Klimley, 1987; Levin & Stunz, 2005; Mucientes et al., 2009).

This study utilizes imperfect citizen science occurrence data, collected by scuba divers in coastal areas of the Canary Islands, alongside carefully selected predictors from open-source environmental databases to explore habitat suitability and the potential distribution of angelsharks. The MaxEnt technique is implemented to (1) investigate sex-differentiated, seasonal angelshark distributions (2) provide an overview of angelshark distribution predictors, and (3) explore the use of bias-corrected imperfect citizen science data in cryptic species HSMs. The ultimate objective is to provide the scientific grounds for evidence-based conservation management decisions, focus scientific sampling efforts and minimise fishing mortality, whilst delivering a flexible framework for the use of biased citizen science data within coastal HSMs for cryptic and threatened marine species.

2. Methods

2.1 Study Region

The Canary Islands lie just over 100km off the north-west coast of Africa in the north-east Atlantic at approximately 28.3° N and 15.5° W. With a total land area of 7,440km^2 the volcanic archipelago consists of eight main islands: (west – east) El Hierro, La Palma, La Gomera, Tenerife, Gran Canaria, Fuerteventura, Lanzarote, La Graciosa, and several islets. Favoured for their mild waters, biodiversity and volcanic seascapes, the Canary Islands are a popular year-round diving destination; particularly in southern and eastern regions which are less exposed to turbulent Atlantic conditions (PADI, 2020). Most sightings data were collected in the easternmost islands (Figure 1), and for this reason, this study has focused on Gran Canaria, Fuerteventura, Lanzarote, and La Graciosa.

2.2 Data Collection: Citizen Science

The majority of data were provided by three databases established to compile citizen science occurrence data on angelsharks and marine biodiversity in the Canary Islands: RedPromar (www.redpromar.com/app/map/report), ePoseidon (www.geoportal.ulpgc.es/poseidon/php/login.php) and the Angel Shark Sightings Map, developed by the Angel Shark Project: Canary Islands, a collaboration between, Universidad de Las Palmas de Gran Canaria, Zoological Research Museum Alexander Koenig and Zoological Society of London (www.angelsharkproject.com/map). Each initiative provided an interactive map for citizen science divers to register their sightings, and log location coordinates alongside species information such a size, abundance, and sex, including dive-specific details like depth and temperature. Sightings data were also provided by several individuals and dive centres working with the Angel Shark Project: Canary Islands. Data collected from March 2014 to August 2018 inclusive were utilised in this study.

Where angelshark occurrences were duplicated across multiple databases (for example if a citizen scientist entered the same sighting into both RedPromar and the Angel Shark Sightings Map), datapoints were condensed to be one datum and the maximum relevant information retained for analysis. As movements can be contingent upon ontogeny (Andrews, Williams & Levin, 2010), only occurrences identified as adult angelsharks were retained to ensure models represented mature individuals. Dive centres reported a minimum-maximum diving range of between 3m and 50m depth. To account for potential land-based and snorkeller sightings, Angelshark occurrences registered at depths between 1m and 50m were retained for analysis.

Based upon a thorough literature review, and long-standing anecdotal evidence from divers in the Canary Islands, data were divided into meteorological seasons: winter (December, January and February), spring (March, April and May), summer (June, July and August) and autumn (September, October and November), and further subdivided by sex to identify sex-segregated distribution in adult angelsharks.

An additional questionnaire was distributed to dive centres across the archipelago ($n = 34$) to ascertain diver effort as a proxy for citizen science sampling effort in order to highlight biases not immediately obvious from the raw occurrence data. A full dive log was also contributed by Buceo La Graciosa dive centre, La Graciosa, from which diver effort (average number of dives per month) was derived from three incomplete years (Figure 7), providing a measure of diver effort seasonality.

2.3 Environmental Variables

Predictor variables were obtained from a variety of open-source databases at varying resolutions, whilst a high resolution digital bathymetric model (DBM), was acquired from the Observatorio Ambiental de Granadilla (see Table 1).

All predictors were processed to ensure a common resolution of 250m x 250m, at depths between 1m and 50m. All processing took place in ARCGIS 10.5.1, with terrain derivatives created using TERRAIN ATTRIBUTE SELECTION FOR SPATIAL ECOLOGY v1.1 (TASSE, Lecours et al., 2017) and BENTHIC TERRAIN MODELER v3.0 (BTM, Walbridge et al., 2018) toolboxes.

Predictors were refined from 51 potential environmental variables, to nine used in the final models. Predictors were reduced to those thought to have both direct and indirect influence on angelshark distribution and movement. Further, as related species are more likely to share ecological preferences (e.g., Wiens et al., 2010; Losos, 2011) variables thought pertinent to elasmobranch ecological or biological processes were also retained. To account for potential movements in relation to the seasonal occurrence of prey species (Byrkjedal & Høines, 2007; Lucifora, García & Worm. 2011), likely predictors of prey species presence were included in explanatory analyses, but the available data were not found to be informative and so were excluded from final model inclusion. To maintain model simplicity and avoid overfitting, indicators of primary productivity were included as a composite variable. As recommended by Lecours et al., (2017), terrain attributes were derived from the digital bathymetric model and included in the analysis. A full list of variables considered can be found in Table S1 of Supplementary Material, while greater detail on variable consideration and rationale can be found in Table S2.

Spearman's rank correlation coefficients and significance tests were then applied to data extracted from remaining predictors with 1,000 random points (Lecours et al., 2017; Stirling et al., 2016). Variables showing significant correlations (p = < 0.05; r > 0.7) were removed and 'vif_func', from the 'fsmb' package, implemented in RSTUDIO VERSION 3.4.3 to stepwise identify and remove variables demonstrating values above a threshold of Variance Inflation Factor of 3, to reduce the risk of type II errors (VIF; Zuur, Ieno & Elphick, 2010).

The final nine predictors were viewed as pairs plots (Figure 2) to examine any persistent relationships between variables and 1,000 randomly generated points (Stirling et al., 2016). Significant correlations of greater than 0.7 between predictors were considered unacceptable for MaxEnt inclusion. Here minimal correlations were seen, with the strongest relationship (r = 0.51) between variables bathymetry and relative deviation from the mean value (RDMV; a measure of topographic position that indicates peaks and pits). As such, all nine variables were appropriate for model inclusion.

Variables selected for inclusion in the final model thus comprised bathymetry, maximum diffuse attenuation (DAMax), minimum diffuse attenuation (DAMin), RDMV, easternness, northernness, sea surface temperature (SST), sea surface salinity (SSS) and substrate (see Table 1).

2.4 Bias File

To account for spatially biased sampling efforts within the data, a biased prior method was used (Phillips et al., 2009). Here, a weighted sampling probability raster layer was created in ArcGIS, using dive site locations provided by participating dive centres, and converted into a kernel density raster (see Figure 3c). This was rescaled from 1 to 20, as recommended by Elith, Kearney & Phillips (2010), before use within the 'biasfile' field of MaxEnt. Comparable spatial extents, showing examples of biased and bias-corrected habitat suitability maps were then produced (Figure 3a and b).

2.5 Model Selection and Settings

MaxEnt was identified as appropriate for use in this study as a presence-only model, with additional benefits including high accuracy and effectiveness in rare species with small sample sizes (Virgili et al., 2018), and its overall performance considered at least as good as, and often better than, alternative modelling techniques, without overfitting (Hernandez et al., 2006; Williams et al., 2009; Aguirre-Gutiérrez et al., 2013).

Model settings, implemented in MaxEnt software version 3.4.1 (Phillips et al., 2017), comprised 10,000 points, 500 iterations, 10^{-5} convergence threshold, regularization value of 1, and 25% test to 75% training data with random seed. Logistic output was employed, producing suitability values between 0 and 1, representing least suitable to most suitable, respectively (Elith et al., 2011). Results were taken from a model average of 100 bootstrap replications, ensuring efficient use of small data sets whilst allowing the partitioning of data for model testing (Phillips, Anderson & Schapire, 2006; Elith et al., 2011; Merow, Smith & Silander, 2013). Outputs were considered to show unsuitable areas (where logistic outputs are between 0 and 0.25), low suitability (0.25 - 0.5), moderate suitability (0.5 – 0.75) and high suitability (0.75 – 1.0), as suggested by Shrestha & Bawa (2014).

2.6 Assessing predictive performance

Area Under Curve (AUC, of the Receiver Operating Characteristic (ROC)) was used in addition to the True Skill Statistic (TSS) as measures of model performance (Table 2). Here, AUC values closer to 1 were considered good, with values of 0.5 considered no better than random with regards their predictive power. TSS values range from −1 to 1, where evaluation values of >0·4 were considered indicative of useful predictions (Eskildsen et al., 2013). Unlike AUC, TSS is threshold dependent; here, the 10-percentile training presence logistic threshold was used to calculate TSS.

3. Results

3.1 Variable Importance

Bathymetry was considered the best individual variable indicator of habitat suitability requirements for both sexes, particularly in autumn and winter, with comparable contributions to models overall (23.35% for females and 29.33% for males). Easternness demonstrated secondary importance to male and female models overall (20.10% and 19.35%, respectively), indicating some dependency on aspect. Substrate also proved important to females during the spring and summer (19.80% and 21.50%, respectively), with an average of 12.83% throughout the year. Substrate was more important for males in winter and spring (16.30% and 24.00%, respectively), with 12.58% overall importance. Salinity was considered highly important to females in the spring (50.20%), but less so overall (14.70), while temperature achieved its highest contribution to summer models of both sexes (25.90% for females; 12.10% for males).

Least significant for female models were variables diffuse attenuation maximum (DAMax, 1.38%), relative deviation from the mean value (RDMV, 4.80%), and diffuse attenuation minimum (DAMin, 6.65%). Meanwhile, of minimum importance to males were sea surface salinity (SSS, 2.93%), diffuse attenuation maximum (DAMax, 3.80%)

and relative deviation from the mean value (RDMV, 4.53%), all of which contributed an average of less than 7% each (see Tables 3 and 4).

To view marginal response curves for all averaged replicate models, see Supplementary Material Figure S3.

3.2 HABITAT SUITABILITY

Overall seasonal habitat suitability maps at depths ≤50m showed highest suitability for females in winter (0.06%) and spring (0.35%), and for males in winter (0.13%). Greatest areas of unsuitable habitat were seen in summer and autumn for females (99.14% and 99.48%, respectively) and males (99.92% and 98.88%, respectively), suggesting a general move away from coastal areas during the warmer months of the year (see Table 5 and Figures 4, 5 and 6).

For female models, highly suitable habitats accounted for between 0.01% and 0.35% of the study area, representing between 0.14km^2 and 4.98km^2. Of the areas considered highly or moderately suitable, the majority were focused along the eastern-most islands of Fuerteventura, Lanzarote and La Graciosa. However, this differed seasonally with greater suitability for females during winter shown along the eastern and southern coasts of Fuerteventura (Figure 5a), Lanzarote and La Graciosa (and 6a) with only small areas of suitability in Gran Canaria in winter (Figure 4a). Areas of moderate to high suitability were much larger in spring models for Fuerteventura (Figure 5b), Lanzarote and La Graciosa (Figure 6b). Minimal suitability was seen for females in the summer and autumn models (Figure 5c and d, respectively).

Areas showing high suitability for males comprised 1.85km^2 of the study area in winter, and 0.43km^2 in both summer and autumn. As with the female models, male habitat suitability was concentrated around the islands of Fuerteventura (Figure 5e), Lanzarote and La Graciosa (Figure 6e) during Winter. In spring there were larger areas of habitat suitability in Fuerteventura (Figure 5f), Lanzarote and La Graciosa (Figure 6f), and also in Gran Canaria (Figure 4f). Suitable areas were reduced in summer across the region, and only minimal areas of suitability were seen on the mid-southern coast of Lanzarote in autumn (Figure 6h).

3.3 OCCURRENCES BY MONTH

Averaged variances in adult angelshark sightings by month across five incomplete years (March 2014 to August 2018, inclusive) are displayed in Figure 7. Most sightings occurred in late autumn and winter, with January alone averaging 41 adult occurrences (male, female and unknown) per month within the modelled area. December and February followed closely with an average of 34 and 32.25 adult occurrences per month, respectively. Sightings of angelshark were lowest in September each year, where only three adults were recorded on average, with none of those identified as male. Males were most often reported in November (14.5 on average), while females were seen most often in January (22 on average) suggesting a temporal asynchrony of the sexes in their use of coastal locations. Over the incomplete five-year period, adult sex-ratios were inclined towards females, with 408 females recorded, while only 243 males were registered in the same timeframe.

In response to a diver effort questionnaire distributed to dive centres across the archipelago, 34 responses were received. Dive hours averaged 817 per centre, per year, with a standard error of 80.47. As dive centre staff are thought to have provided the majority of occurrence data, a measure of diver effort was estimated by multiplying average dive hours (817) by the number of active dive centres (78 PADI registered centres in the Canary Islands at time of writing; PADI, 2019): This produced an estimated contribution of dive hours at 63,726 per year.

3.4 Bias File Comparisons

The use of a bias file within MaxEnt showed some difference between Habitat Suitability Models (HSMs) using biased and bias-corrected data (Figure 3a and b). Notably, HSMs utilizing a bias file during model fitting produced slightly higher suitability throughout the archipelago, whilst uncorrected models produced decreased areas of suitability (Table S3 within Supplementary Materials).

4. Discussion

Habitat Suitability Models (HSMs) play a critical role in both spatial ecology research and conservation planning, with citizen science initiatives able to contribute considerable data where traditional science-led sampling of rare or cryptic species is difficult or resource heavy. Despite well-documented sampling biases in citizen science data, few HSM studies attempt to mitigate these issues, resulting in unidentified over- or, under-prediction in specific areas (Kramer-Schadt et al., 2013). This study explicitly accounts for spatial biases, thereby enhancing model performance and improving efficacy of species conservation planning by comparing results for biased and bias-controlled habitat suitability models.

Models showed variable habitat suitability for *S. squatina* between seasons and by sex, with highest suitability prevalent in the eastern half of the Canary Island archipelago, largely in north-east regions of Fuerteventura, Lanzarote and La Graciosa. Notwithstanding minimal changes in sampling effort, bathymetry was validated as being of high importance to the angelshark with greatest unsuitable areas found in summer and autumn at depths of ≤50m. This suggest that angelsharks move away from shallow waters during the warmer months; corroborating anecdotal evidence from dive centres and explaining the importance of sea surface temperature as a predictor in summer models. Although pupping is suspected to take place year-round, increased female habitat suitability in spring may coincide with a peak in pupping between April and July (Meyers et al. 2017; Jiménez et al. 2020). Angelsharks' absence from shallow waters in summer months may be explained by their nocturnal behaviour, alongside possible diel vertical migrations. With the Canary Islands thought to be the southernmost tip of angelshark range, and thus likely representing the thermal limit of the species, the availability of deeper, cooler waters surrounding the volcanic archipelago may serve to assist thermoregulation during warmer periods. A number of demersal elasmobranchs have shown such behaviours; moving to deeper waters during the day, only becoming more active in shallow waters during the night (Humphries, Simpson & Sims, 2017; Coffey et al., 2020; DeGroot et al., 2020). While this may explain a lack of detection by divers during daylight hours, it highlights a need for more focussed night surveys and greater efforts to sample at depths beyond the recreational dive limits to confirm this. This may involve using methods such as telemetry or fisheries data to ascertain individual movements or occurrence along depth gradients.

As a prominent predictor for both sexes, bathymetry may also be related to reproductive strategy, with results largely supporting prior research on elasmobranchs (Byrkjedal & Høines, 2007; Vaz et al., 2007; Vögler, Milessi & Quiñones, 2008; Meyers et al., 2017; Sequeira et al., 2014). This may explain greater overall suitability for both sexes in winter, with the mating season thought to occur during the cooler months (Meyers et al., 2017). Given more sex-specific occurrence data, identification of movement patterns and habitat association at a higher temporal resolution (e.g., monthly) is required to develop more detailed conservation and managements strategies (Dingle, 1996; Speed et al., 2012).

Areas of southern and eastern aspect generally demonstrated greater suitability, likely acting as a proxy for more sheltered habitats, away from the open Atlantic and the dominant wind direction experienced in the Canary Islands. As ambush predators, angelsharks rely on fine substrate to bury into for camouflage; as such, the overall low influence of the substrate variable was unexpected. However, substrate remains one of the most influential variables for females during spring (19.80%) and summer (21.5%), when areas consisting of mud to muddy-sand and sea grass beds were preferred. As these coincide with the suggested peak in pupping (Meyers et al., 2017), areas of fine substrate and seagrass may be sought by females as nursery areas to provide the most suitable habitats for offspring to remain hidden, thus enhancing juvenile survival.

Given such findings, it is possible to focus resources by initiating a habitat-based conservation framework, identifying areas of highly suitable habitat to enable spatial protection at locations critical for species persistence. For instance, by limiting exploitative activities in shallow, fine substrate areas during the pupping season, disturbances to gravid / birthing females, and neonates would be avoided. With species distribution a key factor in the assessment of conservation status (Crees et al., 2016; Akçakaya et al., 2018), sex-partitioned models also minimise the overestimation of angelshark range by identifying overlaps and allowing for more accurate evaluations of spread. Moreover, with the expansion of tagging initiatives in the archipelago, models also provide a starting point from which long-term movement studies may benefit.

Responses from the diver effort questionnaire (n = 34) emphasize the temporal biases of occurrence data collection, where sampling is largely restricted to hours between 09:00 and 17:00, with most sightings correspondingly logged between 09:00 and 14:00. Despite the angelshark’s nocturnal tendencies (Tonachella, 2010), only two of the 34 diver effort questionnaire respondents indicated that night dives were undertaken by their centre, notwithstanding the angelshark’s likely sedentary state during daylight hours.
Accordingly, increasing night dives and implementing telemetry studies are recommended to provide further insight into the activity estimates for the species. As a

rare species, but with a significant presence in the Canary Islands, angelshark sightings may be desirable on SCUBA excursions, and thus it is appropriate to note that relative effort may be increased on dives specifically targeting *S.squatina*.

A common problem in marine modelling (and particularly in coastal areas) is the low availability, or resolution, of seabed predictor layers (e.g., maximum and minimum diffuse attenuation; 5 arcminutes) when compared to sea surface values (e.g., sea surface salinity and sea surface temperature; 30 arcseconds). MaxEnt's necessity for predictors of equal spatial resolution and extent further exacerbates this issue by requiring grain size to be artificially reduced or increased. This requires additional processing of predictor layers, potentially deviating from source data and providing reduced value to modelled areas of suitability. It is therefore challenging for coastal researchers to accurately identify habitats using sub-surface layers alone; hence the combination of sea surface and benthic layers employed within the final models of this study. Thus, to create a model truly inclusive of variables pertinent to coastal species, complete sets of both benthic and sea surface variables at higher starting resolutions is required.

Alongside citizen-contributed occurrence data, many records used in this study included environmental information relating to the sighting, e.g., depth, habitat (e.g., rock, sand, seagrass) and water temperature. Though, when compared to predictor layer values at corresponding occurrence points, data were rarely consistent, reiterating that a cautionary approach is required for both unvalidated sightings data and coarse-resolution environmental layers. For example, of 613 adult records where habitat type was provided by citizen scientists, only 74 (12.07%) agreed with the corresponding points within the substrate predictor layer. As a broad, modelled prediction of habitat cover, EMODnet is likely to contain inaccuracies, yet no comparable habitat data exists with a spatial coverage incorporating the Canary Islands. Thus, given the paucity of environmental data specific to the study area, an important aim for future studies would be the development of high-accuracy benthic habitat layers for the archipelago.

In addition, the average depth discrepancy between citizen science records and predictor layer values was 7.59m (SD±6.55m). Given that the greatest tidal amplitude in the Canary Islands stands at 84.23cm (at Arrecife, Lanzarote, Gómez et al., 2015), the larger discrepancies may relate to either coarser resolutions, or a lack of spatial specificity and accuracy in citizen science data entry. Although HSMs are capable of coping with minor location errors (Kramer-Schadt et al., 2013), efforts to lessen common inaccuracies are recommended via additional training (Aceves-Bueno et al., 2017) and by increasing detail in the maps widely employed to collect spatial data from citizen scientists. For example, the addition of bathymetric contour lines to maps used for data collection in this study would have mitigated the numerous occurrences lost, due to their being logged at depths beyond recreational dive limits. Such recommendations are very relevant, with applications extending throughout ecological systems, via the inclusion of attributes such as altitude, visual landmarks, human settlements and grid systems to contextualize maps for citizen scientists during data entry; improving data quality and negating the need for expensive and time-consuming data validation.

MAXENT's use as a presence-only model recognizes that absence data, particularly in citizen science studies, is rarely available or reliable; creating opportunities to utilize sparse, irregularly sampled data (Kramer-Schadt et al., 2013). The lack of absence data means that estimating species prevalence is not possible (Phillips & Elith, 2013) yet, even if a presence-absence model were viable, it may not provide meaningful estimates for such cryptic and mobile species. With angelsharks considered as such, prevalence is difficult to ascertain, and unreliable data remain a major limitation (Mengersen et al., 2017), particularly with the challenges of estimating underwater locations. To account for this, the use of occupancy models, although often difficult to fit, would counteract the impacts of imperfect detection in the modelling of cryptic species (Welsh, Lindenmayer & Donnelly, 2013).

Misidentification can impact suitability models, with citizen scientists more prone to such errors (McClintock et al., 2010; Sillero et al., 2014). Yet, despite their cryptic nature, misidentification is unlikely to be significant in this study due to the angelshark's status as a flagship species for the Canary Island diving community. The misidentification of sex, however, may be likely in less experienced divers or when an angel shark is deeply buried in sediment. For instance, male claspers may be confused with pelvic fins, or less visible in immature males. This may cause an apparent increase in female sightings, but would be less likely in the mature individuals modelled in this study, and given that many occurrences were reported by seasoned dive centre staff.

Spatial filtering of occurrence points is the preferred method to achieve model consistency in the face of sampling bias; however, with an insufficient sample size for seasonal, sex-segregated subsets, a bias kernel density file was created for use in this study (Kramer-Schadt et al., 2013). Representative of trends across the models in this study, comparative panels within Figure 3 illustrate slightly more generous predictions when sampling bias is accounted for in this scenario (also see Supplementary Materials Table S3 for a comparison of logistic model outputs). As a potentially widespread effect when bias files are not utilised, the possible implications of under-prediction are broad, and should be considered during interpretation of HSMs, during subsequent sampling endeavours, and in future proposals of conservation action, to maintain the efficient use of research time and funding.

The identification of seasonally varied, sex-differentiated habitat suitability for angelsharks in the Canary Islands provides the evidence base for protection of key habitats across the archipelago. Following protection through the Spanish Endangered Species List, the government is mandated to develop a Recovery Plan which identifies critical and sensitive areas for the species. Model outputs from this project will be fed into the Recovery Plan process to identify these important sites. For example, models highlight areas around southern Lanzarote and Fuerteventura as being particularly important to females during the spring (Figures 5b and 6b). Moreover, with several of these moderate-high suitability areas seen where no occurrences or dive sites have been recorded (for instance, mid-southern Lanzarote, Figure 6), targeted surveys may be able to confirm the presence of angelsharks at these sites, and advance spatial protections in locations not before considered.

Accidental capture of angelsharks in fisheries could be further minimised if the model outputs were overlaid with fishing effort to ascertain possible "high risk" areas for angel sharks. Focused engagement with government authorities, commercial fishers and recreational fishers to gather fishing effort data will benefit the development of the Recovery Plan. For example, seasonal restrictions of fishing gear most likely to encounter angel sharks, e.g., bottom set gear, at these high risk sites in winter and spring could protect angelsharks, with minimal impact on recreational and commercial fisheries. Moreover, by shielding angelsharks through spatial or seasonal measures, and raising their profile outside of the country, a continued resource for ecotourism could be provided, creating a mutually beneficial and enduring relationship between Canary Island communities, visitors and the angelshark. A code of conduct for diving with angelsharks in the Canary Islands, widely distributed amongst the diving community, would help ensure minimal impact to the angelshark whilst safeguarding the long-term viability of the Canary Island's diving tourism, by maximising recovery in its flagship species.

Using innovative citizen science approaches, a clear and adaptive framework for modelling cryptic and data deficient species is given; providing clear comparisons of bias-corrected habitat suitability models and clarifying appropriate interpretation for application throughout coastal systems.

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AUTHOR CONTRIBUTIONS

J.B., E.E.K.M. and D.J.A. conceptualised the study and developed the citizen science data collection initiative. D.M.P.J., N.N., C.M. and J.B. developed manuscript direction and focus. N.N. performed analyses and produced the manuscript and figures, with C.M. contributing to data analysis. All co-authors contributed substantially to revisions.

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TABLES

Table 1 | Variables utilised in final MAXENT models

Variable	Starting resolution (m)	Data Collection	Source
Bathymetry	2	Multibeam	Observatorio Ambiental Granadilla (2016)
Easterness	250	Multibeam-derived	DBM-derived
Substrate	250	The European Nature Information System (EUNIS) habitat classification	EUSeaMap: EMODnet (2016)
Northernness	250	Multibeam-derived	DBM-derived
Diffuse Attenuation Maximum	9200	Satellite- based and in situ measurements	Bio-Oracle (2017)
Diffuse Attenuation Minimum	9200	Satellite- based and in situ measurements	Bio-Oracle (2017)
Relative Deviation from the Mean	250	Multibeam-derived	DBM-derived
Sea Surface Salinity Range	1000	Satellite- based and in situ measurements	Marspec (2013)
Mean Annual Sea Surface Temperature	1000	Satellite- based and in situ measurements	Marspec (2013)

Environmental variables selected for Canary Island angelshark (*Squatina squatina*) model inclusion with corresponding abbreviations, spatial resolutions, data collection method and source. DBM = digital bathymetric model.

Table 2 | MaxEnt model evaluation metrics

		AUC (±SD)	TSS (±SD)
Female	*Winter*	0.989 (±0.005)	0.715 (±0.165)
	Spring	0.942 (±0.021)	0.548 (±0.310)
	Summer	0.996 (±0.004)	0.832 (±0.366)
	Autumn	0.995 (±0.007)	0.840 (±0.188)
Male	*Winter*	0.960 (±0.019)	0.612 (±0.206)
	Spring	0.962 (±0.021)	0.344 (±0.461)
	Summer	1.000 (±0.00)	0.000 (±0.000)
	Autumn	0.996 (±0.006)	0.777 (±0.196)

Averaged values with standard deviation (SD) for AUC (Area Under Curve) and TSS (True Skill Statistic) of 100 MaxEnt replicate runs for the angelshark (*Squatina squatina*) in the Canary Islands. TSS was calculated using respective 10 percentile training presence logistic thresholds.

Table 3 | Variable contributions to each Female MaxEnt model

Variable	Female				
	Winter	*Spring*	*Summer*	*Autumn*	*Average*
Bathymetry	**20.80**	**13.80**	5.40	**53.40**	23.35
Diffuse attenuation maximum	0.80	0.50	3.30	0.90	1.38
Diffuse attenuation minimum	5.10	9.60	**10.70**	1.20	6.65
Easternness	**41.30**	2.20	**24.80**	9.10	19.35
Northernness	**16.30**	2.20	3.70	**18.10**	10.08
Relative deviation from the mean value	5.30	1.60	1.10	**11.20**	4.80
Sea surface salinity range	2.60	**50.20**	3.60	2.40	14.70
Mean average sea surface temperature	1.00	0.20	**25.90**	0.60	6.90
Substrate	6.80	**19.80**	**21.50**	3.20	12.83

Percent contribution of variables to each of the four female MaxEnt models for the angelshark (*Squatina squatina*) in the Canary Islands, including average values across the four models combined. Contributions ≥10% are shown in bold.

Table 4 | Variable contributions to each Male MaxEnt model

Variable	Male				
	Winter	*Spring*	*Summer*	*Autumn*	*Average*
Bathymetry	**44.30**	**15.40**	1.00	**56.60**	29.33
Diffuse attenuation maximum	1.80	**12.70**	0.00	0.70	3.80
Diffuse attenuation minimum	**11.20**	0.30	**21.10**	5.50	9.53
Easternness	**11.80**	**31.50**	**26.90**	**10.20**	20.10
Northernness	2.40	4.60	**30.10**	**11.80**	12.23
Relative deviation from the mean value	4.80	4.60	5.00	3.70	4.53
Sea surface salinity range	6.30	2.20	1.10	2.10	2.93
Mean average sea surface temperature	1.10	4.80	**12.10**	2.10	5.03
Substrate	**16.30**	**24.00**	2.60	7.40	12.58

Percent contribution of variables to each of the four male MaxEnt models for the angelshark (*Squatina squatina*) in the Canary Islands, including average values across the four models combined. Contributions ≥10% are shown in bold.

Table 5 | Percentage of Habitat Suitability levels for each MaxEnt model

		High suitability (%)	Moderate suitability. (%)	Low Suitability (%)	Unsuitable (%)
Female	*Winter*	0.06	1.13	6.77	92.04
	Spring	0.35	3.14	16.41	80.09
	Summer	0.01	0.05	0.80	99.14
	Autumn	0.02	0.08	0.42	99.48
Male	*Winter*	0.13	1.23	5.86	92.78
	Spring	0.00	2.97	25.65	71.38
	Summer	0.03	0.02	0.02	99.92
	Autumn	0.03	0.24	0.85	98.88

Percentage of habitat suitability levels of the total study area for the angelshark (*Squatina squatina*) in the Canary Islands, where logistic outputs of 0.75 – 1.0 = high suitability; 0.5 – 0.75 = moderate suitability; 0.25 – 0.5 = low suitability and 0 – 0.25 = unsuitable areas.

FIGURE LEGENDS

Figure 1 | Canary Island study area.
Map showing the focal study area (Gran Canaria, Lanzarote, Fuerteventura and La Graciosa) with location of dive sites and adult angelshark (*Squatina squatina*) records differentiated by sex; Female (n = 408) and male (n = 243). Location and 100m contour lines provided for reference. Coordinate system WGS84.

Figure 2 | Pairs plots of variables used within models.
Pairs plots illustrating residual relationships between 1000 randomly generated points and predictor variables. Spearman's rank correlation coefficients are also displayed alongside respective significance values (* = p = ≤0.05, ** = p = ≤0.01, *** = p = ≤0.001) and histograms demonstrating variability amongst explanatory variables and random points.

Figure 3 | Comparison of model outputs before and after sampling bias correction.
Example of the differences in Habitat Suitability Model (HSM) outputs before and after correction using the bias file. Here, the northernmost point of Lanzarote and La Graciosa are displayed, and the winter male model is used as an example, (a) model output without use of a bias file, and (b) bias file incorporated in model fitting. Panel (c) shows bias file used within MaxEnt (scaled 1 to 20) for all models in this study, alongside the dive sites used to create it. Outputs were considered to show unsuitable areas (where logistic outputs are between 0 and 0.25), low suitability (0.25 - 0.5), moderate suitability (0.5 – 0.75) and high suitability (0.75 – 1.0). Coordinate system WGS84.

Figure 4 | Seasonal habitat suitability models for Gran Canaria.
Seasonal habitat suitability maps for comparison of adult male and female angelshark (*Squatina squatina*) models, showing Gran Canaria. (a) Male Winter (n = 126), (b) Male Spring (n = 34), (c) Male Summer (n = 13), (d) Male Autumn (n = 70), (e) Female Winter (n = 215) (f) Female Spring (n = 88) (g) Female Summer (n = 50), and (h) Female Autumn (n = 55). Outputs were considered to show unsuitable areas (where logistic outputs are between 0 and 0.25), low suitability (0.25 - 0.5), moderate suitability (0.5 – 0.75) and high suitability (0.75 – 1.0). Coordinate system WGS84.

Figure 5 | Seasonal habitat suitability models for Fuerteventura.
Seasonal habitat suitability maps for comparison of adult male and female angelshark (*Squatina squatina*) models, showing Fuerteventura. (a) Male Winter (n = 126), (b) Male Spring (n = 34), (c) Male Summer (n = 13), (d) Male Autumn (n = 70), (e) Female Winter (n = 215) (f) Female Spring (n = 88) (g) Female Summer (n = 50), and (h) Female Autumn (n = 55). Outputs were considered to show unsuitable areas (where logistic outputs are between 0 and 0.25), low suitability (0.25 - 0.5), moderate suitability (0.5 – 0.75) and high suitability (0.75 – 1.0). Coordinate system WGS84.

Figure 6 | Seasonal habitat suitability models for Lanzarote and La Graciosa.
Seasonal habitat suitability maps for comparison of adult male and female angelshark (*Squatina squatina*) models, showing Lanzarote and La Graciosa. (a) Male Winter (n = 126), (b) Male Spring (n = 34), (c) Male Summer (n = 13), (d) Male Autumn (n = 70), (e) Female Winter (n = 215) (f) Female Spring (n = 88) (g) Female Summer (n = 50), and (h) Female Autumn (n = 55). Outputs were considered to show unsuitable areas (where logistic outputs are between 0 and 0.25), low suitability (0.25 - 0.5), moderate suitability (0.5 – 0.75) and high suitability (0.75 – 1.0). Coordinate system WGS84.

Figure 7 | Angelshark occurrences with diver effort.
Average sex-differentiated occurrences of angelshark (Squatina squatina) in the Canary Islands between March 2014 and August 2018 separated by month. Monthly average dive effort (dives per month) also included (2016-2018).