



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

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1 TITLE Modelling Critically Endangered marine species: bias-corrected
2 citizen science data informs habitat suitability for the angelshark
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4

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29 1.

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

38 2.

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

44 3.

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

53 4.

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

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

60 KEYWORDS

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

63 1. INTRODUCTION

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

76 The use of citizen science data has already proven instrumental to policy changes
77 relating to the distribution of rare and threatened species (see Hyder et al., 2015), and is
78 predicted to become ever more important in future decision-making. Enhancing public
79 participation and engagement throughout the marine spatial planning process, citizen
80 science provides a viable and efficient method of coastal data collection where full
81 scientific monitoring may be unfeasible, whilst delivering community benefits and cost-
82 effective use of research funding (Hyder et al., 2015; Jarvis et al., 2015, see examples:
83 Bradsworth et al., 2017; Coxen et al., 2017; Tiago, Pereira & Capinha, 2017) .With over
84 27 million scuba diver certifications issued globally since 1967 (PADI, 2019), the public
85 represents a huge, untapped resource for marine citizen science initiatives which, when
86 effectively managed, may contribute important data to inform research and monitoring

87 initiatives for rare and invasive species, climate change, marine protected areas, and fish
88 conservation (Arin & Kramer, 2002; Ditton et al., 2002; Rudd & Tupper, 2002). For
89 example, the Seasearch initiative (www.seasearch.co.uk), a citizen science project
90 gathering data on marine species and habitats in the UK and Ireland, has been used by
91 government bodies to promote Marine Conservation Zones and identify priority species
92 for conservation (Seasearch, 2013; see Hyder et al., 2015), corroborating the value of
93 non-specialist data collectors.

94 Yet, despite the provision of many advantages, the use of citizen science is not without
95 its limitations; data quality has proven a major constraint, particularly regarding
96 imperfect detection, a pertinent concern for cryptic, nocturnal species like the angelshark
97 (*Squatina squatina*) (Mengersen et al., 2017; Dwyer et al., 2019). Likewise, dive-specific
98 limitations can include weather conditions, dive-site, depth, accessibility, turbidity and
99 avoidance of areas such as pollution points (Reddy & Dávalos, 2003; Schmeller et al.,
100 2009; Botts, Erasmus & Alexander, 2011; Hassall, 2012).

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

112 With suspected declines of $\geq 80\%$ within three generations, the angelshark is listed as
113 Critically Endangered on the IUCN Red List of threatened species (Morey et al., 2019).
114 The Canary Islands have been identified as a unique stronghold for angelsharks (Barker
115 et al., 2016; Jiménez-Alvarado et al., 2020), but here the species is under threat from
116 accidental bycatch (Barker et al., 2016), with habitat degradation, pollution and human
117 disturbance identified as other potential threats in the Canary Islands. Hence, baseline
118 ecological data for the angelshark is urgently required for ensuring appropriate

119 conservation and management actions (Barker et al., 2016). With an understanding of
120 species distribution critical to this, HSMs have become integral in expanding our
121 knowledge of data-poor and cryptic species (Huveneers et al., 2009; Aguirre-Gutiérrez et
122 al., 2013; Araujo et al., 2017; Meyers et al., 2017), whilst providing critical justification
123 for marine protected area planning, material for fisheries interactions and as a visual
124 tool, accessible to scientists and non-specialists alike (Young & Carr, 2015). Moreover,
125 greater knowledge of angelshark habitat requirements and movements can inform future
126 management decisions in the Canary Islands, following the inclusion of angelsharks on
127 the Spanish Endangered Species List as in "in danger of extinction" - the highest category
128 of protection.

129 Found in coastal marine waters, including estuaries and brackish waters, the historic
130 range for angelshark extends from northern Scotland and southern Scandinavia to
131 Western Sahara and Canary Islands, including the Mediterranean Sea and Sea of
132 Marmara (Compagno, 1984; OSPAR Commission, 2010; Lawson et al., 2020). Seasonal
133 migrations are thought to take place within its northern ranges, with individuals moving
134 north as water temperatures rise in the summer months (OSPAR Commission, 2010);
135 though Ellis et al. (2021) also highlight seasonal inshore-offshore migrations occurring
136 within the *Squatina* family. Dorsoventrally flattened and demersal, Angelsharks
137 typically inhabit areas of soft, benthic sediment at depths of 0.3m to 150m (OSPAR
138 Commission, 2010; Meyers et al., 2017; Morey et al., 2019). Sexual dimorphism in the
139 angelshark is largely defined by size, with such differences generally associated with
140 behavioural divergence, and varying degrees of sexual segregation, as has widely been
141 observed within shark populations (Springer, 1967; Ruckstuhl & Neuhaus, 2002; Safi,
142 König & Kerth, 2007; van Toor, Jaberg & Safi, 2011; Munroe, Simpfendorfer & Heupel,
143 2014).

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

151 highlighting areas of differential exploitation and disturbance between the sexes
152 (Klimley, 1987; Levin & Stunz, 2005; Mucientes et al., 2009).

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

164 2. METHODS

165 2.1 STUDY REGION

166 The Canary Islands lie just over 100km off the north-west coast of Africa in the north-
167 east Atlantic at approximately 28.3° N and 15.5° W. With a total land area of 7,440km²
168 the volcanic archipelago consists of eight main islands: (west – east) El Hierro, La
169 Palma, La Gomera, Tenerife, Gran Canaria, Fuerteventura, Lanzarote, La Graciosa,
170 and several islets. Favoured for their mild waters, biodiversity and volcanic seascapes,
171 the Canary Islands are a popular year-round diving destination; particularly in southern
172 and eastern regions which are less exposed to turbulent Atlantic conditions (PADI,
173 2020). Most sightings data were collected in the easternmost islands (Figure 1), and for
174 this reason, this study has focused on Gran Canaria, Fuerteventura, Lanzarote, and La
175 Graciosa.

176 2.2 DATA COLLECTION: CITIZEN SCIENCE

177 The majority of data were provided by three databases established to compile citizen
178 science occurrence data on angelsharks and marine biodiversity in the Canary Islands:
179 RedPromar (www.redpromar.com/app/map/report), ePoseidon
180 (www.geoportal.ulpgc.es/poseidon/php/login.php) and the Angel Shark Sightings Map,

181 developed by the Angel Shark Project: Canary Islands, a collaboration between,
182 Universidad de Las Palmas de Gran Canaria, Zoological Research Museum Alexander
183 Koenig and Zoological Society of London (www.angelsharkproject.com/map). Each
184 initiative provided an interactive map for citizen science divers to register their sightings,
185 and log location coordinates alongside species information such a size, abundance, and
186 sex, including dive-specific details like depth and temperature. Sightings data were also
187 provided by several individuals and dive centres working with the Angel Shark Project:
188 Canary Islands. Data collected from March 2014 to August 2018 inclusive were utilised
189 in this study.

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

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

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

210 2.3 ENVIRONMENTAL VARIABLES

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

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

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

233 Spearman's rank correlation coefficients and significance tests were then applied to data
234 extracted from remaining predictors with 1,000 random points (Lecours et al., 2017;
235 Stirling et al., 2016). Variables showing significant correlations ($p < 0.05$; $r > 0.7$) were
236 removed and 'vif_func', from the 'fsmb' package, implemented in RSTUDIO VERSION
237 3.4.3 to stepwise identify and remove variables demonstrating values above a threshold
238 of Variance Inflation Factor of 3, to reduce the risk of type II errors (VIF; Zuur, Ieno &
239 Elphick, 2010).

240 The final nine predictors were viewed as pairs plots (Figure 2) to examine any persistent
241 relationships between variables and 1,000 randomly generated points (Stirling et al.,

242 2016). Significant correlations of greater than 0.7 between predictors were considered
243 unacceptable for MaxEnt inclusion. Here minimal correlations were seen, with the
244 strongest relationship ($r = 0.51$) between variables bathymetry and relative deviation
245 from the mean value (RDMV; a measure of topographic position that indicates peaks
246 and pits). As such, all nine variables were appropriate for model inclusion.

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

251 2.4 BIAS FILE

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

259 2.5 MODEL SELECTION AND SETTINGS

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

265 Model settings, implemented in MAXENT SOFTWARE VERSION 3.4.1 (Phillips et al.,
266 2017), comprised 10,000 points, 500 iterations, 10^{-5} convergence threshold, regularization
267 value of 1, and 25% test to 75% training data with random seed. Logistic output was
268 employed, producing suitability values between 0 and 1, representing least suitable to
269 most suitable, respectively (Elith et al., 2011). Results were taken from a model average
270 of 100 bootstrap replications, ensuring efficient use of small data sets whilst allowing the
271 partitioning of data for model testing (Phillips, Anderson & Schapire, 2006; Elith et al.,

272 2011; Merow, Smith & Silander, 2013). Outputs were considered to show unsuitable
273 areas (where logistic outputs are between 0 and 0.25), low suitability (0.25 - 0.5),
274 moderate suitability (0.5 – 0.75) and high suitability (0.75 – 1.0), as suggested by
275 Shrestha & Bawa (2014).

276 2.6 ASSESSING PREDICTIVE PERFORMANCE

277 Area Under Curve (AUC, of the Receiver Operating Characteristic (ROC)) was used in
278 addition to the True Skill Statistic (TSS) as measures of model performance (Table 2).
279 Here, AUC values closer to 1 were considered good, with values of 0.5 considered no
280 better than random with regards their predictive power. TSS values range from –1 to 1,
281 where evaluation values of >0.4 were considered indicative of useful predictions
282 (Eskildsen et al., 2013). Unlike AUC, TSS is threshold dependent; here, the 10-percentile
283 training presence logistic threshold was used to calculate TSS.

284 3. RESULTS

285 3.1 VARIABLE IMPORTANCE

286 Bathymetry was considered the best individual variable indicator of habitat suitability
287 requirements for both sexes, particularly in autumn and winter, with comparable
288 contributions to models overall (23.35% for females and 29.33% for males). Easternness
289 demonstrated secondary importance to male and female models overall (20.10% and
290 19.35%, respectively), indicating some dependency on aspect. Substrate also proved
291 important to females during the spring and summer (19.80% and 21.50%, respectively),
292 with an average of 12.83% throughout the year. Substrate was more important for males
293 in winter and spring (16.30% and 24.00%, respectively), with 12.58% overall importance.
294 Salinity was considered highly important to females in the spring (50.20%), but less so
295 overall (14.70), while temperature achieved its highest contribution to summer models of
296 both sexes (25.90% for females; 12.10% for males).

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

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

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

305 3.2 HABITAT SUITABILITY

306 Overall seasonal habitat suitability maps at depths $\leq 50\text{m}$ showed highest suitability for
307 females in winter (0.06%) and spring (0.35%), and for males in winter (0.13%). Greatest
308 areas of unsuitable habitat were seen in summer and autumn for females (99.14% and
309 99.48%, respectively) and males (99.92% and 98.88%, respectively), suggesting a general
310 move away from coastal areas during the warmer months of the year (see Table 5 and
311 Figures 4, 5 and 6).

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

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

330 3.3 OCCURRENCES BY MONTH

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

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

350 3.4 BIAS FILE COMPARISONS

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

356 4. DISCUSSION

357 Habitat Suitability Models (HSMs) play a critical role in both spatial ecology research
358 and conservation planning, with citizen science initiatives able to contribute considerable
359 data where traditional science-led sampling of rare or cryptic species is difficult or
360 resource heavy. Despite well-documented sampling biases in citizen science data, few
361 HSM studies attempt to mitigate these issues, resulting in unidentified over- or, under-

362 prediction in specific areas (Kramer-Schadt et al., 2013). This study explicitly accounts
363 for spatial biases, thereby enhancing model performance and improving efficacy of
364 species conservation planning by comparing results for biased and bias-controlled habitat
365 suitability models.

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

389 As a prominent predictor for both sexes, bathymetry may also be related to reproductive
390 strategy, with results largely supporting prior research on elasmobranchs (Byrkjedal &
391 Høines, 2007; Vaz et al., 2007; Vögler, Milessi & Quiñones, 2008; Meyers et al., 2017;
392 Sequeira et al., 2014). This may explain greater overall suitability for both sexes in
393 winter, with the mating season thought to occur during the cooler months (Meyers et al.,

394 2017). Given more sex-specific occurrence data, identification of movement patterns and
395 habitat association at a higher temporal resolution (e.g., monthly) is required to develop
396 more detailed conservation and managements strategies (Dingle, 1996; Speed et al.,
397 2012).

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

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

418 Responses from the diver effort questionnaire (n = 34) emphasize the temporal biases of
419 occurrence data collection, where sampling is largely restricted to hours between 09:00
420 and 17:00, with most sightings correspondingly logged between 09:00 and 14:00. Despite
421 the angelshark's nocturnal tendencies (Tonachella, 2010), only two of the 34 diver effort
422 questionnaire respondents indicated that night dives were undertaken by their centre,
423 notwithstanding the angelshark's likely sedentary state during daylight hours.

424 Accordingly, increasing night dives and implementing telemetry studies are
425 recommended to provide further insight into the activity estimates for the species. As a

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

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

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

453 In addition, the average depth discrepancy between citizen science records and predictor
454 layer values was 7.59m (SD±6.55m). Given that the greatest tidal amplitude in the
455 Canary Islands stands at 84.23cm (at Arrecife, Lanzarote, Gómez et al., 2015), the larger
456 discrepancies may relate to either coarser resolutions, or a lack of spatial specificity and
457 accuracy in citizen science data entry. Although HSMs are capable of coping with minor

458 location errors (Kramer-Schadt et al., 2013), efforts to lessen common inaccuracies are
459 recommended via additional training (Aceves-Bueno et al., 2017) and by increasing
460 detail in the maps widely employed to collect spatial data from citizen scientists. For
461 example, the addition of bathymetric contour lines to maps used for data collection in
462 this study would have mitigated the numerous occurrences lost, due to their being logged
463 at depths beyond recreational dive limits. Such recommendations are very relevant, with
464 applications extending throughout ecological systems, via the inclusion of attributes such
465 as altitude, visual landmarks, human settlements and grid systems to contextualize maps
466 for citizen scientists during data entry; improving data quality and negating the need for
467 expensive and time-consuming data validation.

468 MAXENT's use as a presence-only model recognizes that absence data, particularly in
469 citizen science studies, is rarely available or reliable; creating opportunities to utilize
470 sparse, irregularly sampled data (Kramer-Schadt et al., 2013). The lack of absence data
471 means that estimating species prevalence is not possible (Phillips & Elith, 2013) yet, even
472 if a presence-absence model were viable, it may not provide meaningful estimates for
473 such cryptic and mobile species. With angelsharks considered as such, prevalence is
474 difficult to ascertain, and unreliable data remain a major limitation (Mengersen et al.,
475 2017), particularly with the challenges of estimating underwater locations. To account
476 for this, the use of occupancy models, although often difficult to fit, would counteract the
477 impacts of imperfect detection in the modelling of cryptic species (Welsh, Lindenmayer
478 & Donnelly, 2013).

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

488 Spatial filtering of occurrence points is the preferred method to achieve model
489 consistency in the face of sampling bias; however, with an insufficient sample size for

490 seasonal, sex-segregated subsets, a bias kernel density file was created for use in this
491 study (Kramer-Schadt et al., 2013). Representative of trends across the models in this
492 study, comparative panels within Figure 3 illustrate slightly more generous predictions
493 when sampling bias is accounted for in this scenario (also see Supplementary Materials
494 Table S3 for a comparison of logistic model outputs). As a potentially widespread effect
495 when bias files are not utilised, the possible implications of under-prediction are broad,
496 and should be considered during interpretation of HSMs, during subsequent sampling
497 endeavours, and in future proposals of conservation action, to maintain the efficient use
498 of research time and funding.

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

511 Accidental capture of angelsharks in fisheries could be further minimised if the model
512 outputs were overlaid with fishing effort to ascertain possible "high risk" areas for angel
513 sharks. Focused engagement with government authorities, commercial fishers and
514 recreational fishers to gather fishing effort data will benefit the development of the
515 Recovery Plan. For example, seasonal restrictions of fishing gear most likely to
516 encounter angel sharks, e.g., bottom set gear, at these high risk sites in winter and spring
517 could protect angelsharks, with minimal impact on recreational and commercial
518 fisheries. Moreover, by shielding angelsharks through spatial or seasonal measures, and
519 raising their profile outside of the country, a continued resource for ecotourism could be
520 provided, creating a mutually beneficial and enduring relationship between Canary
521 Island communities, visitors and the angelshark. A code of conduct for diving with

522 angelsharks in the Canary Islands, widely distributed amongst the diving community,
523 would help ensure minimal impact to the angelshark whilst safeguarding the long-term
524 viability of the Canary Island's diving tourism, by maximising recovery in its flagship
525 species.

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

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544 AUTHOR CONTRIBUTIONS

545 J.B., E.E.K.M. and D.J.A. conceptualised the study and developed the citizen science
546 data collection initiative. D.M.P.J., N.N., C.M. and J.B. developed manuscript direction
547 and focus. N.N. performed analyses and produced the manuscript and figures, with
548 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)
Easternness	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 (\pmSD)	TSS (\pmSD)
Female	<i>Winter</i>	0.989 (\pm 0.005)	0.715 (\pm 0.165)
	<i>Spring</i>	0.942 (\pm 0.021)	0.548 (\pm 0.310)
	<i>Summer</i>	0.996 (\pm 0.004)	0.832 (\pm 0.366)
	<i>Autumn</i>	0.995 (\pm 0.007)	0.840 (\pm 0.188)
Male	<i>Winter</i>	0.960 (\pm 0.019)	0.612 (\pm 0.206)
	<i>Spring</i>	0.962 (\pm 0.021)	0.344 (\pm 0.461)
	<i>Summer</i>	1.000 (\pm 0.00)	0.000 (\pm 0.000)
	<i>Autumn</i>	0.996 (\pm 0.006)	0.777 (\pm 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				
	<i>Winter</i>	<i>Spring</i>	<i>Summer</i>	<i>Autumn</i>	<i>Average</i>
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 $\geq 10\%$ are shown in bold.

Table 4 | Variable contributions to each Male MAXENT model

Variable	Male				
	<i>Winter</i>	<i>Spring</i>	<i>Summer</i>	<i>Autumn</i>	<i>Average</i>
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 $\geq 10\%$ are shown in bold.

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

		High suitability (%)	Moderate suitability. (%)	Low Suitability (%)	Unsuitable (%)
Female	<i>Winter</i>	0.06	1.13	6.77	92.04
	<i>Spring</i>	0.35	3.14	16.41	80.09
	<i>Summer</i>	0.01	0.05	0.80	99.14
	<i>Autumn</i>	0.02	0.08	0.42	99.48
Male	<i>Winter</i>	0.13	1.23	5.86	92.78
	<i>Spring</i>	0.00	2.97	25.65	71.38
	<i>Summer</i>	0.03	0.02	0.02	99.92
	<i>Autumn</i>	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 (* = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$) 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).