



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

Noviello, N., McGonigle, C., Jacoby, D., Meyers, E., Alvarado, D., & Barker, J. (2021). Modelling Critically Endangered marine species: Bias-corrected citizen science data inform habitat suitability for the angelshark ( *Squatina squatina* ). *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(12), 3451-3465. <https://doi.org/10.1002/aqc.3711>

[Link to publication record in Ulster University Research Portal](#)

### Published in:

Aquatic Conservation: Marine and Freshwater Ecosystems

### Publication Status:

Published (in print/issue): 27/09/2021

### DOI:

[10.1002/aqc.3711](https://doi.org/10.1002/aqc.3711)

### Document Version

Author Accepted version

### General rights

Copyright for the publications made accessible via Ulster University's Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

### Take down policy

The Research Portal is Ulster University's institutional repository that provides access to Ulster's research outputs. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact [pure-support@ulster.ac.uk](mailto:pure-support@ulster.ac.uk).

1 TITLE Modelling Critically Endangered marine species: bias-corrected  
2 citizen science data informs habitat suitability for the angelshark  
3 (*Squatina squatina*).

4

5 AUTHORSHIP **Nicola Noviello\***

6 School of Biological Sciences, University of Bristol.

7 **Christopher McGonigle**

8 School of Geography and Environmental Sciences, Ulster  
9 University.

10 **David M P Jacoby**

11 Institute of Zoology, Zoological Society of London.

12 **Eva K M Meyers**

13 Zoological Research Museum Alexander Koenig (ZMFK).

14 **David Jiménez Alvarado**

15 Grupo en Biodiversidad y Conservación, IU-ECOQUA,  
16 Universidad de Las Palmas de Gran Canaria.

17 **Joanna Barker**

18 Conservation and Policy Department, Zoological Society of  
19 London.

20

21 ABSTRACT: 289

22 MAIN TEXT (INCLUDING CITATIONS): 5427

23 TABLES: 5

24 FIGURES: 7

25

26 \*CORRESPONDING AUTHOR: Nicola Noviello

27 EMAIL ADDRESS: nicolanoviello@outlook.com

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](http://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 7,440km<sup>2</sup>  
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](http://www.redpromar.com/app/map/report)), ePoseidon  
180 ([www.geoportal.ulpgc.es/poseidon/php/login.php](http://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](http://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  $0.14\text{km}^2$  and  $4.98\text{km}^2$ . 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  $1.85\text{km}^2$  of the study area in winter,  
323 and  $0.43\text{km}^2$  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  $\leq 50$ 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.

#### 530 ACKNOWLEDGEMENTS

531 All contributing dive centres and their continued engagement with the Angel Shark  
532 Project: Canary Islands, particularly Oceanos de Fuego, Buceo La Graciosa, Deep Blue  
533 Diving and David Thompson for providing long term datasets. Universidad de  
534 Las Palmas de Gran Canaria for providing ePoseidon data and Gobierno de Canarias  
535 for providing RedPromar data. José Andrés Sevilla Hernández at the Observatorio  
536 Ambiental de Granadilla for providing bathymetry data; Maria Belén Caro, Micheal  
537 Sealey for assisting with data acquisition; and Charlotte Pike for her support with data  
538 cleaning. The Angel Shark Sightings Map and Angel Shark Project: Canary Islands diver  
539 engagement was made possible through grants provided by Shark Conservation Fund,  
540 Disney Conservation Fund, CRESSI, Save Our Seas Foundation, Oceanário de Lisboa,  
541 WWF Netherlands and Deutsche Elasmobranchier-Gesellschaft. DMPJ was supported  
542 by a research grant from the Bertarelli Programme in Marine Science. Authors of this  
543 paper have no conflict of interest to declare.

#### 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.

#### 549 REFERENCES

550 Aceves-Bueno, E., Adeleye, A.S., Feraud, M., Huang, Y., Tao, M., Yang, Y. et al.

551 (2017). The Accuracy of Citizen Science Data: A Quantitative Review. *The Bulletin of the*  
552 *Ecological Society of America*, 98(4), 278–290. <https://doi.org/10.1002/bes2.1336>

553 Aguirre-Gutiérrez, J., Carvalheiro, L.G., Polce, C., van Loon, E.E., Raes, N., Reemer,  
554 M. et al. (2013). Fit-for-Purpose: Species Distribution Model Performance Depends on  
555 Evaluation Criteria – Dutch Hoverflies as a Case Study. *PLoS ONE*, 8(5), e63708.  
556 <https://doi.org/10.1371/journal.pone.0063708>

557 Akçakaya, H.R., Bennett, E.L., Brooks, T.M., Grace, M.K., Heath, A., Hedges, S. et al.  
558 (2018). Quantifying species recovery and conservation success to develop an IUCN  
559 Green List of Species. *Conservation Biology*, 32(5), 1128–1138.  
560 <https://doi.org/10.1111/cobi.13112>

561 **Andrews**, K.S., Williams, G.D. & Levin, P.S. (2010). Seasonal and Ontogenetic  
562 Changes in Movement Patterns of Sixgill Sharks. *PLoS ONE*, 5(9): e12549.  
563 <https://doi.org/10.1371/journal.pone.0012549>

564 Araujo, G., Snow, S., So, C.L., Labaja, J., Murray, R., Colucci, A. et al. (2017).  
565 Population structure, residency patterns and movements of whale sharks in Southern  
566 Leyte, Philippines: results from dedicated photo-ID and citizen science. *Aquatic*  
567 *Conservation: Marine and Freshwater Ecosystems*, 27(1), 237–252.  
568 <https://doi.org/10.1002/aqc.2636>

569 **Arin, T. &** Kramer, R.A. (2002). Divers' willingness to pay to visit marine sanctuaries:  
570 An exploratory study. *Ocean and Coastal Management*, 45(2-3), 171–183.  
571 [https://doi.org/10.1016/S0964-5691\(02\)00049-2](https://doi.org/10.1016/S0964-5691(02)00049-2)

572 Awruch, C.A., Nostro, F.L.L., Somoza, G.M. & Di Giacomo, E. (2008). Biología  
573 reproductiva del tiburón ángel *Squatina guggenheim* (Chondrichthyes: Squatinidae en la costa  
574 de Patagonia (Argentina, Atlántico suroeste). *Ciencias Marinas*, 34(1), 17–28.  
575 <https://doi.org/10.7773/cm.v34i1.1232>

576 Barker, J., Bartoli, A., Clark, M., Dulvy, N.K., Gordon, C., Hood, A. et al. (2016).  
577 *Angelshark Action Plan for the Canary Islands*. London.

578 **Botts, E.A.**, Erasmus, B.F.N. & Alexander, G.J. (2011). Geographic sampling bias in the  
579 South African Frog Atlas Project: Implications for conservation planning. *Biodiversity and*

580 *Conservation*, 20(1), 119–139. <https://doi.org/10.1007/s10531-010-9950-6>

581 Bradsworth, N., White, J.G., Isaac, B. & Cooke, R. (2017). Species distribution models  
582 derived from citizen science data predict the fine scale movements of owls in an  
583 urbanizing landscape. *Biological Conservation*, 213, 27–35.  
584 <https://doi.org/10.1016/j.biocon.2017.06.039>

585 **Bridge**, N.F., Mackay, D. & Newton, G. (1998). Biology of the ornate angel shark  
586 (*Squatina tergocellata*) from the Great Australian Bight. *Marine and Freshwater Research*,  
587 49(7), 679–686. <https://doi.org/10.1071/MF97075>

588 **Byrkjedal**, I. & Høines, Å. (2007). Distribution of demersal fish in the south-western  
589 Barents Sea. *Polar Research*, 26(2), 135–151. <https://doi.org/10.1111/j.1751->  
590 [8369.2007.00030.x](https://doi.org/10.1111/j.1751-8369.2007.00030.x)

591 Chapman, D.D., Feldheim, K.A., Papastamatiou, Y.P. & Hueter, R.E. (2015). There  
592 and Back Again: A Review of Residency and Return Migrations in Sharks, with  
593 Implications for Population Structure and Management. *Annual Review of Marine Science*,  
594 7(1), 547–570. <https://doi.org/10.1146/annurev-marine-010814-015730>

595 Coffey, D.M., Royer, M.A., Meyer, C.G. & Holland, K.N. (2020). Diel patterns in  
596 swimming behavior of a vertically migrating deepwater shark, the bluntnose sixgill  
597 (*Hexanchus griseus*). *PLoS ONE*, 15(1): e0228253.  
598 <https://doi.org/10.1371/journal.pone.0228253>

599 Compagno, L.J.V. (1984). *FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated*  
600 *and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes*. FAO  
601 Fisheries Synopsis, 125(4/2), 251–655.

602 Coxen, C.L., Frey, J.K., Carleton, S.A. & Collins, D.P. (2017). Species distribution  
603 models for a migratory bird based on citizen science and satellite tracking data. *Global*  
604 *Ecology and Conservation*, 11, 298–311. <https://doi.org/10.1016/j.gecco.2017.08.001>

605 Crees, J.J., Collins, A.C., Stephenson, P.J., Meredith, H.M.R., Young, R.P., Howe, C.  
606 et al. (2016). A comparative approach to assess drivers of success in mammalian  
607 conservation recovery programs. *Conservation Biology*, 30(4), 694–705.  
608 <https://doi.org/10.1111/cobi.12652>

609 DeGroot, B.C., Roskar, G., Brewster, L. & Ajemian, M.J. (2020) Fine-scale movement  
610 and habitat use of whitespotted eagle rays *Aetobatus narinari* in the Indian River  
611 Lagoon, Florida, USA. *Endangered Species Research*, 42(109), 124.  
612 <https://doi.org/10.3354/esr01047>

613 Dingle, H. (1996). *Migration: The biology of life on the move*. Oxford University Press, New  
614 York.

615 Ditton, R.B., Thailing, C.E., Riechers, R. & Osburn, H.R. (2002). The economic impact  
616 of sport divers using artificial reefs in Texas offshore waters, in: Creswell, R.L. (Ed.),  
617 *Proceedings of the 53rd Annual Gulf and Caribbean Fisheries Institute*. Biloxi, Mississippi, pp.  
618 344–377.

619 Dwyer, R.G., Campbell, H.A., Pillans, R.D., Watts, M.E., Lyon, B.J., Guru, S.M. et al.  
620 (2019). Using individual- based movement information to identify spatial conservation  
621 priorities for mobile species. *Conservation Biology*, 33(6), 1426–1437.  
622 <https://doi.org/10.1111/cobi.13328>

623 Ellis, J.R., Barker, J., McCully Phillips, S.R., Meyers, E.K.M. & Heupel, M. (2021).  
624 Angel sharks (Squatinae): A review of biological knowledge and exploitation. *Journal*  
625 *of Fish Biology*. 2021; 98: 592– 621. <https://doi.org/10.1111/jfb.14613>

626 Elith, J., Kearney, M. & Phillips, S. (2010). The art of modelling range-shifting species.  
627 *Methods in Ecology and Evolution*, 1(4), 330–342. <https://doi.org/10.1111/j.2041->  
628 [210X.2010.00036.x](https://doi.org/10.1111/j.2041-210X.2010.00036.x)

629 Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011). A  
630 statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17(1), 43–57.  
631 <https://doi.org/10.1111/j.1472-4642.2010.00725.x>

632 Eskildsen, A., le Roux, P.C., Heikkinen, R.K., Høye, T.T., Kissling, W.D., Pöyry, J. et  
633 al. (2013). Testing species distribution models across space and time: High latitude  
634 butterflies and recent warming. *Global Ecology and Biogeography*, 22(12), 1293–1303.  
635 <https://doi.org/10.1111/geb.12078>

636 Gómez, M., Pérez- Gómez, B., De Alfonso, M., Pérez, S. & Ruiz, M. I. (2015).  
637 *Waves and tides in the Canary Current Large Marine Ecosystem*. In: *Oceanographic and biological*

638 *features in the Canary Current Large Marine Ecosystem*. Valdés, L. & Déniz- González, I.  
639 (eds). IOC- UNESCO, Paris. IOC Technical Series, 115, 115- 131.  
640 <http://hdl.handle.net/1834/9182>.

641 Hassall, C. (2012). Predicting the distributions of under- recorded Odonata using species  
642 distribution models. *Insect Conservation and Diversity*, 5(3), 192–201.  
643 <https://doi.org/10.1111/j.1752-4598.2011.00150.x>

644 Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006). The effect of  
645 sample size and species characteristics on performance of different species distribution  
646 modeling methods. *Ecography*, 29(5), 773–785. [https://doi.org/10.1111/j.0906-](https://doi.org/10.1111/j.0906-7590.2006.04700.x)  
647 [7590.2006.04700.x](https://doi.org/10.1111/j.0906-7590.2006.04700.x)

648 **Humphries**, N.E., Simpson, S.J. & Sims, D.W. (2017) Diel vertical migration and  
649 central place foraging in benthic predators. *Marine Ecology Progress Series*, 582, 163-  
650 180. <https://doi.org/10.3354/meps12324>

651 Huveneers, C., Luo, K., Otway, N.M. & Harcourt, R.G. (2009). Assessing the  
652 distribution and relative abundance of wobbegong sharks (*Orectolobidae*) in New South  
653 Wales, Australia, using recreational scuba-divers. *Aquatic Living Resources*, 22(3), 255–  
654 264. <https://doi.org/10.1051/alr/2009046>

655 Hyder, K., Townhill, B., Anderson, L.G., Delany, J. & Pinnegar, J.K. (2015). Can  
656 citizen science contribute to the evidence-base that underpins marine policy? *Marine*  
657 *Policy*, 59, 112–120. <https://doi.org/10.1016/j.marpol.2015.04.022>

658 Jarvis, R.M., Breen, B.B., Krägeloh, C.U. & Billington, D.R. (2015). Citizen science and  
659 the power of public participation in marine spatial planning. *Marine Policy*, 57, 21–26.  
660 <https://doi.org/10.1016/j.marpol.2015.03.011>

661 Jiménez- Alvarado, D., Meyers, E.K.M., Caro, M.B., Sealey, M.J. & Barker, J.  
662 (2020). Investigation of juvenile angelshark (*Squatina squatina*) habitat in the Canary  
663 Islands with recommended measures for protection and management. *Aquatic*  
664 *Conservation: Marine and Freshwater Ecosystems*. 30(10), 2019-1025,  
665 <https://doi.org/10.1002/aqc.3337>

666 Klimley, A.P. (1987). The determinants of sexual segregation in the scalloped

667 hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes*, 18(1), 27–40.  
668 <https://doi.org/10.1007/BF00002325>

669 Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder,  
670 V. et al. (2013). The importance of correcting for sampling bias in MaxEnt species  
671 distribution models. *Diversity and Distributions*, 19(11), 1366–1379.  
672 <https://doi.org/10.1111/ddi.12096>

673 Lawson, J.M., Pollom, R.A., Gordon, C.A., Barker, J., Meyers, E.K.M., Zidowitz, H.  
674 et al. (2020). Extinction risk and conservation of critically endangered angel sharks in the  
675 Eastern Atlantic and Mediterranean Sea. *ICES Journal of Marine Science*, 77(1), 12–29.  
676 <https://doi.org/10.1093/icesjms/fsz222>

677 Lecours, V., Devillers, R., Simms, A.E., Lucieer, V.L. & Brown, C.J. (2017). Towards a  
678 framework for terrain attribute selection in environmental studies. *Environmental*  
679 *Modelling and Software*, 89, 19–30. <https://doi.org/10.1016/j.envsoft.2016.11.027>

680 Levin, P.S. & Stunz, G.W. (2005). Habitat triage for exploited fishes: Can we identify  
681 essential “Essential Fish Habitat?,” in: *Estuarine, Coastal and Shelf Science*. Academic  
682 Press, pp. 70–78. <https://doi.org/10.1016/j.ecss.2005.02.007>

683 Losos, J.B. (2011). Seeing the forest for the trees: The limitations of phylogenies in  
684 comparative biology. *American Naturalist*, 177(6), 709–727.  
685 <https://doi.org/10.1086/660020>

686 **Lucifora, L.O.**, García, V.B. & Worm, B. (2011). Global Diversity Hotspots and  
687 Conservation Priorities for Sharks. *PLoS ONE*, 6(5), e19356.  
688 <https://doi.org/10.1371/journal.pone.0019356>

689 McClintock, B.T., Bailey, L.L., Pollock, K.H. & Simons, T.R. (2010). Unmodeled  
690 observation error induces bias when inferring patterns and dynamics of species  
691 occurrence via aural detections. *Ecology*, 91(8), 2446–2454. <https://doi.org/10.1890/09-1287.1>

693 Mengersen, K., Peterson, E.E., Clifford, S., Ye, N., Kim, J. & Bednarz, T. (2017).  
694 Modelling imperfect presence data obtained by citizen science. *Environmetrics*, 28(5),  
695 e2446. <https://doi.org/10.1002/env.2446>

696 Merow, C., Smith, M.J. & Silander, J.A. (2013). A practical guide to MaxEnt for  
697 modeling species' distributions: what it does, and why inputs and settings matter.  
698 *Ecography*, 36(10), 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>

699 Meyers, E.K.M., Tuya, F., Barker, J., Jiménez Alvarado, D., Castro-Hernández, J.J. &  
700 Haroun, R. (2017). Population structure, distribution and habitat use of the Critically  
701 Endangered Angelshark, *Squatina squatina*, in the Canary Islands. *Aquatic Conservation:  
702 Marine and Freshwater Ecosystems*, 27(6), 1133–1144. <https://doi.org/10.1002/aqc.2769>

703 Morey, G., Barker, J., Hood, A., Gordon, C., Bartolí, A. & Meyers, E.K.M. (2019).  
704 *Squatina squatina*. *The IUCN Red List of Threatened Species*.  
705 <https://doi.org/e.T39332A117498371>

706 Mucientes, G.R., Queiroz, N., Sousa, L.L., Tarroso, P. & Sims, D.W. (2009). Sexual  
707 segregation of pelagic sharks and the potential threat from fisheries. *Biology Letters*, 5(2),  
708 156–159. <https://doi.org/10.1098/rsbl.2008.0761>

709 Munroe, S.E.M., Simpfendorfer, C.A. & Heupel, M.R. (2014). Defining shark ecological  
710 specialisation: Concepts, context, and examples. *Reviews in Fish Biology and Fisheries*,  
711 24(1). 317-331, <https://doi.org/10.1007/s11160-013-9333-7>

712 OSPAR Commission. (2010). *Background document for angel shark Squatina*. UK.

713 PADI. (2020). *Diving in the Canary Islands* | PADI [WWW Document]. URL  
714 <https://www.padi.com/diving-in/canary-islands/> (accessed 6.27.20).

715 PADI. (2019). *Worldwide Corporate Statistics. Data for 2013-2018* [WWW Document].  
716 URL <https://travel.padi.com/d/canary-islands/> (accessed 6.27.20).

717 Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017). Opening  
718 the black box: an open-source release of Maxent. *Ecography*, 40(7), 887–893.  
719 <https://doi.org/10.1111/ecog.03049>

720 **Phillips**, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of  
721 species geographic distributions. *Ecological Modelling*, 190, 231–259.  
722 <https://doi.org/10.1016/j.ecolmodel.2005.03.026>

723 Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A. & Leathwick, J. (2009).

724 Sample selection bias and presence-only distribution models: implications for  
725 background and pseudo-absence data. *Ecological Applications*, 19(1), 181–197.  
726 <https://doi.org/10.1890/07-2153.1>

727 Phillips, S.J. & Elith, J. (2013). On estimating probability of presence from use-  
728 availability or presence-background data. *Ecology*, 94(6), 1409–1419.  
729 <https://doi.org/10.1890/12-1520.1>

730 Reddy, S. & Dávalos, L.M. (2003). Geographical sampling bias and its implications for  
731 conservation priorities in Africa. *Journal of Biogeography*, 30(11), 1719–1727.  
732 <https://doi.org/10.1046/j.1365-2699.2003.00946.x>

733 Ruckstuhl, K.E. & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative  
734 test of three hypotheses. *Biological Reviews*, 77(1), 77–96.  
735 <https://doi.org/10.1017/S1464793101005814>

736 Rudd, M.A. & Tupper, M.H. (2002). The impact of Nassau grouper size and abundance  
737 on scuba diver site selection and MPA economics. *Coastal Management*, 30(2), 133–151.  
738 <https://doi.org/10.1080/089207502753504670>

739 Safi, K., König, B. & Kerth, G. (2007). Sex differences in population genetics, home  
740 range size and habitat use of the parti-colored bat (*Vespertilio murinus*, Linnaeus 1758) in  
741 Switzerland and their consequences for conservation. *Biological Conservation*, 137(1), 28–  
742 36. <https://doi.org/10.1016/j.biocon.2007.01.011>

743 Schmeller, D.S., Henry, P.Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F. et al.  
744 (2009). Ventajas del monitoreo de biodiversidad basado en voluntarios en Europa.  
745 *Conservation Biology*, 23(2), 307–316. <https://doi.org/10.1111/j.1523-1739.2008.01125.x>

746 Seasearch. (2013). *Annual Report*. Ross-on-Wye.

747 Sequeira, A.M.M., Mellin, C., Fordham, D.A., Meekan, M.G. & Bradshaw, C.J.A.  
748 (2014). Predicting current and future global distributions of whale sharks. *Global Change*  
749 *Biology*, 20(3), 778–789. <https://doi.org/10.1111/gcb.12343>

750 Shrestha, U.B. & Bawa, K.S. (2014). Impact of Climate Change on Potential  
751 Distribution of Chinese Caterpillar Fungus (*Ophiocordyceps sinensis*) in Nepal Himalaya.

752 *PLoS ONE*, 9(9), e106405. <https://doi.org/10.1371/journal.pone.0106405>

753 Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.A. et al. (2014).  
754 Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia*  
755 *Reptilia*, 35(1), 1–31. <https://doi.org/10.1163/15685381-00002935>

756 Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Harcourt, R.G., Stevens, J.  
757 et al. (2012). Marine parks for reef sharks: shark movements at Ningaloo Reef., in: *Book*  
758 *of Abstracts. 12th International Coral Reef Symposium*, 9–13 July 2012. Cairns, Queensland,  
759 Australia, p. 309.

760 Springer, S. (1967). Social organization of shark populations, in: Gilbert, P.W.,  
761 Mathewson, R.F., Rall D.P. (Eds.), *Sharks, Skates and Rays*. Johns Hopkins Press,  
762 Baltimore, pp. 149–174.

763 Stirling, D.A., Boulcott, P., Scott, B.E. & Wright, P.J. (2016). Using verified species  
764 distribution models to inform the conservation of a rare marine species. *Diversity and*  
765 *Distributions*, 22(7), 808–822. <https://doi.org/10.1111/ddi.12447>

766 Stratmann, T., Barrett, K. & Floyd, T. (2016). Locating suitable habitat for a rare  
767 species: Evaluation of a species distribution model for bog turtles (*Glyptemys muhlenbergii*)  
768 in the southeastern United States. *Herpetological Conservation and Biology*, 11(1), 199–213.

769 **Tiago, P.**, Pereira, H.M. & Capinha, C. (2017). Using citizen science data to estimate  
770 climatic niches and species distributions. *Basic and Applied Ecology*, 20, 75–85.  
771 <https://doi.org/10.1016/j.baae.2017.04.001>

772 Tonachella, N. (2010). *Focus on GFCM- SAC priority species*. Rome, Italy.

773 van Toor, M.L., Jaberg, C. & Safi, K. (2011). Integrating sex-specific habitat use for  
774 conservation using habitat suitability models. *Animal Conservation*, 14(5), 512–520.  
775 <https://doi.org/10.1111/j.1469-1795.2011.00454.x>

776 Vaz, S., Martin, C.S., Eastwood, P.D., Ernande, B., Carpentier, A., Meaden, G.J. et al.  
777 (2007). Modelling species distributions using regression quantiles. *Journal of Applied*  
778 *Ecology*, 45(1), 204–217. <https://doi.org/10.1111/j.1365-2664.2007.01392.x>

779 Virgili, A., Authier, M., Monestiez, P. & Ridoux, V. (2018). How many sightings to  
780 model rare marine species distributions. *PLoS ONE*, 13(3), e0193231.  
781 <https://doi.org/10.1371/journal.pone.0193231>

782 Vögler, R., Milessi, A.C. & Quiñones, R.A. (2008). Influence of environmental variables  
783 on the distribution of *Squatina guggenheim* (*Chondrichthyes*, *Squatinidae*) in the Argentine-  
784 Uruguayan Common Fishing Zone. *Fisheries Research*, 91(2-3), 212–221.  
785 <https://doi.org/10.1016/j.fishres.2007.11.028>

786 Walbridge, S., Slocum, N., Pobuda, M. & Wright, D.J. (2018). Unified  
787 Geomorphological Analysis Workflows with Benthic Terrain Modeler. *Geosciences*, 8(3),  
788 94. <https://doi.org/10.3390/geosciences8030094>

789 Welsh, A.H., Lindenmayer, D.B. & Donnelly, C.F. (2013). Fitting and Interpreting  
790 Occupancy Models. *PLoS ONE*, 8(1), 52015.  
791 <https://doi.org/10.1371/journal.pone.0052015>

792 Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H. V. et  
793 al. (2010). Niche conservatism as an emerging principle in ecology and conservation  
794 biology. *Ecology Letters*, 13(10), 1310–1324. [https://doi.org/10.1111/j.1461-  
795 0248.2010.01515.x](https://doi.org/10.1111/j.1461-0248.2010.01515.x)

796 Williams, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M. et al. (2009).  
797 Using species distribution models to predict new occurrences for rare plants. *Diversity and  
798 Distributions*, 15(4), 565–576. <https://doi.org/10.1111/j.1472-4642.2009.00567.x>

799 Young, M. & Carr, M.H. (2015). Application of species distribution models to explain  
800 and predict the distribution, abundance and assemblage structure of nearshore temperate  
801 reef fishes. *Diversity and Distributions*, 21(12), 1428–1440.  
802 <https://doi.org/10.1111/ddi.12378>

803 Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid  
804 common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14.  
805 <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

TABLES

**Table 1 | Variables utilised in final MAXENT models**

<b>Variable</b>	<b>Starting resolution (m)</b>	<b>Data Collection</b>	<b>Source</b>
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**

		<b>AUC (<math>\pm</math>SD)</b>	<b>TSS (<math>\pm</math>SD)</b>
<b>Female</b>	<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)
<b>Male</b>	<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	<b>20.80</b>	<b>13.80</b>	5.40	<b>53.40</b>	23.35
Diffuse attenuation maximum	0.80	0.50	3.30	0.90	1.38
Diffuse attenuation minimum	5.10	9.60	<b>10.70</b>	1.20	6.65
Easternness	<b>41.30</b>	2.20	<b>24.80</b>	9.10	19.35
Northernness	<b>16.30</b>	2.20	3.70	<b>18.10</b>	10.08
Relative deviation from the mean value	5.30	1.60	1.10	<b>11.20</b>	4.80
Sea surface salinity range	2.60	<b>50.20</b>	3.60	2.40	14.70
Mean average sea surface temperature	1.00	0.20	<b>25.90</b>	0.60	6.90
Substrate	6.80	<b>19.80</b>	<b>21.50</b>	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	<b>44.30</b>	<b>15.40</b>	1.00	<b>56.60</b>	29.33
Diffuse attenuation maximum	1.80	<b>12.70</b>	0.00	0.70	3.80
Diffuse attenuation minimum	<b>11.20</b>	0.30	<b>21.10</b>	5.50	9.53
Easternness	<b>11.80</b>	<b>31.50</b>	<b>26.90</b>	<b>10.20</b>	20.10
Northernness	2.40	4.60	<b>30.10</b>	<b>11.80</b>	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	<b>12.10</b>	2.10	5.03
Substrate	<b>16.30</b>	<b>24.00</b>	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**

		<b>High suitability (%)</b>	<b>Moderate suitability. (%)</b>	<b>Low Suitability (%)</b>	<b>Unsuitable (%)</b>
<b>Female</b>	<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
<b>Male</b>	<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).