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RESEARCH ARTICLE

Population structure, distribution and habitat use of the Critically Endangered Angelshark, *Squatina squatina*, in the Canary Islands

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Abstract

1. Angel sharks are among the most threatened fish worldwide, facing regional and global extinction. In Europe, populations of the three Critically Endangered angel sharks (*Squatina aculeata*, *Squatina oculata* and *Squatina squatina*) have been severely depleted.
2. Taking advantage of the last global 'hotspot' of the angelshark, *Squatina squatina*, this study gathered data through a citizen science programme to describe the occurrence of this shark in the coastal waters of the Canary Islands. Specifically, this study described (1) the population structure, and (2) habitat use of this species, which was used in a Species Distribution Model to (3) examine realized and potential distribution patterns, and to (4) determine the relative importance of environmental predictors on the occurrence of *S. squatina*.
3. Over the 12 months sampling period (April 2014 – March 2015), 678 sightings were reported. Individuals ranged from 20 to 200 cm (total length). Larger sightings of both females and neonates occurred mostly in April to July, i.e. during the pupping season. Males were significantly more frequent in November to January, i.e. during the mating season. Angelsharks were encountered at depths from <1 m to a maximum of 45 m. Small-sized individuals (i.e. neonates) exclusively occurred in shallow water (0–25 m). Most sharks occurred on sandy bottoms adjacent to reefs.
4. Even though sightings were recorded at all seven islands in the archipelago, there were fewer encounters in the western than the eastern islands.
5. The Species Distribution Model indicated that the probability of occurrence mainly correlated with sea surface temperature, chlorophyll, salinity and depth. Areas with the greatest habitat suitability were in shallow water.
6. The angelshark displayed spatial (vertical and horizontal) and temporal segregation by size and sex. This information is vital to inform conservation of this Critically Endangered shark in its last stronghold.

KEYWORDS
coastal, distribution, endangered species, fish, modelling, ocean

1 | INTRODUCTION

Chondrichthyans are key to the world's oceans as they play a significant functional role as predators (Heithaus, Wirsing, & Dill, 2012), and have gained important value in the wildlife tourism sector (Vianna, Meekan, Pannell, Marsh, & Meeuwig, 2012). However, one-quarter of all chondrichthyan species are threatened with extinction, with angel sharks found to be the second most threatened family of elasmobranchs in the world (Dulvy et al., 2014). Several populations of sawfishes, skates and angel sharks have been locally and/or regionally extirpated (Dulvy & Forrest, 2010; Dulvy, Sadovy, & Reynolds, 2003) across their distribution ranges, or have not been reported for many decades, highlighting the necessity of urgent conservation and management (Dulvy et al., 2014).

Research efforts to assess the status of species and, in particular, to identify those that are at risk are essential in any conservation planning (Simpfendorfer, Heupel, White, & Dulvy, 2011). It is particularly challenging to develop conservation and recovery strategies for species with limited scientific data on their basic ecology and distribution, especially for those species that already have reduced population sizes and are rarely caught or reported in fisheries. Considering that many studies on elasmobranch trends have used data from fisheries, there is a greater challenge to collect scientific data on rare or declining species with no commercial interest. One approach to tackle data gaps is to include information from alternative sources, such as those provided through citizen science programmes, an approach increasingly used for marine and coastal conservation worldwide (Cigliano et al., 2015). Data provided by observers and volunteers has often been highlighted as an adequate alternative (Delaney, Sperling, Adams, & Leung, 2007; Goffredo et al., 2010). In particular, this approach is a cost-effective solution to obtain large datasets covering wide geographic areas (Bernard, Götz, Kerwath, & Wilke, 2013; Cohn, 2008; Newman, Buesching, & Macdonald, 2003; Pattengill-Semmens & Semmens, 2003). This strategy has been useful, for example, to gather information on the distribution, abundance, habitat use and population structure of elasmobranchs such as grey reef sharks, *Carcharhinus amblyrhynchos* (Hussey, Stroh, Klaus, Chekchak, & Kessel, 2013); manta rays, *Manta alfredii* (Jaine et al., 2012) and *Manta birostris* (Luiz, Balboni, Kodja, Andrade, & Marum, 2009); yellow stingrays, *Ueobatis jamaicensis* (Ward-Paige, Pattengill-Semmens, Myers, & Lotze, 2011); smalltooth sawfish, *Pristis pectinata* (Waters et al., 2014; Wiley & Simpfendorfer, 2010); wobbegong sharks, *Orectolobus* spp. (Huveneers, Luo, Otway, & Harcourt, 2009); and whale sharks, *Rhincodon typus* (Graham & Roberts, 2007; Meekan et al., 2006). The efficacy of citizen science as a tool to monitor shark populations has also been validated in comparative studies. For example, data gathered by experienced dive guides to estimate the abundance of reef sharks in Palau was consistent with a comparative study using long-term telemetry data to estimate abundance of the same population (Vianna, Meekan, Bornovski, & Meeuwig, 2014). Moreover, public sightings data to monitor the smalltooth sawfish population in the south-east USA provided important information on the current distribution of the species and additional valuable information used for conservation efforts (Wiley & Simpfendorfer, 2010). However, it is recognized that there are a variety of concerns with the quality of datasets provided by recreational divers (Ward-Paige & Lotze, 2011). For example, underwater surveys conducted by divers are limited by diving conditions (e.g. wave action, accessibility, turbidity) and the limits of recreational diving depths.

Understanding distribution patterns of species and their habitat use is crucial for many aspects of their conservation and environmental management (Brooks, Sloman, Sims, & Danylchuk, 2011; Colton & Swearer, 2010; Franklin, 2009). Species Distribution Models (SDMs), also known as ecological niche models, link species occurrences or abundances at a range of sites with environmental drivers and/or spatial characteristics of the sites (Franklin, 2009). Species Distribution Models can be applied on varying scales, ranging from continental to microhabitats. However, when using SDMs to estimate the potential distribution of a species within a subset of its range, extrapolation beyond this range may be associated with high uncertainty. In marine systems, SDMs have become particularly important in terms of conservation planning (Robinson et al., 2011). For example in the design of marine protected areas; the implementation of certain habitat conservation strategies; understanding fisheries interactions; and predicting impacts of climate change and exotic species invasions (Embling et al., 2010; Hannah et al., 2007; Maxwell, Stelzenmuller, Eastwood, & Rogers, 2009; Sequeira, Mellin, Fordham, Meekan, & Bradshaw, 2014; Sundblad, Bergström, & Sandström, 2011). Species Distribution Models have now been applied successfully to a wide range of marine species, including seaweeds (Martinez, Viejo, Carreno, & Aranda, 2012), seabirds (Oppel et al., 2011), reef fishes (Mellin, Bradshaw, Meekan, & Caley, 2010), whales (Druon et al., 2012) and sharks (McKinney, Fulford, Wu, Hoffmayer, & Hendon, 2012; Sequeira, Mellin, Rowat, Meekan, & Bradshaw, 2012; Sequeira et al., 2014).

The angelshark, *Squatina squatina* (Linnaeus, 1758), is a dorsoventrally flattened, bottom-dwelling, shark listed as Critically Endangered by the IUCN Red List of Threatened Species in 2006 and 2015 (Ferretti et al., 2015). This species inhabits continental shelves down to 200 m depth (Compagno, Dando, & Fowler, 2005) and can also be found in estuaries and brackish waters (OSPAR Commission, 2010). The angelshark was historically distributed from Norway to the West Sahara and the Canary Islands, including the Baltic, Mediterranean and Black seas (Compagno et al., 2005). Although there are no data on current or historical abundance, historical records from fisheries landings and research survey data have revealed that *S. squatina* was very abundant throughout its entire distribution range, including the North Sea, the English Channel (Day, 1880) and the Mediterranean Sea (Psomadakis, Maio, & Vacchi, 2009). However, in the past 50 to 100 years, it has suffered severe population declines and is currently absent from research vessel surveys and fisheries landings throughout its entire range (International Council for the Exploration of the Sea, ICES, 2014; OSPAR, 2010). Recent studies have reported occasional sightings in the Black Sea, the Sea of Marmara, the Aegean Sea, the Levantine Sea and the Northern Adriatic Sea (Bilecenoğlu, Kaya, Cihangir, & Çiçek, 2014; Fortibuoni, Borme, Franceschini, Giovanardi, & Raicevich, 2016; Kabasakal & Kabasakal, 2014). Importantly, to date, there are no population estimates for this species. As a result, baseline information on the current spatial distribution patterns, habitat use, abundance and population structure of the angelshark are lacking, which are necessary to promote urgent conservation policies. Seasonal coastal migrations linked to warming water temperature have been described in the northern part of its range (Compagno et al., 2005; Wheeler, Blacker, & Pirie, 1975), which fits observations for other species within the same genus, e.g. *Squatina californica* (Compagno et al., 2005; Eschmeyer, Herald, & Hammann, 1983; Kato, Springer, & Wagner, 1967; Natanson & Cailliet, 1986). A tagging study conducted in Irish waters reported that *S. squatina* undertakes seasonal migrations into deeper waters during a certain season and may return to the same area, or be resident, for a certain period of time (Green, 2007).

However, data on the migratory behaviour of angelsharks are very scarce and should be further investigated.

In the Canary Islands, benthic elasmobranch species are often sighted and the angelshark is, in particular, one of the most commonly encountered species by recreational scuba divers (Narvaez, 2013; Tuya, Sanchez-Jerez, Dempster, Boyra, & Haroun, 2006). This represents a unique opportunity to gain vital biological and ecological data on this Critically Endangered species. Diving tourism is an important industry in the Canary Islands; the large number of scuba diving operators who regularly visit the same sites throughout the entire year represents an important opportunity to gather information on angelsharks. In this sense, the aims of this study were to identify and describe the spatio-temporal distribution patterns of juvenile and adult angelsharks in the coastal waters of the Canary Islands. Specifically, data were obtained from recreational scuba divers through a citizen science programme, and through parallel underwater visual surveys to validate sightings and gather extra information, to (1) describe the population structure, (2) identify the habitat use, (3) examine realized and potential distribution patterns, and (4) determine the relative importance of environmental predictors on the occurrence of *S. squatina* in the Canary Islands.

2 | METHODS

2.1 | Study region

The Canary Island archipelago comprises seven main islands and four islets (Chinijo Archipelago) that have emerged after successive volcanic events from the ocean basin. All together, the islands have a surface area of 7490 km^2 and a coastline covering 1501 km. They are located west of the African coast, situated between latitude 27.68–29.58 N and longitude 18.28–14.58 E. The easternmost part of the archipelago (Fuerteventura) lies only 90 km away from the shore of the African mainland, while La Palma island is almost 400 km from the African coast (Fernández-Palacios & Martín Esquivel, 2001). The Canary Islands are a very popular tourist destination (12 million tourists in 2015) particularly for scuba divers. There are 84 official diving centres distributed across the archipelago. The most popular islands for diving are El Hierro, Fuerteventura, Gran Canaria, Lanzarote and Tenerife. Divers reach dive sites either from land or by boat, but due to the exposure and hydrodynamics of the islands, most dive sites are located in eastern and southern regions of each island.

2.2 | Angelshark presence data

Data on angelshark encounters were obtained through a citizen science tool, POSEIDON (www.programaposeidon.eu), which was initiated by the Universidad de Las Palmas de Gran Canaria to monitor marine biodiversity in the Canary Islands. Within this ongoing programme a specific online tool was developed for the Angel Shark Project, to compile data of angelshark encounters. The project and its database were promoted through available social media (Facebook, Twitter), media releases (local newspaper, local TV), a website (www.angelsharkproject.com) and educational materials that were distributed to dive centres. Dive schools, centres and shops in all seven islands were also individually approached, or contacted via email, to encourage their participation in the project and to receive training and educational material on the database and on angelsharks.

Recreational scuba divers were encouraged to use the database to register the exact location on a map (latitude and longitude) of their angelshark encounters within the archipelago and record specific data on: date and time of encounter; number of sharks; estimated total length (categorized as: < 30 cm, 30–100 cm, >100 cm); sex of the shark, if able to identify (male/female/unknown); habitat type where the shark was seen (categorized as sand, reef, rock and sand and seagrass); water depth (m); water temperature (°C); behaviour of the shark at the time of the encounter; and the total diving time of the observer (Figure S1, Supporting information). To submit data into the database, observers had to register as a user and fill out a 'profile' with contact data, age, occupation, level of diving experience, diving certification and affiliations to any diving club/centre/school. In addition, participating diving centres submitted a record of the number of dives per month, which was used as a measure of diving effort. The effort was quantified as the average number of dives that were undertaken by each diving centre per month, as well as the number of participating diving centres per island. This information was subsequently used to standardize the number of sightings per island, to account for varying sampling effort between islands.

The reliability of supplied data was validated in the following ways: (i) personal contact with observers to evaluate their level of expertise and reliability; (ii) level of diving experience of the observer; (iii) regular scientific dive surveys to locations where encounters were registered to confirm the presence of angelsharks.

Scientific diving surveys to areas of predicted occurrence of angelsharks, or to exact locations indicated in the database by observers, were carried out to validate the citizen science data. The survey consisted of a visual exploration of the area during a 60 minute dive. During these surveys, more detailed information was collected on the habitat types, population structure and site affinity in 'hotspots' (i.e. areas with a high sighting frequency) that were identified via the database.

2.3 | Data processing

Only validated records based on the previously described criteria were used for the analysis. Effort-based analyses, as described earlier, were used to avoid an overestimation or underestimation of sightings according to varying sampling effort among islands and seasons. To describe the population structure, size estimates were classified into three body length categories: neonates: <30 cm, pre-adults: 30–100 cm and adults: > 100 cm, and were distinguished between males, females and unknown sex. Deviation from an expected 1:1 sex ratio for the overall study was tested through a chi square test. Correlation between sightings of females and neonates was calculated with a Pearson product moment correlation. To investigate the habitat use of angelsharks, a correlation analysis between the body size of each individual and the depth of the sighting was carried out by means of a Pearson product moment correlation. Furthermore, a factorial one-way Analysis of Variance (ANOVA) was used to test for significant differences in the overall number of sightings (standardized by the number of participating diving centres per island) between three groups of islands distributed along an east to west gradient through the archipelago: the eastern (Lanzarote and Fuerteventura), central (Gran Canaria and Tenerife) and western islands (La Gomera, La Palma and El Hierro). Data were square-root transformed to achieve parametric assumptions (homogeneous variances and normality).

2.4 | Environmental data

To determine the potential distribution of angelshark according to environmental drivers, monthly level-3 pre-processed environmental data were acquired from Aqua-MODIS (http://oceancolor.gsfc.nasa.gov/) at 4 km resolution (2.5 arc min) with a temporal coverage of 12 months (September 2013 to October 2014). In addition, environmental data were derived from the Bio-ORACLE online platform (http://www.oracle.ugent.be/), a climate dataset designed for marine species distribution modelling at a spatial resolution of 9.2 km (5 arc min) (Tyberghein et al., 2012). Bathymetry data were derived from the General Bathymetric Chart of the Oceans (GEBCO). Spatial data (environmental predictor variables) were resampled to the same cell size using ArcToolBox functions from ArcGIS 10.2.2 (ESRI Corporation).

The monthly sets of the following variables were used for SDM development (see Table S1 for further information on the source of each variable): chlorophyll *a* concentration (Chl), cloud cover, diffuse attenuation, dissolved oxygen (dissox), nitrate concentration, photosynthetically active radiation (PAR), pH, phosphate, particulate organic carbon (POC), salinity, silicate, sea surface temperature (SST) (daytime and night-time) and bathymetry. In order to extract a subset of variables covering the most important environmental variations, all (monthly) variables were summarized by a Principal Component Analysis (PCA) using Cran *R* 3.2.2. Ten principal components (PCs) with eigenvalues greater than 1 were used as predictors for the SDM.

All environmental variables were selected based on their direct or indirect (e.g. because they serve as a proxy for prey availability) influence on elasmobranch distribution and movement. For example a study conducted by Vögler, Milessi, and Quiñones (2008), identified that temperature, salinity and bathymetry were the environmental variables that affected the distribution of *Squatina guggenheim*, in the south-west Atlantic. For whale sharks, Chl, bathymetry and SST were the main drivers for habitat suitability (McKinney et al., 2012; Sequeira et al., 2014). Diffuse attenuation, PAR and Chl were also used because they characterize areas of high productivity (Jaud, Dragon, Garcia, & Guinet, 2012; Sequeira et al., 2012), which are preferentially occupied by many marine species (Block et al., 2011).

2.5 | Modelling approach

Ideally, species distribution data should be generated from entirely randomized data collection surveys; however, such data may be difficult to obtain in many cases, for example through citizen science programmes. Hence, this study used a maximum entropy approach, via Maxent 3.3.2 (Phillips, Anderson, & Schapire, 2006; http://www.cr.princeton.edu/~shapire/Maxent), to calculate a species distribution model. Maxent is a programme for modelling potential distributions from presence-only data and random background data (Elith et al., 2011). This method estimates the probability that the environmental conditions are suitable for a targeted species at a given site (Elith et al., 2011; Phillips et al., 2006) and is particularly suitable for presence-only data of species where systematic survey data are limited (Elith et al., 2011).

Applying the default settings, the species records were 100 times randomly split into 70% training and 30% testing subsets. The area under the receiver operating characteristic curve (AUC) was used to measure model performance (Fielding & Bell, 1997; Swets, 1988). AUC values above 0.7 indicate that the performance of the model is acceptable (Phillips et al., 2006). Variable importance was estimated using a permutation approach, as well as a jack-knife test, implemented in Maxent. A map showing the potential distribution of angelsharks was generated applying the 10% training presence logistic threshold as a non-fixed presence–absence threshold. In order to derive a biologically meaningful training background for the SDM, a bathymetry layer of the Canary Islands was re-classed in DIVA-GIS 5.4 to indicate areas up to 200 m depth, highlighting the areas with the maximum depth at which angelsharks occur (Compagno et al., 2005).

3 | RESULTS

Over the 12 months sampling period (April 2014 – March 2015), 678 sightings of *S. squatina* were registered through the citizen science programme. In total, 39 citizen scientists submitted their sightings to the POSEIDON database, corresponding to 22 independent scuba diving centres located at Lanzarote (n = 6), Fuerteventura (n = 4), Gran Canaria (n = 7), Tenerife (n = 2), La Gomera (n = 1), La Palma (n = 1) and El Hierro (n = 1). There was not an equal number of sightings from each island, nor from each diving centre. The average number of dives that were undertaken by each diving centre per month during the study period was 60.5 dives per month.

In total, 40 scientific dive surveys were conducted across the archipelago (except La Gomera), in those spots where *S. squatina* were either encountered, as indicated by the POSEIDON database users, or where the habitat requirements (according to our predictions) seemed to be suitable. Sharks were encountered in 55% of these scientific dive surveys (n = 22). Most encounters and aggregations (for this study, more than two sharks reported in one particular area were considered as an aggregation) of angelsharks occurred during night dives.

3.1 | Population structure

Over the study period, June was the month with the highest number of encounters (n = 143; 25% of total encounters), followed by May (n = 65; 12% of total encounters), December (n = 62; 11% of total encounters) and April (n = 43; 8% of total encounters). Taking into account the diving effort (average number of dives per month), there are two peaks in encounters, one in spring/early summer (April–July) and one in winter (December–February) (Figure 1). September was the month with the least reported sightings (n = 13; 2% of total encounters), despite repeated dives (at day and night) in spots where encounters have been commonly reported during other months. Most

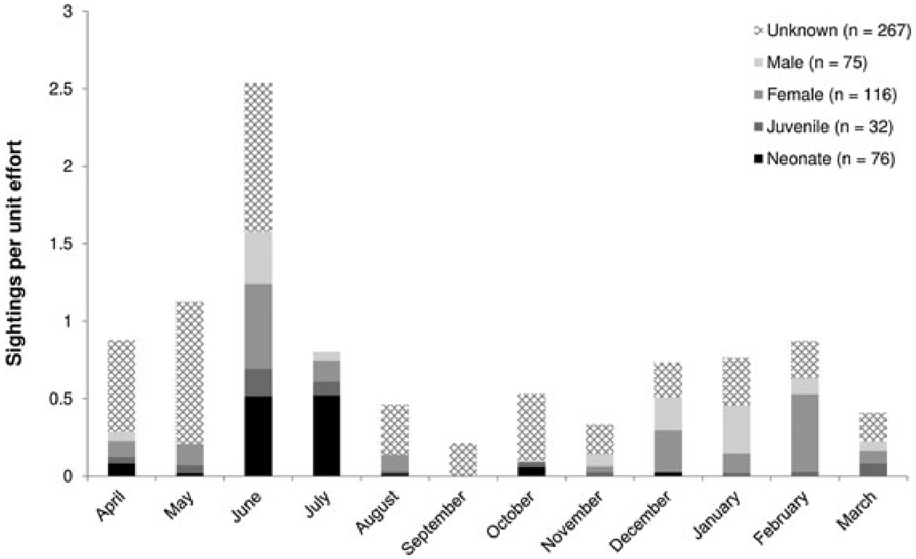

FIGURE 1 Overall number of sightings per month (April 2014 – March 2015) of the angelshark, *Squatina squatina*, in the Canary Islands; data were standardized by the average number of dives per month of the 22 participating diving centres. Sightings are categorized according to neonates(< 30 cm TL), juveniles (30–100 cm TL), adult males and females (> 100 cm) and unknown estimated total length

neonates were sighted between April and July (*n* = 70 out of 76), particularly in June and July. Sightings of females and neonates correlated positively ($r_s = 0.73$, $P < 0.01$), with a greater number recorded during those months (Figure 1).

Sex was identified in *n* = 170 cases; there were significantly more females than males ($\chi^2 = 4.840$, df = 1, $P = 0.0278$). Male sharks were encountered in lower numbers throughout the study (39.3%), with a peak in June (early summer) and between November and January (winter, Figure 1). Male observations were significantly more frequent in winter (*n* = 44) than in summer (*n* = 24) ($\chi^2 = 5.882$, df = 1, $P = 0.015$). Moreover, except for two sightings, all male sharks were >100 cm TL.

Overall, angelsharks ranged in size from 20 to 200 cm (total length (TL)). The most common reported sizes were >100 cm (*n* = 237). The estimated TL of the largest individual was a 200 cm female. Maturity data for angelsharks (Osaer, Narváez, Pajuelo, & Lorenzo, 2015) suggests that 53% of encountered sharks had not yet reached sexual maturity, while 47% were considered to be sexually mature. Two females were observed giving birth in June, while 12 gravid females were registered (three in February, two in March, five in June/July and two in December), some with mating scars.

The total number of encounters per island (standardized according to sampling effort per island) showed a clear gradient from the eastern to the western islands; the overall number of sightings in the eastern and central islands (Lanzarote, Fuerteventura, Gran Canaria and Tenerife) was significantly larger than those at the western islands (La Gomera, La Palma and El Hierro) (Figure 2, one-way ANOVA, $p = 0.02$). The number of neonates was particularly elevated in Tenerife (36 out of a total of 69), at a nursery area that is currently being monitored in an ongoing study. Another possible

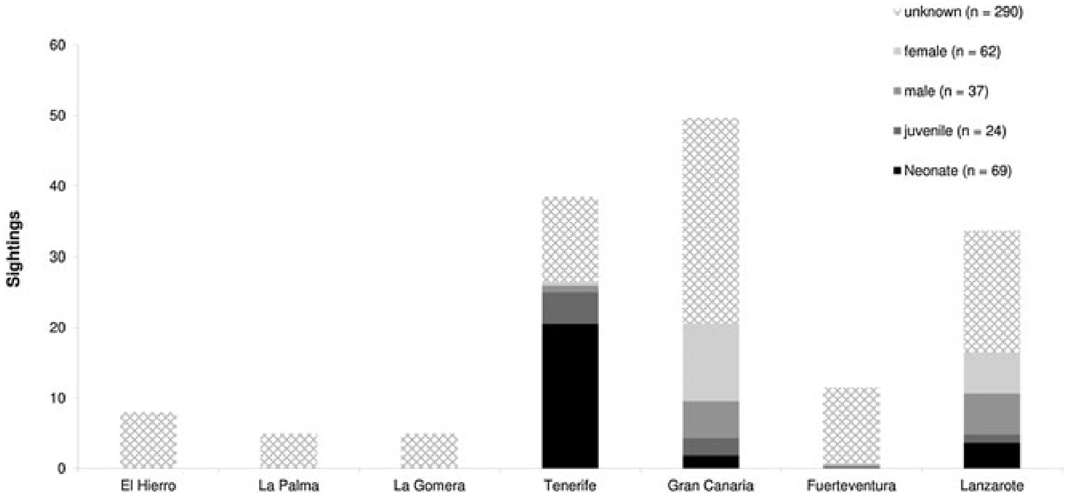

FIGURE 2 Number of sightings of the angelshark, *Squatina squatina*, at each of the seven islands (shown in west to east order) from April 2014 to March 2015; data were pooled through time and standardized by the number of participating diving centres per island. Sightings are categorized according to neonates (< 30 cm TL), juveniles (30–100 cm TL), adult males and females (> 100 cm) and unknown estimated total length

nursery area was identified in Lanzarote, where 21 neonates were reported.

Angelsharks were encountered in water depths from <1 m to a maximum of 45 m; most encounters occurred between 10 and 15 m depth (n = 189) (Figure 3a). Neonate and juvenile angelsharks were encountered only within the first 25 m. Sharks observed in deeper areas (>15 m) increased in TL (Figure 3a; $r_s = 0.79$, $P < 0.01$). Most sharks (88.9%) were observed associated with sandy bottoms, either close to reefs or strips of sand. A small proportion of individuals were also encountered on reefs and seagrass beds (Figure 3b). Angelshark presence was reported to the database at temperatures between 18°C and 22°C.

3.2 | Species distribution modelling (SDM)

Among a set of 10 PCs, representing 119 environmental variables, two PCs (PC4 and PC5) were the most influential set of variables characterizing the potential spatial distribution of *S. squatina* in the Canary Islands (Table S2). PC4 was positively correlated with SST, salinity and pH, but negatively correlated with Chl, POC, diffuse attenuation coefficient (kd490) and bathymetry. PC5 was positively correlated with cloud cover, dissolved oxygen, phosphate, bathymetry and negatively correlated with Chl, diffuse attenuation coefficient, SST, PAR, POC (Table S3). In addition, the Maxent model's jackknife test of variable importance also showed that these variables accounted for most variation to explain the potential distribution of angelsharks. The remaining PCs are not discussed further, as their contribution was negligible (< 5%).

Maxent's response curves showed how each PC influenced the prediction of the model. Curves showed that the logistic prediction change as each PC varied, leaving all other PCs at their average sample value (Figure S2). Analysis of the PC4 response curve suggested that the probability of species presence was affected particularly by the SST, salinity, and pH, as well as Chl, POC, diffuse attenuation coefficient (kd490) and bathymetry, with a truncated response curve. The opposite is true for PC5, which showed a bell-shaped response curve, indicating reduced suitability after a certain threshold of the environmental predictors. On the other hand, the response curves indicated a Maxent model using only the corresponding PCs. The response curve using only the PC4 showed that the variables which correlated with this principal component increase or decrease the probability of occurrence beyond a threshold. The PC5, however, has a similar bell-shaped

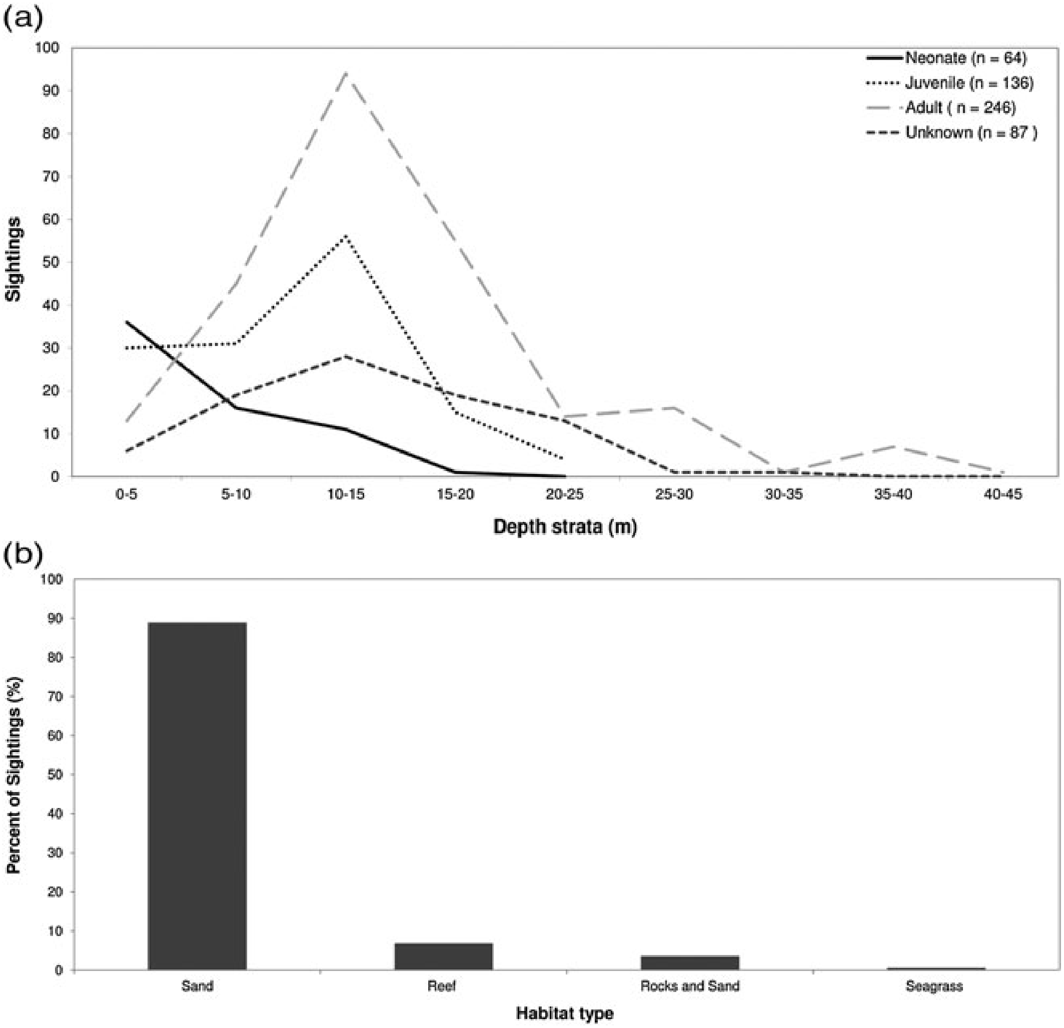

FIGURE 3 (a) Number of sightings of the angelshark, *Squatina squatina* at different water depths. Sightings are categorized according to neonates (< 30 cm TL), juveniles (30–100 cm TL), adult males and females (> 100 cm) and unknown estimated total length. (b) Percentage of sightings of the angelshark, *Squatina squatina*, associated with four different habitat types

response curve, indicating, again, a threshold at which the environmental variables of this PC become a limiting factor on angelshark occurrence (Figure S3).

The SDM has a strong predictive power with an AUC value of 0.973 and a Test AUC of 0.961. The minimum training presence logistic threshold of the SDM was <0.1 (0.0217), while the value for the 10 percentile training presence logistic threshold was 0.4559. The 10 percentile training presence threshold indicates the probability value where 10% of the presence points do not fall in the potential area.

Sightings of angelshark were recorded at all seven islands (Figure 4a). The potential distribution map denotes suitable habitat at all seven islands, with a higher suitability around the easternmost (Lanzarote, Fuerteventura) and central islands (Gran Canaria and Tenerife). Areas with the largest habitat suitability were at shallow depth, close to the shore. For example, on the north-eastern side of Gran Canaria, the bay of Sardina was particularly highlighted. In Lanzarote, the northern Chinijo archipelago and almost the entire eastern coast, particularly the area of 'Puerto del Carmen', was predicted as a highly suitable habitat. There were also areas with high suitability in the south-east of Fuerteventura. A high frequency of sightings per cell was observed at four sites: in 'Las Teresitas' (Tenerife), in 'Sardina del Norte' and in 'El Cabrón' (Gran Canaria) and in 'Puerto del Carmen' (Lanzarote) (Figure 4b). Three of these sites have also been identified as potential nursery areas, due to the elevated number of sightings of juvenile sharks.

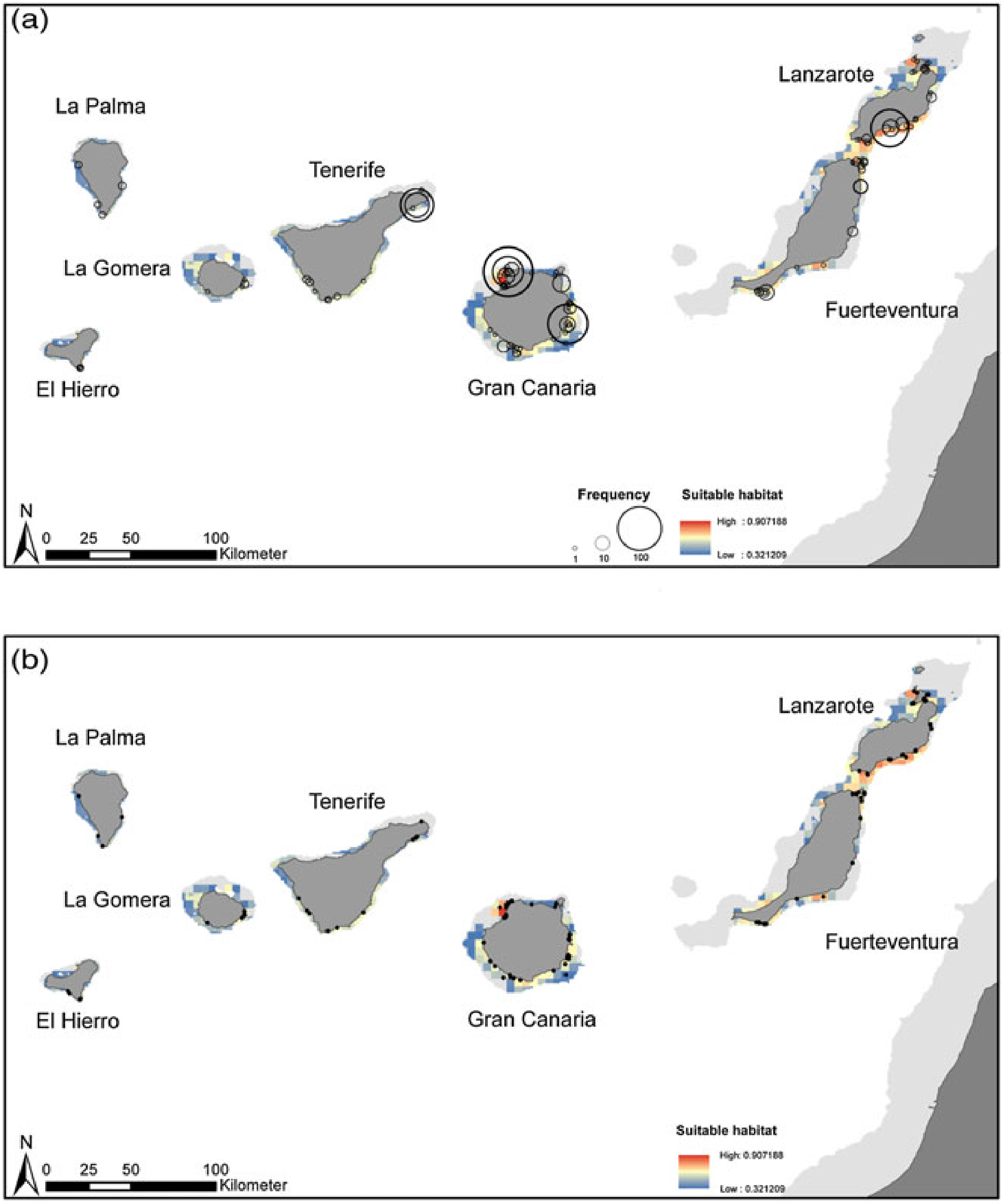

FIGURE 4 Habitat suitability map, from the maximum entropy model, for the angelshark, *Squatina squatina*. (a) Frequencies of sightings per cell are indicated as unfilled circles; (b) sightings are shown as black dots. Warmer colours indicate higher suitability areas; light grey colour denotes areas up to 200 m depth

4 | DISCUSSION

This study is the first to analyse the spatio-temporal occurrence patterns, population structure, distribution and habitat use of the angelshark, *Squatina squatina*, in the Canary Islands. The results of the study demonstrated that angelsharks exhibit highly structured and reproductively active populations, distributed along coastal shallow areas in the entire archipelago. Angelsharks were encountered throughout the entire year, but not consistently over different months.

Almost the full range of sizes (20 to 200 cm TL; i.e. neonates, juveniles and adult sharks) were reported. Adult sharks have been observed all year-round; however, the occurrence of very large-sized individuals (> 200 cm) was rare. According to the literature, angelsharks can reach up to 244 cm TL (Capapé, Quignard, & Mellinger, 1990; Compagno, 1984; Quigley, 2006). The largest shark encountered in this study was, however, a female of 200 cm. This could be due to either an underestimation of sizes, or because large sharks remain absent from these areas or move to deeper areas. Small to middle sized sharks that may have not yet reached sexual maturity, i.e. between 30 and 100 cm TL (Compagno, 1984; Osaer et al., 2015; Tonachella, 2010) were reported throughout the entire study period. There were two peaks in the number of sightings, corresponding to summer (June–July) and winter (December–February). The majority of neonate encounters occurred between April and July, which corresponded with an increased number of female sightings. This suggests that the pupping season starts in early spring (April) and reaches its peak at the end of summer (July). Moreover, this hypothesis is strengthened by the observation of seven gravid females during this period, which fits previous observations between 2006 and 2008 at Gran Canaria Island (Narvaez, 2013). The second peak in sightings was in winter (December–February), which may correspond to the mating season. This hypothesis is strengthened, as mating, mating scars and gravid females were observed or reported during this period. In addition, large-sized male sharks were significantly more frequent in winter, thus it is plausible that during summer, male sharks either undertake horizontal or vertical migrations to different areas (deeper or offshore), which could explain the significantly greater proportion of female sightings. Despite the reproductive behaviour of the angelshark being poorly understood, Narvaez (2013) and Osaer (2009) have also indicated that active males were predominantly found during winter and that the pupping season started in spring at Gran Canaria Island, as has been demonstrated here. Sexual segregation, either seasonal or spatial, has also been observed for other species of the same genus, including *Squatina californica* (Pittenger, 1984), *Squatina tergocellata* (Bridge, Mackay, & Newton, 1998) and *Squatina guggenheim* (Awruch, Nostro, Somoza, & Di Giacomo, 2008). For example, similar to *S. squatina*, adult *S. guggenheim* females migrate to shallow coastal areas (< 40 m depth) to breed (Vooren & Da Silva, 1991). The fact that 79 neonates and 12 gravid females were sighted clearly demonstrates that the population still remains reproductively active.

The angelshark is currently distributed along the entire coastline of the Canary Islands. However, the occurrence of angelsharks significantly decreased from the easternmost towards the westernmost islands, i.e. angelsharks were observed predominantly in the central (Gran Canaria, Tenerife) and easternmost (Lanzarote and Fuerteventura) islands. This was further corroborated by the SDM, as *S. squatina* exhibited a high predicted probability of occurrence towards the easternmost islands. The presence of angelsharks around the westernmost islands (La Palma, El Hierro and La Gomera) was rare, and not confounded by varying sampling effort. For example, despite the elevated number of diving centres in El Hierro Island (nine diving companies and >20 000 divers per year), angelsharks have been only infrequently encountered there. Differences in the composition and abundance of marine species across the Canary Island archipelago have been previously detected for fishes (Tuya, Boyra, Sanchez-Jerez, Barbera, & Haroun, 2004) and macroalgae (Tuya & Haroun, 2009). It is thought that this is a result of large-scale oceanographic variability associated with the proximity of the Canary Islands to the continental shore of Africa. The eastern side of the Canary Islands is routinely influenced by the seasonal coastal upwelling off the African coast, while the western part of the archipelago is situated towards the oligotrophic 'open' ocean (Davenport, Never, Helmke, Pérez-Moreno, & Llinas, 2002). Thus, the easternmost islands (Lanzarote and Fuerteventura) are regularly influenced by cooler sea water that results in higher primary productivity (Chl), while the westernmost islands (La Palma and El Hierro) often have a higher sea surface temperature (by *c*. 2°C). This oceanographic gradient seems to be important to explain the inter-island distribution patterns of angelsharks and the contrasting number of sightings between the easternmost and central, and westernmost islands. Sea temperature among other abiotic factors, has been successfully used to predict occurrences and influence movement of many sharks and rays (McKinney et al., 2012; Sequeira et al., 2014; Vaudo & Heithaus, 2009; Vooren & Da Silva, 1991).

For *S. squatina*, temperature and light dependent variables such as SST, Chl, kd400 and PAR were predicted to have the greatest effect on its occurrence. Similarly, Narvaez (2013) found a seasonal variance, possibly related to sea temperature, for the number of angelshark observations at a diving spot ('El Cabrón') in Gran Canaria. These results revealed more sightings during winter and spring, corresponding to a sea temperature between 17°C and 21°C. Despite occurring mainly in temperate waters, thermal tolerance and related ecological adaptations of *S. squatina* have not been studied in detail. A study conducted on the impact of climate change on threatened species (including *S. squatina*) in UK waters using a set of environmental variables (e.g. temperature) revealed that the potential distribution of *S. squatina* in the North Sea would not be severely affected by climate change (Jones et al., 2013). Thus, this may indicate that angelsharks are able to tolerate temperature fluctuations and, more likely, also cope with other environmental factors. In the marine system, however, abiotic factors such as water temperature, salinity and nutrient concentration may be inter-correlated and do not act in isolation (Schlaff, Heupel, & Simpfendorfer, 2014). Thus, determining the main drivers of distribution may be more complex and requires careful consideration of abiotic and biotic factors such as food, shelter and predator avoidance.

In addition to the hypothesis that varying oceanographic patterns across the archipelago influence angelshark distribution, there are three alternative hypotheses for this change. First, proximity to the African coast per se could also have influenced past and present colonization events and, therefore, provide an alternative/complementary explanation for the decrease of angelshark occurrences towards the westernmost islands. Second, the older islands are located in the eastern and central part of the archipelago; these islands have therefore wider continental platforms compared with the most recent islands (La Palma and El Hierro, in particular) (Mitchell, Dade, & Masson, 2003). This suggests that, potentially, there is more suitable habitat for angelsharks in the eastern and central relative to the western islands. Third, abyssal barriers between adjacent islands, except between Lanzarote and Fuerteventura, may also constrain connectivity between islands. It still remains unclear whether angelsharks possess the biological adaptations to undertake large migrations through the water column, and so whether the populations among the Canary Islands and the rest of the distribution range are connected.

The SDMs highlighted a high frequency of sightings and a high predictive occurrence of sharks at two particular sites (Sardina del Norte in Gran Canaria and Puerto del Carmen in Lanzarote), which correspond with the most popular diving spots in the Canary Islands. Two additional localities, one at Tenerife (Las Teresitas) and the other at Gran Canaria (El Cabrón) also included a high frequency of sightings per grid cell. Sightings are lacking in some suitable areas predicted by the SDM, such as those located off the north and west coasts of most islands. These areas are not frequented by recreational scuba divers because of rough sea conditions (wave action and restricted accessibility) and hence remain mostly unexplored. In general, it was not possible to validate the predictive map, by comparing the sighting frequency per cell with the probability of occurrence per cell. This resulted from an uneven survey effort among the islands.

The distribution of angelsharks is connected with a number of habitat features, including the bathymetry and the type of substrate. The angelshark predominantly uses areas composed of sand strips, in most cases adjacent to reefs, but it was also observed directly resting on reefs and within seagrass meadows. Angelsharks typically prefer soft substrates, which is associated with their behaviour of burying in sand for camouflage (Compagno, 1984; Compagno et al., 2005). The SDM predicted that the likelihood of angelshark occurrence was driven by a set of environmental variables, which may encapsulate the ecological niche of this shark. Our data showed that the habitat use of *S. squatina* changes according to their body size and, subsequently, their sex. Deeper waters were exclusively inhabited by large sharks (> 100 cm TL), while neonate and juvenile sharks exclusively occurred in shallow waters (< 25 m depth). This may indicate that small-sized sharks are subjected to predation and, therefore, choose the safety of shallow water habitats to evade predators. A similar behaviour has been observed for other shark species (DeAngelis, McCandless, Kohler, Recksiek, & Skomal, 2008; Heupel, Carlson, & Simpfendorfer, 2007). However, predator avoidance may not be the only factor causing segregation; for example, the availability of prey may also have an influence on their preference for shallow habitats. Vooren and Da Silva (1991) revealed that juvenile *Squatina guggenheim* of both sexes occurred close to shore, while adult sharks were distributed offshore up to 100 m depth. Vögler et al. (2008) also found that the different habitat preferences of *S. guggenheim* are linked to an increase in body size. For other sharks (e.g. Port Jackson sharks, nurse sharks and reef sharks), particularly for those that are coastal residents, segregation along depth gradients was linked to temperature tolerances (Speed, Field, Meekan, & Bradshaw, 2010), foraging behaviour (Sims et al., 2008) or predator avoidance (Dicken, Smale, & Booth, 2006). Shallow coastal areas are linked to more elevated temperatures, compared with deeper areas. It is likely that angelsharks, similar to leopard sharks (Hight & Lowe, 2007; Nosal, Caillat, Kisfaludy, Royer, & Wegner, 2014; Nosal et al., 2013), may take advantage of warm shallow areas to speed the development of their offspring. However, more research is needed to further investigate the influence of elevated temperatures in shallow habitats on angelshark physiology.

Mindful of the caveats of citizen science data (Ward-Paige & Lotze, 2011), this study has demonstrated that using scuba divers to report sightings is an effective method to obtain valuable data on angelsharks in the Canary Islands. It should be noted that data were collected in a depth range between 0 and 45 m depth, however, similar to other marine systems (Robinson et al., 2011), sampling effort was biased towards shallow sites close to the coast. Because of sampling limitations, certain assumptions can only be made for areas below 45 m depth. In this sense, it is necessary to conduct further long-term studies (e.g. acoustic telemetry) to validate citizen science data and to explore the distribution and the migratory behaviour of angelsharks, including areas greater than 40 m in depth.

5 | CONCLUSIONS: IMPLICATIONS FOR CONSERVATION

Understanding life-history strategies of sharks has important implications for their conservation (Simpfendorfer et al., 2011). This study demonstrated that angelsharks display spatial (vertical and horizontal) and temporal segregation by size and sex. Angelshark distribution is driven by a combination of factors, including environmental and geographical/geological variation across the archipelago as well as biotic factors, e.g. reproductive behaviour, prey abundance and predator avoidance, which require further investigation.

This information has recently been used to develop the Angelshark Action Plan for the Canary Islands (Barker et al., 2016). Improved understanding of the spatial distribution of angelsharks, in particular through the identification of critical habitats, can be used to design spatial protective measures, taking into account segregation by size and sex. Effective protective measures for the angelshark can be developed through the understanding of timing of key life-history events, e.g. pupping and mating. For example, the results of this study could be used to limit recreational and commercial fishing in certain shallow waters during the mating (winter) and pupping (spring/summer) seasons. Similarly, this knowledge can be used to better target public awareness raising campaigns, e.g. when angelsharks are more vulnerable to disturbance, for divers or beach users during the pupping season, or in areas where angelsharks are seen more often.

This study identified three potential nursery areas. It is clear that (1) long-term monitoring studies to determine whether these areas are used as nursery areas for angelsharks, according to Heupel et al. (2007), should be conducted here. In addition, other key research areas to prioritize include: (2) long-term tagging and acoustic monitoring of sharks to understand their vertical and horizontal habitat use, taking into account different life stages, sex and seasons; (3) identification of critical habitats in nearshore areas in terms of mating and pupping; (4) movement and connectivity of angelsharks at multiple scales; and (5) estimates of relative abundance. Prioritizing research based on conservation needs both optimizes capacity and available resources, as well as ensuring that conservation strategies/action plans are implemented effectively to minimize the threats to angelsharks in the Canary Islands.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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