The distribution, ecology and predicted habitat use of the Critically Endangered angelshark (*Squatina squatina*) in coastal waters of Wales and the central Irish Sea

Joanna Barker | Jake Davies | Monika Goralczyk | Surshti Patel | John O’Connor | Jim Evans | Rowland Sharp | Matthew Gollock | Fenella R. Wood | James Rosindell | Charlie Bartlett | Brett J. Garner | Dafydd Jones | Declan Quigley | Ben Wray

1 Zoological Society of London, Regent’s Park, London, UK
2 Natural Resources Wales, Maes y Ffynnon, Bangor, UK
3 Department of Life Sciences, Imperial College London, Berkshire, UK
4 Welsh Federation of Sea Anglers, Pembrokeshire, UK
5 Welsh Fishermen’s Association, Ceredigion, UK
6 School of Biological Sciences, University of Aberdeen, Aberdeen, UK
7 Fisher, Gwynedd, UK
8 Sea Fisheries Protection Authority, Co Dublin, Ireland

**Abstract**

The angelshark (*Squatina squatina*) has the northernmost range of any angel shark species, but there is limited information on its distribution, habitat use and ecology at higher latitudes. To address this, Angel Shark Project: Wales gathered 2231 *S. squatina* records and 142 anecdotal resources from fishers, coastal communities and archives. These spanned the coastal waters of Wales and the central Irish Sea and were dated from 1812 to 2020, with 97.62% of records within 11.1 km (6 nm) of the coast. Commercial, recreational and charter boat fishers provided the majority of *S. squatina* records (97.18%), with significantly more sightings from three decades (1970s, 1980s and 1990s) and in the months of September, June, August and July (in descending order). The coastal area between Bardsey Island and Strumble Head had the most *S. squatina* records (*n* = 1279), with notable concentrations also found in Carmarthen Bay, Conwy Bay and the Outer Severn Estuary. Species distribution models (SDM) identified four environmental variables that had significant influence on *S. squatina* distribution, depth, chlorophyll-a concentration, sea surface temperature (SST) and salinity, and these varied between the quarters (Q) of the year. SDM model outputs predicted a larger congruous area of suitable habitat in Q3 (3176 km²) compared to Q2 (2051 km²), with suitability along the three glacial moraines (Sarn Badrig, Sarn-y-Bwch and Sarn Cynfelyn) strongly presented. Comparison of modelled environmental variables at the location of *S. squatina* records for each Q identified reductions in depth and salinity, and increases in chlorophyll-a and SST when comparing Q2 or Q3 with Q1 or Q4. This shift may suggest *S. squatina* are making seasonal movements to shallow coastal waters in Q2 and Q3. This is supported by 23 anecdotal resources and may be driven by reproductive behaviour, as there were

Joanna Barker and Jake Davies should be considered joint first authors.

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INTRODUCTION

There are at least 23 species of angel shark in the family Squatinidae, a group of demersal sharks with a dorso-ventrally flattened body shape, with a global distribution across warm temperate and tropical seas (Ebert et al., 2013; Ellis et al., 2021; Gordon et al., 2017; Weigmann, 2016). Squatinidae are one of the most globally threatened families of chondrichthians (Dulvy et al., 2014; Kyne et al., 2020) and are particularly susceptible to accidental capture in fisheries and habitat loss due to their demersal coastal ecology, low reproductive output and presumed slow growth rates (Barker et al., 2016; Dulvy et al., 2014; Ellis et al., 2021). The angelshark, Squatina squatina, is listed as Critically Endangered on the IUCN Red List of Threatened Species (Morey et al., 2019) and has the northernmost range for any angel shark species: south-west Scandinavia (62°N) to north-west Africa (21°N), including the Mediterranean and parts of the Black Sea close to the Sea of Marmara (Lawson et al., 2020; Morey et al., 2019). However, the geographic extent of S. squatina has contracted by 58% in the last 100 years, with evidence of a few contemporary populations remaining in the north-east Atlantic (Canary Islands and Celtic Sea Ecoregion) and Mediterranean (Adriatic Sea, Aegean Sea, Ionian Sea, Tyrrenhenian Sea and waters off Algeria, Libya, Malta, North Cyprus, Tunisia and Turkey) (Lawson et al., 2020). Of these, the Canary Islands have been identified as a uniquely large stronghold for S. squatina, with the species commonly sighted by divers and fishers around the archipelago (Barker et al., 2016; Meyers et al., 2017; Gordon et al., 2017).

S. squatina are present in coastal waters to at least 150 m in depth (Morey et al., 2019). The species shows broad habitat use, with individuals documented on sand, gravels and mud (Akyol et al., 2015; Jiménez-Alvarado et al., 2020; Meyers et al., 2017; Morey et al., 2019; Noviello et al., 2021); reefs (Meyers et al., 2017) and seagrass beds (Lapinski & Giovos, 2019; Meyers et al., 2017), and able to adapt to varying salinities: coastal marine waters (Morey et al., 2019), lagoons (Lapinski & Giovos 2019) and estuaries (Aflalo, 1904; Morey et al., 2019). Tagging studies conducted in Tunisia and Ireland suggest that S. squatina do not demonstrate long-distance movements; in the former, all recaptures were within 44 km of the tagging site (Capapé et al., 1990; Quignard & Capapé 1971) and in the latter, 96% of recaptures were in coastal Irish waters (Quigley, 2006) on average 61 km from the tagging location (Fitzmaurice et al., 2003). Additional research suggests that S. squatina may make seasonal inshore migrations to reproduce (Bom et al., 2020; Ellis et al., 2021; Fitzmaurice et al., 2003; Meyers et al., 2017; Noviello et al., 2021).

S. squatina demonstrate lecithotrophic viviparity and give birth to between seven and 25 pups that are 24–34 cm in length (Capapé et al., 1990; Ellis et al., 2021; Lo Blanco, 1899; Osseo et al., 2015; Patterson, 1905). S. squatina are thought to have a biennial reproductive period (Capapé et al., 1990, 2005; Ellis et al., 2021), with the ability to give birth year-round (Jiménez-Alvarado et al., 2020). The peak pupping period is believed to be between April and July in the Canary Islands (Meyers et al., 2017), July in the Mediterranean (Capapé et al., 2005), and June and July in the UK (Norman & Fraser, 1948; Wheeler & Blacker, 1969).

Within the Celtic Sea Ecoregion, near the northermmost part of the S. squatina range, important areas have been identified due to recent confirmed records: the west coast of Ireland, specifically Tralee Bay and Clew Bay (Fitzmaurice et al., 2003; Shephard et al., 2019), coastal waters of Wales (Barker et al., 2020) and the Irish Sea (Quigley, 2021). Further research and conservation efforts at these locations are of particular importance as several studies have suggested a decline in S. squatina records – and potentially abundance – within and around the area (Bom et al., 2020; Fitzmaurice et al., 2003; Hiddink et al., 2019; ICES, 2019; Rogers & Ellis, 2000; Shephard et al., 2019).

In Ireland, analysis of angling logbooks, the Irish Specimen Fish Committee and the Irish Marine Sportfish Tagging Programme indicate a decline in S. squatina records between 1955 and 2011 (Fitzmaurice et al., 2003; Shephard et al., 2019). In the North Sea, S. squatina is considered as extirpated (ICES, 2019); a review of historical literature identified a decline in S. squatina records between 1945 and 1970 (Bom et al., 2020), with only four S. squatina records reported since 1970 (Zidowitz et al., 2017). In the English Channel, two studies interrogated research vessel survey data and identified very few records of S. squatina, particularly in contemporary surveys (Martin et al., 2010; Rogers & Ellis, 2000).

In Wales, a recent analysis of S. squatina records between 1970 and 2016 ‘estimated a 70% decline in abundance over 46 years’ and ‘distribution contracted to a central core of Cardigan Bay’ (Hiddink et al., 2019). The estimated decline in S. squatina abundance was inferred from changes in observations per unit effort, calculated by adjusting records collected through phone interviews with fishers for recall bias and assuming that there was a constant observer effort over space and time (Hiddink et al., 2019). The authors highlighted that ‘the ultimate challenge in the interpretation of opportunistic records is separating true population trends from changes in the observation effort. As we could not quantify observation effort
directly, we made the simplifying assumption that observers were active at a constant effort in space and time’ (Hiddink et al., 2019).

Quantifying spatial and temporal changes in fishing effort, for example the number of fishers, the number of vessels, the size of vessel, the frequency of fishing, the fishing location, the type and usage of gear, and the seasonal changes in these factors, is important to interpret any changes in S. squatina records over time and/or to use these to infer change in abundance. This is extremely difficult, especially in complex, multinational, polyvalent fleets such as those in the Celtic Seas Ecoregion. Further data are needed to quantify changes in fishing effort over time to allow for more precise estimates of species abundance and any changes.

Additionally, there are several limitations in using research vessel survey data to monitor rare species, as they are designed to target commercially targeted fish species to enable stock assessments (Maxwell & Jennings, 2005) and are often completed in offshore regions, where there is low spatial overlap with shallow-water species and habitats (Shephard et al., 2019).

Commercial landings data for S. squatina from across the Food and Agriculture Organization of the United Nations (FAO) Area 27, North East Atlantic, have been collated by the International Council for the Exploration of the Sea (ICES) Working Group on Elasmobranch Fishes (ICES, 2019). These data indicate decadal declines in S. squatina landings from the 1970s (20 t per year), 1980s (13.2 t per year) and 1990s (1.4 t per year), with few landings since then (Ellis et al., 2021; ICES, 2019). The latter studies highlighted that legal protection for S. squatina, introduced in 2008 under the UK Wildlife and Countryside Act (1981) and in 2009 under the EU Common Fisheries Policy, is likely to have contributed to fewer reported landings in the last two decades. Two further limitations in using commercial landings data to monitor and assess elasmobranchs exploited in mixed fisheries are (a) any animal that was discarded at sea prior to landing would not be included and (b) local or regional changes in fishing effort are not taken into account (Martin et al., 2010).

To date, there has been no attempt to describe S. squatina ecology in the Celtic Sea Ecoregion, likely due to a sparsity of records. This is a critical data gap: without a baseline understanding of S. squatina distribution, habitat use, movement and other aspects of their ecology in higher latitudes, it is difficult to assess and adapt conservation measures and outline research priorities for the species (Barker et al., 2020). Most information on S. squatina ecology comes from studies in the Canary Islands, historic research in the Mediterranean Sea and/or more studied angel shark species as a proxy, for example S. californica.

Angel Shark Project: Wales (ASP:W) is a collaborative project led by Natural Resources Wales and the Zoological Society of London. This article aims to share key insights into S. squatina distribution, habitat use and ecology in Wales, using a mixed methods analysis of S. squatina records and anecdotal resources dating back 200 years. It will outline a baseline understanding of S. squatina in coastal waters of Wales and the central Irish Sea to inform future research, conservation, management and policy decisions contained in the Wales Angelshark Action Plan (Barker et al., 2020). Two specific research questions will be answered: (a) what are the spatial and temporal trends in S. squatina distribution in Wales and (b) what ecological parameters are driving these?

2 | MATERIALS AND METHODS

2.1 | Geographic scope

Data collection methods were focused on gathering S. squatina ‘records’ (specific observations of S. squatina, obtained through capture during fishing, being observed underwater or found dead-stranded on the shore) and ‘anecdotal resources’ (information on S. squatina ecology or biology, provided anecdotally or published in literature) from Wales, using both the English and Welsh language. Data analysis encompassed the UK Exclusive Economic Zone (EEZ) around Wales, up until the midline between Wales and England (herein referred to as ‘UK EEZ around Wales’), and the bordering area of the central Irish Sea, facilitated by S. squatina records from the east coast of Ireland being provided to the project by Sea Fisheries Protection Authority (D. Quigley).

2.2 | Gathering S. squatina records and anecdotal resources with fishers

Semistructured informal interviews were designed to gather local ecological knowledge (LEK) on S. squatina from the fishing community across Wales. This LEK study was carefully designed to fit the socio-historical and cultural context of fishing in Wales, to build long-term collaboration with responders and to enable collation of relevant, detailed and accurate data on S. squatina (Gilchrist et al., 2005; Early-Capistrán et al., 2020). It was co-designed with the fishing community and respondents were recruited through snowball sampling, with a total of 65 fishers contributing to the LEK study over the period of July 1, 2017 to December 31, 2020. Researchers led the interviews in either English or Welsh. The LEK study had five stages, as outlined below, and only 21 fishers completed all stages, with the rest (n = 44) completing every stage except stage 4.

2.2.1 | Stage 1

A fisher stakeholder map for Wales was developed by (a) working with fisher associations to identify key individuals, (b) gathering contacts from social media, fishing websites and forums, and (c) personal recommendations from fishers as to who to talk to about S. squatina.

2.2.2 | Stage 2

An initial in-person meeting or phone call was completed to explain the aims of ASP:W, why S. squatina records and anecdotal resources were sought and to obtain verbal consent to work with the project.
2.2.3 | Stage 3

Data gathering meetings were completed in-person or by phone. Meetings were designed as informal conversations structured using a participatory guide (Supporting Information S1) to gather information on fishers (age, location and year started fishing), fishing practices (fishing areas, gears used and target species), S. squatina records, S. squatina anecdotal resources and perceptions on how fishing has changed (practices, fishing behaviour, species abundance) in Wales. To verify that records were of S. squatina, not anglerfish (Lophius piscatorius), which shares the common name ‘monkfish’ in some parts of Wales, an identification guide was shown and descriptions of the record were used to assign confidence in identification (Supporting Information S2). Fishers were asked to share any contacts who may be willing to participate in the project for snowball sampling.

2.2.4 | Stage 4

Historical timelines and participatory mapping exercises were completed to support the recall of information in a systematic way. Time-lines were provided outlining significant national and fishing-related events (e.g., harsh winter in 1962, decimalization in 1971 and the Sea Empress oil spill in 1996) and fishers provided information using the timeline as a contextual frame. A nautical chart from the area the fisher operated was provided and this was used to map where they had encountered S. squatina, their fishing locations and how these varied spatially and temporally. One commercial fisher and two charter boat skippers shared their logbooks, which had detailed S. squatina records, including weight and location of capture, and information on fishing effort.

2.2.5 | Stage 5

Data were validated and refined through repeat meetings with fishers and fisher associations. Project outputs were also shared to explain how their input had contributed to S. squatina conservation.

2.3 | Collation of additional historic S. squatina records and anecdotal resources

An extensive search of historical literature (books, magazines, newspapers, reports, paintings, illustrations and online databases) and community photographs and letters were used to gather S. squatina records and anecdotal resources, using four data collection strategies.

2.3.1 | Online literature search

Online searches were completed on social media platforms, online natural history databases and forums using the keywords ‘angelshark’, ‘monkfish’, ‘maelgi’, ‘fiddlefish’ and ‘squatina’. When a S. squatina record or anecdotal resource was identified, the owner was contacted and added to the stakeholder map.

2.3.2 | Non-digitized literature search

Ten citizen scientists were recruited and trained to search local museums, libraries and archives for S. squatina records and anecdotal resources. Training involved S. squatina identification and historical research techniques. To standardize information, data-gathering forms were used and citizen scientists took photographs where copyright permissions allowed. Searches involved looking for the same keywords described above, as well as wider information on Welsh maritime heritage. The search was targeted on information from Wales, but records and anecdotal resources from a wider region were also documented.

2.3.3 | Collation of community information

Posters, social media and a press release were used to promote five Angelshark History Roadshows, completed to gather S. squatina records and anecdotal resources. The roadshows were held between January and February 2019, located in community hubs at five strategic locations across Wales (Aberystwyth, Holyhead, Milford Haven, Nefyn and Swansea). Visitors were encouraged to share photographs, logbooks, diaries and oral memories on S. squatina.

2.3.4 | Collation of records and anecdotal resources from the Sea Angler archive

The recreational sea-fishing magazine Sea Angler (monthly issues from March 1972, when the magazine launched, and March 2020) was searched to identify S. squatina records and anecdotal resources. Reports of S. squatina submitted to the magazine were mainly referred to by the common name ‘monkfish’.

2.4 | Collation of recent S. squatina records

Sightings submitted to the Angel Shark Sightings Map (www.angelsharkproject.com/map) were downloaded monthly. Where consent was granted, reporters were contacted by ASP:W for further detail.

2.5 | Data management and validation

Three cross-referenced database tables were developed: the personal database held information from fishers who had completed interviews, including data on their fishing effort, the record database held
S. squatina records and the resources database held S. squatina anecdotal resources separated into four categories (information specific to Wales, the rest of the UK, outside of the UK and those with no geographic reference).

2.6 Quantitative analysis

To enable quantitative analysis, data within the records database were ranked using four confidence scales related to identification (ID) (how confident the record is S. squatina and not another species), abundance (how well fishers can recall the number of S. squatina caught during one event), temporal (whether an exact date, month, year or year range was provided) and spatial (how the location of the encounter was recorded or whether it was estimated) (Supporting Information S2). Any record where identification confidence was assigned the lowest score (1) was removed prior to analysis (n = 7). To reduce known subjectivity in LEEK data, the data were reviewed across confidence scales and cross-checked to aid accuracy and reliability (Early-Capistrán et al., 2020; Gilchrist et al., 2005; O’Donnell et al., 2010).

Duplicate records were identified and that with the lower overall confidence was removed. To enable temporal analysis across the year, data were assigned a quarter: Q1 (January to March), Q2 (April to June), Q3 (July to September) and Q4 (October to December). To enable analysis of life-history stages, data were categorized into four length groups associated with inferred life-history stages: ≤39 cm total length (TL) was inferred as recently born, 40–60 cm TL was inferred as juvenile, 61–100 cm TL was inferred as subadult and ≥101 cm TL was inferred as adult.

To test for the difference in the number of S. squatina records between any two discrete categories, pairwise chi-square tests with a Bonferroni correction were used.

2.7 Qualitative analysis

A total of 142 S. squatina anecdotal resources were collated. Given that data collection focused on Wales, only those anecdotal resources with Wales-specific information (n = 64) and UK-wide information (n = 26) were used in the qualitative analysis to reduce regional bias. Each resource was transcribed and categorized depending on what aspect of S. squatina ecology it described: frequency of encounters, seasonality and/or movement, prey species, habitat preference or reproduction. Some anecdotal resources covered more than one category. Results presented on frequency of encounters and seasonality and/or movement include only Wales-specific anecdotal resources; results presented on prey, habitat preference and reproduction include both Wales specific and UK-wide anecdotal resources.

On review of the personal database it was identified that further data covering a wider range of fishing vessels was needed to meaningfully interpret any changes in fishing effort, thus this is not included in the present article nor do we infer how S. squatina abundance may have changed in the region.

2.8 Species distribution modelling

2.8.1 Environmental predictors

The R packages used in the analysis are listed in Supporting Information S3. Species distribution models (SDMs) were fitted using inferred seabed substrate type (substrate), depth of the seafloor (depth), log-transformed chlorophyll-a concentration (chlorophyll-a), salinity (salinity), sea surface temperature (SST) and standard deviation of SST (sdSST) (Table 1). These variables were chosen following a literature review of other elasmobranch species, including other angel shark species and S. squatina populations in different parts of its range. The temporal range of records used to fit the models was limited to records from 1980 to align with the temporal resolution of the environmental predictors and prevent introducing false temporal accuracy (Table 1). Each dynamic predictor (chlorophyll-a, SST and salinity) was averaged across its temporal coverage to create daily (chlorophyll-a, SST) and monthly (salinity) climatological layers. These layers were then averaged across Q2 and Q3 to create seasonal-scale predictors. Standard deviation of SST was calculated across both quarters to account for the variation in temperature. Environmental predictor variables were resampled to 0.0083° × 0.0083° horizontal resolution (around 1 km by 1 km), which was selected based on the resolution of the environmental datasets, a recommended approach for studies of species distributions that use observations from fisheries (Mannocci et al., 2017). As S. squatina records used in this study had different spatial resolutions, the chosen intermediate model resolution had a secondary benefit of reducing the chance of introducing false accuracy in model outputs. Temperature was resampled using bilinear interpolation and substrate was aggregated using modal values.

2.8.2 Pseudo-absence points

Most algorithms applied in SDMs require information about environmental conditions at sites where a species is absent. As absence data were not available in this study, pseudo-absence points were sampled using a target group background sampling technique, which transfers the sampling bias in presence records to the pseudo-absence points and can minimize over-fitting (Elith & Leathwick, 2009; Phillips et al., 2009, Phillips et al., n.d.). Pseudo-absence points were sampled from areas within a 20 km distance from the presence points, as this was an intermediate size for the study region (Derville et al., 2018; VanDerWal et al., 2009). The number of pseudo-absence points was equal to 10 times the number of presence records used to fit the model, selected to maximize model performance (Barbet-Massin et al., 2012).

2.9 Model fitting

In this study, an ensemble of bivariate models MaxEnt (Phillips et al., 2009), generalized linear models (GLMs) and generalized boosted models (GBMs) were built in the ‘biomod2’ (Thuiller et al., 2020) and
‘ecospat’ (Broennimann et al., 2021) packages in R Studio (R Studio Team, 2020). These were fitted using an ensemble approach, where all possible combinations of predictors were combined into a single model based on selected evaluation statistics (Araújo & New, 2007; Lomba et al., 2010). This approach was chosen to overcome sample size limitations for rare species, such as *S. squatina*, which cannot align with recommendations that the number of predictors used to fit a model should not exceed the number of presence records multiplied by 10 (Araújo & New, 2007; Breiner et al., 2018; Guisan & Zimmermann, 2000; Lomba et al., 2010).

The models were calibrated by applying a k-fold cross-validation procedure in the ‘ecospat’ package (Broennimann et al., 2021). At each partition, 80% of the dataset was drawn at random to build the model and the remaining 20% was used to test its performance. This was repeated 10 times to evaluate each model, resulting in a total of 900 models (10 iterations × 15 bivariate models × 3 algorithms × 2 seasons) (Hijmans, 2012; Hijmans & Elith, 2013) (Supporting Information S4). An overall ensemble forecast of the habitat suitability for *S. squatina* was created as an area under the receiver operating characteristic (ROC) curve (AUC)-weighted mean of the individual models. Variable importance was calculated using the ‘ecospat.var.importance’ function in the ‘ecospat’ package (Broennimann et al., 2021) (Table 1).

### Table 1 Percentage contribution of each environmental predictor variable used in the species distribution models fitted using *Squatina squatina* records

| Variable                                | Source                                                                 | Temporal resolution | Spatial resolution          | Quarter 2 | Quarter 3 |
|-----------------------------------------|------------------------------------------------------------------------|---------------------|-----------------------------|-----------|-----------|
| Sea surface temperature (SST)           | Hoyer & Karagali (2016); IFREMER (2019).                              | 1982–2011           | 0.03° latitude/longitude    | 0.182     | 0.172     |
| Standard deviation of SST               |                                                                        |                     |                             | 0.164     | 0.176     |
| Depth of the seafloor                   | Sbrocco & Barber (2013)                                               | NA                  | 0.0083° latitude/longitude  | 0.198     | 0.17      |
| Inferred seabed substrate type          | EMODnet Seabed Habitats data (2021)                                   | NA                  | 0.000278° latitude/longitude| 0.154     | 0.147     |
| Log of chlorophyll-a concentration      | Mercator Ocean International (2016).                                  | 1997–2018           | 0.0104° latitude/longitude  | 0.156     | 0.169     |
| Salinity                                | Sbrocco & Barber (2013)                                               | 1955–2002           | 0.0083° latitude/longitude  | 0.147     | 0.159     |

**Figure 1** Number of *Squatina squatina* records each year, spanning a 208 year period between 1812 and 2020. Only those records where a specific year was provided are shown (n = 2099). Bars are stacked with different kinds of shading representing the different ID confidence levels (Supporting Information S2). ( ) 2, ( ) 3, ( ) 4, ( ) 5.
To compare the distributions of suitable sites between quarters, continuous habitat suitability values were converted into binary values (1 = presence, 0 = absence) using the true skill statistic (TSS) threshold as a cut-off value to maximize the sum of sensitivity and specificity so that habitat suitability scores could be converted into maps showing *S. squatina* predicted presence and absence; it has been shown to be independent of prevalence (Allouche et al., 2006).

### 2.9.1 | Habitat preference

Environmental variables used for SDMs were extracted for *S. squatina* records and summarized for each quarter to assess variation across the year. Distribution of environmental data across quarters was non-normal with unequal variance, therefore nonparametric Wilcoxon tests were used to test for a difference between means of environmental variables. Statistical difference could not be tested across all quarters.
**FIGURE 3** Comparison of the number of female, male and sex not recorded (nr) Squatina squatina records reported in each month. Specific month not recorded is plotted on a secondary axis as the majority of records spanned more than a month period (shown to the right of the dashed line). □ Female, ■ male, (□) nr

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**FIGURE 4** Spatial variation in Squatina squatina records across the UK EEZ around Wales and the central Irish Sea, shown as counts per 20 km grid squares. Coastal areas of Wales are divided using biogeography and extend out to 12 nm or the mid-line: 1, Dee Estuary to North Stack; 2, North Stack to Bardsey Island; 3, Bardsey Island to Strumble Head; 4, Strumble Head to St Govan’s Head; 5, St Govan’s head to Rhossilli; 6, Rhossili to Barry; 7, Barry to Chepstow. The numbers provided under each area label show how many S. squatina records were reported in that area.
due to low sample sizes in Q1 and Q4, so the significance results presented below relate to comparison between Q2 and Q3 only.

3 | RESULTS

3.1 | Results of quantitative analysis

3.1.1 | Source of S. squatina records

A total of 510 reports containing 2231 S. squatina records, spanning 1912 to 2020, were provided to ASP:W and used for quantitative analysis; 86.28% (n = 1925) of records were categorized in the two highest ID confidence levels (Figure 1). In total, 97.18% (n = 2168) of S. squatina records were provided by fishers, with the majority originating from direct fisher interviews (93.05%, n = 2076) (Supporting Information S5). In addition, 1260 records were from commercial fishers, 660 records from charter boat skippers, 182 records from recreational fishers from shore and 66 records from recreational fishers from boats (Figure 2a). There was significant difference in the number of S. squatina records provided by each of the fisher categories ($X^2 = 1699.5$, d.f. = 3, $P < 0.001$).

3.1.2 | Temporal variation in S. squatina records

There was a significant difference in the number of S. squatina records reported between decades ($X^2 = 5855.3$, d.f. = 12, $P < 0.0001$); three decades [1970s (n = 337), 1980s (n = 774) and 1990s (n = 805)] contributed 85.88% of records. Fewer S. squatina records were provided in the 2000s (n = 82) and 2010s (n = 126) (Figure 1).

There was a significant difference in the number of S. squatina records reported each month (d.f. = 11, $X^2 = 3438.7$, $P < 0.0001$), with September, June, August and July having statistically higher numbers of records (in descending order) (Figure 3). This trend was also reflected when S. squatina records were analysed in each fisher category, with more S. squatina recorded in Q3 than in Q1, Q2 or Q4 for commercial fishers (Q1 $X^2 = 434$, d.f. = 1, $P < 0.0001$; Q2 $X^2 = 68.1$, d.f. = 1, $P < 0.0001$; Q4 $X^2 = 465$, d.f. = 1, $P < 0.0001$) and charter

FIGURE 5  Comparison of environmental variables extracted at Squatina squatina records for each quarter, including depth (m) (a), chlorophyll-a (mg m$^{-3}$) (b), sea surface temperature (°C) (c) and salinity (ppt) (d). ***Identifies statistical significance between variables in Q2 and Q3; sample sizes were too low for statistical analysis of Q1 and Q4.
boat skippers (Q1 $X^2 = 52, \text{d.f.} = 1, P < 0.0001$; Q2 $X^2 = 17.8, \text{d.f.} = 1, P < 0.01$; Q4 $X^2 = 38.8, \text{d.f.} = 1, P < 0.0001$) (Figure 2a).

3.1.3 | Biological information from *S. squatina* records

*S. squatina* records from all inferred life-history stages were reported to the project: recently born ($n = 4$), juvenile ($n = 81$), subadult ($n = 10$) and adult ($n = 2079$) (Figure 2b). The majority were adult *S. squatina* (93.19%, $n = 2079$), significantly more than any other inferred life-history stage (recently born $X^2 = 2067, \text{d.f.} = 1, P < 0.0001$; subadult $X^2 = 2049.19, \text{d.f.} = 1, P < 0.0001$; juvenile $X^2 = 1848.15, \text{d.f.} = 1, P < 0.0001$) (Figure 2b). More adult *S. squatina* were reported in Q3 compared with Q1 ($X^2 = 646, \text{d.f.} = 1, P < 0.01$), Q2 ($X^2 = 142, \text{d.f.} = 1, P < 0.0001$) or Q4 ($X^2 = 620, \text{d.f.} = 1, P < 0.0001$) (Figure 2b).

3.1.4 | Spatial variation in *S. squatina* records

*S. squatina* records were present across the entire coast of Wales, with most located between Bardsey Island and Strumble Head (58.59%, $n = 1279$) (Figure 4). The majority of records were located close to the coast, within 11.1 km (6 nm) (97.62%, $n = 2178$), significantly more than any other distance from the coast: 6-12 nm ($X^2 = 2151, \text{d.f.} = 1, P < 0.0001$), 12 nm to UK EEZ around Wales.
| Source | Name/author | Year | Month | Source text description |
|--------|------------|------|-------|-------------------------|
| Newspaper | North Wales Chronicle | 1858 | September | A strange nautical visitor ... the fishermen ... came in contact with a species of fish, which the oldest of them (having been employed ... for upwards of 45 years) never observed before |
| Newspaper | The Aberystwyth Observer | 1870 | August | Carefully preserved by Mr Colleman, the pier manager, and it was exhibited during the past week to crowds of spectators |
| Newspaper | Irish Times | 1874 | September | Taken to Manchester Aquarium to be exhibited. |
| Newspaper | Cambrian News | 1875 | September | It was handed to Mr Bamber, fishmonger, Terrace Road, who kept it alive until Monday morning |
| Newspaper | Cambrian News | 1875 | September | This is the third 'shark' that has been caught in the (Aberystwyth) bay this summer |
| Newspaper | Cambrian News | 1878 | August | Exhibited in a boat on the beach |
| Newspaper | The Aberystwyth Observer | 1893 | September | Exhibited on the beach |
| Newspaper | The Carmarthen Weekly Reporter | 1897 | September | Wild Beast Show – a dead 'angel shark' caught in Carmarthen Bay reposed in peace alongside ... |
| Newspaper | Evening Express | 1899 | September | For some times past it has been reported that a shark had been several times sighted in the (Aberystwyth) bay |
| Newspaper | The Cardigan Bay Visitor | 1903 | September | It attracted much curiosity while exhibited by Mr Shears in Terrace Road |
| Newspaper | The Cardiff Times | 1905 | August | Shown to visitors at a penny ahead |
| Book | H.E. Forrest | 1907 | Not recorded | Frequently met ... not uncommon ... |
| Newspaper | The Aberystwyth Observer | 1908 | July | Shark was exhibited on Saturday in a tent erected on the beach |
| Newspaper | Llangollen Advertiser Denbighshire Merionethshire and North Wales Journal | 1918 | May | Visitors and the inhabitants viewed it in large numbers, the proceeds going to the Red Cross funds |
| Newspaper | Llangollen Advertiser Denbighshire Merionethshire and North Wales Journal | 1918 | May | First fish of this kind caught in Cardigan Bay |
| Newspaper | Western Mail | 1923 | September | Some angelsharks caught |
| Book | Clive Gammon | 1974 | Not recorded | Common off Lleyn, South Pembrokeshire and sometimes in the Swansea area, in late summer |
| Magazine | Sea Angler | 1975 | May | In the past year the competition has yielded ... monkfish |
| Magazine | Sea Angler | 1975 | July | Two or three in an afternoon is not unknown |
| Magazine | Sea Angler | 1976 | August | Monkfish are caught along the stretch of the coast every year, but this year they have shown up in greater numbers than usual. In one day off Port Talbot 14 monkfish were boated |
| Magazine | Sea Angler | 1977 | August | Returned with a good catch of monkfish and tope |
| Magazine | Sea Angler | 1979 | August | Divers of Rhosneigr (Anglesey) reported large angler and monkfish. These are not common to the area, other than reports of the species taken on rod and line every for our five years |
| Magazine | Sea Angler | 1979 | August | Producing some monkfish |
| Magazine | Sea Angler | 1980 | November | Porthcawl, a mark for possible monkfish encounters |
| Magazine | Sea Angler | 1984 | July | Long-lining boats report good catches of spurs and monkfish |
TABLE 2 (Continued)

| Source   | Name/author | Year | Month | Source text description |
|----------|-------------|------|-------|-------------------------|
| Magazine | Sea Angler  | 1986 | August| Monkfish appear to be going through a lean time, fish to 50 lb can be expected |
| Magazine | Sea Angler  | 1989 | July  | Monkfish are not now so abundant, and are more likely to be caught by the shore angler as they like the shallower water |
| Magazine | Sea Angler  | 1990 | September | Not many monkfish have been reported so far this year |
| Magazine | Sea Angler  | 1993 | July  | There’s always a chance of landing a big monkfish ... Large monkfish come inshore and regularly appear ... |
| Magazine | Sea Angler  | 1994 | September | Area fishing well for monkfish |
| Magazine | Sea Angler  | 1995 | September | Take the odd monkfish |
| Magazine | Sea Angler  | 1997 | May   | Really heavy monkfish are generally on offer |

\( (X^2 = 2104, \text{d.f.} = 1, P < 0.0001) \) or outside of UK EEZ around Wales \( (X^2 = 2166, \text{d.f.} = 1, P < 0.0001) \) (Figure 4).

3.2 | SDM outputs

3.2.1 | Habitat preference in S. squatina records

S. squatina depth was highly variable, with mean depth in Q1 (38.3 m ± 19.4 s.e.) and Q4 (42.4 m ± 15.6 s.e.) deeper than in Q2 (12.5 m ± 0.43 s.e.) and Q3 (9.39 m ± 0.26 s.e.), with depths in Q2 and Q3 showing a statistically significant difference (Figure 5a). Chlorophyll-a at S. squatina records followed a similar pattern, with Q1 (1.49 mg m\(^{-3}\) ± 0.39 s.e.) and Q4 (2.17 mg m\(^{-3}\) ± 0.32 s.e.) lower than Q2 (5.13 mg m\(^{-3}\) ± 0.11 s.e.) and Q3 (4.48 mg m\(^{-3}\) ± 0.03 s.e.), and chlorophyll-a in Q2 and Q3 showing a statistically significant difference (Figure 5b). Average SST at S. squatina records was significantly greater in Q3 (16.6°C ± 0.02 s.e.) compared with Q1 (7.92°C ± 0.59 s.e.), Q2 (10.9°C ± 0.03 s.e.) and Q4 (11.6°C ± 0.21 s.e.) (Figure 5c). Salinity levels at S. squatina records were relatively constant in Q1 (34.4 ppt ± 0.22 s.e.), Q3 (34.4 ppt ± 0.01 s.e.) and Q4 (34.3 ppt ± 0.08 s.e.), but significantly lower in Q2 (34.1 ppt ± 0.01 s.e.) (Figure 5d).

The majority of S. squatina records were present on sand habitats (67.07%, n = 688), with significantly more S. squatina records on ‘sand’ or ‘coarse-grained sediment’ than any other habitat type in Q2, and significantly more S. squatina records on ‘sand’, ‘mud to muddy sand’ and ‘coarse-grained sediment’ in Q3 (Supporting Information S6).

3.2.2 | Ensemble model predictions

In both Q2 and Q3, MaxEnt, GBM and GLM models performed strongly in predicting suitable habitats for S. squatina (Supporting Information S4). Both the ensemble habitat suitability model (Figure 6) and binary model outputs (Figure 7) predicted highly suitable habitat for S. squatina across the coast of Wales, the majority within 1 nm of the coast in Q2 (Figures 6a and 7a) and within 6 nm of the coast in Q3 (Figures 6b and 7b). The ensemble habitat suitability model identified several areas with strongest habitat suitability (70 or higher): Swansea Bay and Porthcawl, Cardigan Bay, Tremadog Bay and the Llŷn Peninsula in Q2 (Figure 6a), with additional areas identified in Carmarthen Bay and estuaries, the OUTER Severn Estuary and the Dee Estuary in Q3 (Figure 6b).

In Q2, suitability along the three glacial moraines (Sarn Badrig, Sarn-y-Bwch and Sarn Cynfelyn) was strongly presented in both the ensemble habitat suitability model (Figure 6a) and the ensemble binary prediction model (Figure 7a). In Q3, a larger congruous area of suitable habitat is predicted around the coast of Wales, which is more prominent in the binary prediction model where 2051 km\(^2\) is predicted as S. squatina present in Q2 (Figure 7a) and 3176 km\(^2\) is predicted as S. squatina present in Q3 (Figure 7b).

A much smaller part of the Irish coast had the strongest predictions in the ensemble habitat suitability model, with some cells present between Dublin Bay and Boyne Estuary, and the mouth of the Waterford Harbour in both Q2 and Q3. However, a greater part of the coast within 1 nm was predicted as S. squatina present in the binary model predictions (Figure 7).

3.3 | Results of qualitative analysis

3.3.1 | Frequency of encounters, seasonality and movement

In total, 33 anecdotal resources provided information of frequency of S. squatina encounters in Wales, and 51.5% (n = 17) of these anecdotal resources included descriptions that suggested S. squatina were not uncommon to Wales and 48.5% (n = 16) of anecdotal resources suggested sightings or captures were rare (Table 2). The inconsistency
### Table 3
Chronological timeline of historical literature that includes text on *Squatina squatina* seasonality or movement in Wales (in several sources, *S. squatina* is referred to as ‘monkfish,’ a common name used in some parts of Wales)

| Source     | Name/author | Year | Month | Source text description |
|------------|-------------|------|-------|-------------------------|
| Magazine   | Sea Angler  | 1974 | September | Big monkfish move into the beaches of South Wales for 1 or 2 weeks of the year |
| Book       | Clive Gammon | 1974 | Not recorded | Common off Llwyngwril, South Pembrokeshire and sometimes in the Swansea area, in late summer |
| Magazine   | Sea Angler  | 1974 | September | September always a month for heavy monkfish |
| Magazine   | Sea Angler  | 1975 | September | September always produces monks to 45 lb |
| Magazine   | Sea Angler  | 1979 | July | Swansea Bay usually produces some hefty monkfish at this time of the year (July)* |
| Magazine   | Sea Angler  | 1980 | June | Tope should start to feature (June)* in catches along with bull huss and monkfish |
| Magazine   | Sea Angler  | 1981 | June | June should see mackerel arriving in useful numbers ... there will be monkfish ... tend to concentrate in the east of the region |
| Magazine   | Sea Angler  | 1981 | July | Most summer species should now be feeding close inshore and boat anglers can expect ... monkfish |
| Magazine   | Sea Angler  | 1982 | July | Expect to hear of monkfish being landed during the next month (August)* |
| Magazine   | Sea Angler  | 1983 | July | Monkfish should be around in fair numbers |
| Magazine   | Sea Angler  | 1984 | November | Large monkfish also started their September wandering and fish taken 35–47.5 lb was taken 15 miles off Aberystwyth |
| Magazine   | Sea Angler  | 1985 | September | Monkfish and black bream will be taken accidentally 20 miles offshore as the end of the month (September)* closes. Sure, sign of their migratory trek south beginning |
| Magazine   | Sea Angler  | 1985 | May | Monkfish were caught regularly from the beach in summer months |
| Magazine   | Sea Angler  | 1985 | June | Monkfish will be taken in the Swansea Bay area (June)*, and some heavy fish are expected |
| Magazine   | Sea Angler  | 1986 | October | Offshore boat anglers will hook black bream and monkfish feeding on outside marks as they make the first few miles of their migration to warmer winter waters |
| Magazine   | Sea Angler  | 1987 | July | Boat results rely on the mackerel arriving followed by shark... including monkfish |
| Magazine   | Sea Angler  | 1987 | June | Inshore boat fishing should improve this month (June)* as tope, bull huss, monkfish and rays establish themselves in the area |
| Magazine   | Sea Angler  | 1988 | September | Monkfish will move from the sandy inshore summer marks and the black bream from the reef systems of mid Wales will be taken offshore as they begin their winter travels to warmer southern waters |
| Magazine   | Sea Angler  | 1988 | October | This is ‘drop back’ month and can be as productive as July for the migratory species: shark, tope mackerel and monkfish. Supplies of monkfish can be taken on marks 20 miles from the shore as they too make their way south. |
| Magazine   | Sea Angler  | 1989 | May | an early monkfish can be expected towards the latter part of the month (May)* |
| Magazine   | Sea Angler  | 1989 | July | Monkfish are not now so abundant (July)*, and are more likely to be caught by the shore angler as they like the shallower water |
| Magazine   | Sea Angler  | 1992 | June | This is the best month (June)* for monkfish |
| Magazine   | Sea Angler  | 1993 | October | The migratory move of black bream and monkfish began some weeks ago (Oct)* |

*Months are taken from the date the Sea Angler magazine was published.
in accounts is present throughout the 130 year dataset (Table 2), with 90.9% of anecdotal resources dated between April and September and eight anecdotal resources describing _S. squatina_ as being exhibited, sometimes to paying crowds, given that it was ‘a strange nautical visitor’ (North Wales Chronicle, 1858) (Table 2). The range of accounts presented in the literature suggests that the perceived rarity of _S. squatina_ in Wales varies both geographically and seasonally.

Twenty-three anecdotal resources describe that _S. squatina_ are present in coastal waters of Wales during the summer months (June to September), of which six specifically mention southward or offshore movement during the months of September or October, suggesting that _S. squatina_ are following their prey and/or moving to warmer waters (Table 3).

### 3.3.2 Prey species, habitat preference and reproduction

Fifteen anecdotal resources from Wales and the UK included information on _S. squatina_ prey species; the majority highlighted that angel sharks feed on a range of bottom-living fishes and/or flatfish. Species mentioned include fish (dab, flounder, gurnard, mackerel, plaice, sole, whiting), elasmobranchs (dogfish, ray), crustaceans (brown crab, crabs, lobster) and molluscs (whelk).

Twenty-seven anecdotal resources from Wales and the UK included information on _S. squatina_ habitat, the majority highlighting shallow/inshore water (n = 11), sand (n = 5), estuaries (n = 3), sand or mud (n = 3), sand next to reefs (n = 3) and deeper water (n = 2) being preferred by _S. squatina_. In addition, 11 anecdotal resources included information about angel sharks reproducing in British waters, suggesting that _S. squatina_ give birth in coastal waters or estuaries during June and July; two of these anecdotal resources were specific to Wales.

## 4 DISCUSSION

The results of our study highlight the importance of working with fishers and the inclusion of diverse data sources to study rare marine species. There is significant spatial and temporal variation in _S. squatina_ records across the UK EEZ around Wales and the central Irish Sea, with most records reported in shallow coastal waters (<6 nm) in Q2 and Q3. A combination of environmental and biological factors is likely to be driving these trends.

### 4.1 What are the temporal trends in _S. squatina_ distribution in Wales?

There was significant annual and decadal variation across years in the number of _S. squatina_ records provided to ASP:W. Several factors are likely to account for these changes but given that 97.18% of records were provided by fishers, the number of _S. squatina_ records will be intrinsically linked with changes to recreational, commercial and charter boat fishing effort in Wales, which have not been quantified in this study.

Changes in fishing effort are difficult to ascertain as there are several influencing factors, which have not been collated systematically in Wales. For example, until recently there has been no obligation for vessels under 10 m to report catch and location information (Welsh Government, 2020). Vessels under 10 m represent 93% of the current Welsh fishing fleet, with 385 vessels under 10 m registered in 2019 (Uberoi et al., 2020). In the last 50 years there has been a large reduction in fleet size (Elliot & Holden, 2019), with the over-10 m commercial fleet reducing from 121 registered vessels in 1996 (Ministry of Agriculture Fisheries and Food Fisheries Statistical Unit, 1996) to 29 registered vessels in 2019 (Uberoi et al., 2020). There has also been a shift in target species to reflect changes in available quota; until the late 1990s part of the fleet operating inshore included a number of trawlers and netters that targeted a range of finfish, skate and ray, but today most vessels target crab, lobster and whelks with pots year-round (J. Evans, pers. comm.). Fisheries statistics show that shellfish now contribute 87% of landings by the Welsh fleet (Uberoi et al., 2020). The substantial change in the number of vessels and target species in the late 1990s may in part explain why there is a noticeable decline in _S. squatina_ records at the end of the century (Figure 1).

Changes in recreational fisheries in Wales, including charter boats that take paying clients fishing, have not been quantified to date, but use of historical resources and online archives indicates a decline over time; 72 charter boats were operating in 1973 (Gammon, 1974), 68 in 1996 (Sea Angler, 1996) and 40 in 2019 (https://www.charterboats-uk.co.uk/).

The decline in the number of _S. squatina_ records provided to this study cannot be directly attributed to a change in the abundance of the _S. squatina_ population in the study area as further data on sampling effort (including fishing effort) are required. It is possible that the decline in fishing activity and shift to the current types of gear used in the UK EEZ around Wales and the central Irish Sea has enabled the _S. squatina_ population to remain, unlike other parts of north-west Europe, but further analyses are needed to investigate this (Barker et al., 2020). However, confirmation of contemporary records, with similar numbers of _S. squatina_ reported in the 2000s (n = 82) and 2010s (n = 126), demonstrates that there is an extant population in the UK EEZ around Wales and the central Irish Sea, one of the last remaining areas in the higher latitudes of its range.

The greater number of _S. squatina_ records in Q3 and Q2 could reflect seasonal changes in fishing effort: both recreational and commercial fishing efforts are likely to increase when weather and sea conditions improve. However, qualitative analyses also described _S. squatina_ as seasonal visitors to coastal waters of Wales during June to September. The quantitative analysis may also support a hypothesis of _S. squatina_ seasonal movement, which would align with similar hypotheses in Ireland, where analysis of the re-capture location of tagged _S. squatina_ specimens suggested seasonal movement inshore during June to September and offshore from October to May ( Fitzmaurice et al., 2003). It is important to note, however, there were too few records in Q1 and Q4 for us to test these quarters statistically.
S. squatina are encountered infrequently in both trawl survey programmes and discard-observer programmes (ICES, 2017; Silva & Ellis, 2019), which may relate to a combination of low spatial overlap between surveys/discard observer programmes with S. squatina habitat, low catchability or insufficient sampling effort to provide census data for rare species (Martin et al., 2020). Thus, other research techniques are needed to investigate S. squatina movement and seasonality in the UK EEZ around Wales and the central Irish Sea. This has been outlined in the research objectives in the Wales Angelshark Action Plan (Barker et al., 2020).

4.2 | What are the spatial and environmental trends in S. squatina distribution in Wales?

The spatial trends in S. squatina record distribution in Wales will also be influenced by fishing effort, with records mainly provided on grounds that are fished by recreational anglers, charter boat skippers or commercial fishers. The majority of commercial, recreational and charter boat fishers that contributed to this study operate within 12 nm of the coast, providing spatial bias of S. squatina records to inshore coastal waters. A total of 97.62% of S. squatina records collated in this study were located within 6 nm of the Welsh coastline in Q2 and Q3, confirming the importance of these inshore waters at those times of the year for the species. The relatively shallow mean depth of S. squatina records in Q2 and Q3 corroborate what has been observed in the Canary Islands (Meyers et al., 2017; Jiménez-Alvarado et al., 2020; Noviello et al., 2021).

The greatest number of S. squatina records was located between Bardsey Island and Strumble Head, but records were also present across coastal waters of Wales, with notable concentrations also found in Carmarthen Bay, Conwy Bay and the Outer Severn Estuary (Figure 4). The variation in the accounts of S. squatina rarity identified in anecdotal resources used for qualitative analysis (Table 2) also suggests an unequal distribution of records in coastal waters. This distribution may be influenced by habitat type, with results aligning with preferences documented for this species elsewhere (Akyol et al., 2015; Meyers et al., 2017; Morey et al., 2019). It may also be influenced by other environmental variables, with habitat suitability models highlighting that depth, chlorophyll-a, SST and salinity have a significant influence on the modelled presence of S. squatina. Modelled environmental variables at the location of S. squatina records showed a reduction in depth and higher chlorophyll-a in Q2 and Q3, higher water temperature in Q3 and lower salinity in Q2. The habitat suitability model predictions of S. squatina presence were mainly restricted to 3 nm in north Wales and the 1 nm limit in west and south Wales in Q2, with three glacial moraines (Sarn Badrig, Sarn-y-Bwch and Sarn Cynfelyn) strongly presented (Figure 6a). The S. squatina predictions in Q3 were broader, reaching the 6 nm limit in North Wales and West Wales and the 3 nm limit in South Wales, which may suggest that there is greater homogeneity of environmental variables across a wider area in Q3. Alternatively, it could be that biological parameters (e.g., mating, feeding, giving birth) during this period are a stronger driver for S. squatina distribution than habitat type or environmental variables, as seen in other elasmobranchs, such as thorny skate Amblyraja radiata (Swain & Benoit, 2006).

4.3 | What biological parameters are influencing S. squatina distribution?

According to our data all life-history stages and both sexes of S. squatina are present in the UK EEZ around Wales and the central Irish Sea, with most records being inferred as adults (≥101 cm TL). Qualitative analyses highlighted that S. squatina are generalist predators that feed on a range of teleosts, elasmobranchs, crustaceans and molluscs. This aligns with published research on S. squatina diet in the region (Ellis et al., 1996). Previous research has highlighted that sand patches next to reefs are particularly important prey habitat for S. squatina (Meyers et al., 2017). The three glacial moraines are important reef features in Cardigan Bay and are likely to have a higher abundance of possible prey species (Countryside Council for Wales, 2009; Wray, 2010), which may have a strong influence on S. squatina distribution. This is further supported by an increased mean temperature extracted at S. squatina records in Q3 and higher mean chlorophyll-a extracted at S. squatina records in Q2 and Q3, which links to well-documented trophic coupling of food web dynamics and availability of prey species (Dutta et al., 2017; Thresher et al., 1989).

One of the anecdotal resources used in qualitative analysis stated that ‘A fish (S. squatina) that once bred in plenty about Sarn Gynfelyn and Sarn-y-Bwch in Cardigan Bay’ (Western Mail South Wales News, 1950). In total, 85 S. squatina records provided to ASP:W were inferred as recently born or juvenile life-history stages, suggesting the possibility that they use the coastal waters of Wales and the central Irish Sea to give birth. Research conducted in the Canary Islands highlights that S. squatina give birth in shallow, sheltered habitats with high densities of prey (Jiménez-Alvarado et al., 2020; Meyers et al., 2017). It may be that reproduction is driving the hypothesized seasonal movement to shallow coastal waters in Q2 and Q3. Indeed, the main concentrations of S. squatina records in this study were generally in close proximity to estuaries, including North Cardigan Bay (Mawddach and Dyfi Estuaries), Tremadog Bay (Dwyryd Estuary), Carmarthen Bay (Taf, Tywi, Gwendraeth and Loughor Estuaries), Conwy Bay (Conway Estuary) and the Outer Severn Estuary. Estuaries in the UK have a greater abundance of juvenile fish species than surrounding waters (Claridge et al., 1986; Elliot & Dewally, 1995), so may provide the conditions needed for S. squatina to be born and grow. Indeed, anecdotal resources mention juvenile S. squatina in UK estuaries: ‘Small examples of from 12 to 18 inches are common in many south coast estuaries, notably at Teignmouth, where a few are brought ashore almost every week during May in the sand-eel seines worked just outside the bar’ (Aflalo, 1904). Research focused on identifying juvenile S. squatina presence in Welsh estuaries and transitional waters is needed to confirm this.
4.4 Study limitations and additional research

There was a spatial bias in the data collection methods, with more fishermen providing records to the project in north Wales, where project staff are based. Replication of the data collection methods with fishermen in south Wales and non-Welsh fishermen that fish in the UK EEZ around Wales and the central Irish Sea will likely provide additional important S. squatina records to improve data analyses. In addition, most commercial fishermen interviewed were from the <10 m fishing fleet, which mainly operates within 12 nm of the coast, providing spatial bias of S. squatina records to inshore waters. Further effort to gather records from the >10 m fishing fleet that operates in the UK EEZ around Wales would benefit future S. squatina research in the region.

A major challenge in SDMs of rare marine species is bias of underlying presence data. The data used in this study were, in the majority, provided by fishermen and thus there is a sampling bias towards shallow, inshore regions. This is a common limitation of marine species distribution studies (Robinson et al., 2011). One solution to minimize the bias would be to maintain consistent sampling effort on the temporal and spatial scales, or, if this is not possible, measure and account for this in the SDMs, but these data are not currently available. A detailed assessment of changes in recreational, charter boat and commercial fishing efforts across the UK EEZ around Wales and the central Irish Sea would benefit future research on S. squatina and other species to quantify and account for bias in analyses.

Additionally, pseudo-replication constitutes another limitation of SDMs. In the case of mobile marine species, it is possible that records are not independent of each other, which violates model assumptions and can lead to spatial autocorrelation (SAC) in model residuals (Dormann et al., 2007). This in effect inflates model prediction and can result in type I errors (Crase et al., 2012). To minimize the effects of SAC, data thinning or accounting for the SAC in the SDMs is recommended (Dormann et al., 2007; Virgili et al., 2018). However, these approaches might not be applicable in studies with a small number of records or if the sampling effort data are not available. For the purpose of this study, the AUC as a measure of discrimination between correctly predicted presences and absences was chosen as an appropriate evaluation technique.

SDMs developed in this study could be extrapolated to other areas of the north-east Atlantic to identify potential suitable habitats of S. squatina in a wider range, where focused projects like ASP:W have not been initiated. However, this must be done with caution and a different evaluation method to assess the model’s calibration power (e.g., the Boyce index; Hirzel et al., 2006) should be considered to choose the best model.

4.5 Using results to inform policy and S. squatina conservation in the UK EEZ around Wales and the central Irish Sea

The results of this study provide a baseline understanding of S. squatina distribution and the possible ecological parameters driving this in the UK EEZ around Wales and the central Irish Sea. In 2020, the Wales Angelshark Action Plan was developed in collaboration with stakeholders across Wales and outlines a priority list of actions to be delivered in partnership over the next 5 years (Barker et al., 2020). Specifically, this study addresses four priority research objectives outlined in the Action Plan to help fill evidence gaps to inform policy decisions.

Immediate next research steps include replicating research techniques in South Wales, completing environmental DNA (eDNA) surveys to assess S. squatina seasonality, pilot the use of telemetry to understand S. squatina seasonal movement, and investigate changes in fishing effort across the UK EEZ around Wales and further research on juvenile or recently born S. squatina habitat preferences. Replication of survey methods in other parts of the north-east Atlantic, including other parts of the Celtic Sea ecoregion and Biscay-Iberian waters, would also be beneficial to provide information on S. squatina across the higher latitudes of their range.

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**CONTRIBUTIONS**

J.B. led project conception, design, analysis, interpretation and manuscript preparation, and secured funding to complete the work. J.D. led data collation, particularly with fishing communities around Wales, and supported project strategy, design, analysis and interpretation, making significant contributions to manuscript preparation. M.Gor. led quantitative analysis, species distribution modelling and interpretation of results, making significant contributions to manuscript preparation. S.P. developed the local ecological knowledge survey design, supported data collection and made major contributions to manuscript preparation. J.O. supported data collection, project design and interpretation, with moderate contributions to manuscript preparation. J.E. supported data collection, project design and interpretation, with minor contributions to manuscript preparation. R.S. supported project conception and design, making major contributions to interpretation of results. M.Gol. supervised J.B. throughout the project, contributing to project design and analysis, and made major contributions to manuscript preparation. F.R.W. supported historical data collation and interpretation, with moderate contributions to manuscript preparation. J.R. supervised M.Gor. and supported quantitative analysis and interpretation, making moderate contributions to manuscript preparation. C.B. provided significant data and supported interpretation of results for the discussion. B.G. provided significant data and supported interpretation of results for the discussion. D.J. provided significant data and supported interpretation of results for the discussion. B.W. supported project conception, design, analysis and interpretation, secured funding to complete the work and made significant contributions to manuscript preparation.

**ORCID**

Joanna Barker [https://orcid.org/0000-0003-1396-6851](https://orcid.org/0000-0003-1396-6851)
Sushri Patel [https://orcid.org/0000-0001-9419-8182](https://orcid.org/0000-0001-9419-8182)
James Rosindell [https://orcid.org/0000-0002-5060-9346](https://orcid.org/0000-0002-5060-9346)

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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