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

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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 km^2) compared to Q2 (2051 km^2), 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

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85 records of *S. squatina* individuals ≤60 cm in the dataset, inferred as recently born or juvenile life-history stages. The results have helped fill significant evidence gaps identified in the Wales Angelshark Action Plan and immediate next research steps are suggested.

KEYWORDS
angel shark, Wales, ecology, local ecological knowledge, modelling

1 | 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 chondrichthyans (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, Tyrrhenian 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 (Lapinksi & 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 Bianco, 1899; Osaer *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 northernmost 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 sociohistorical 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. Timelines 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', 'angel shark', '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 LEK 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 $0.0083^\circ \times 0.0083^\circ$ 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

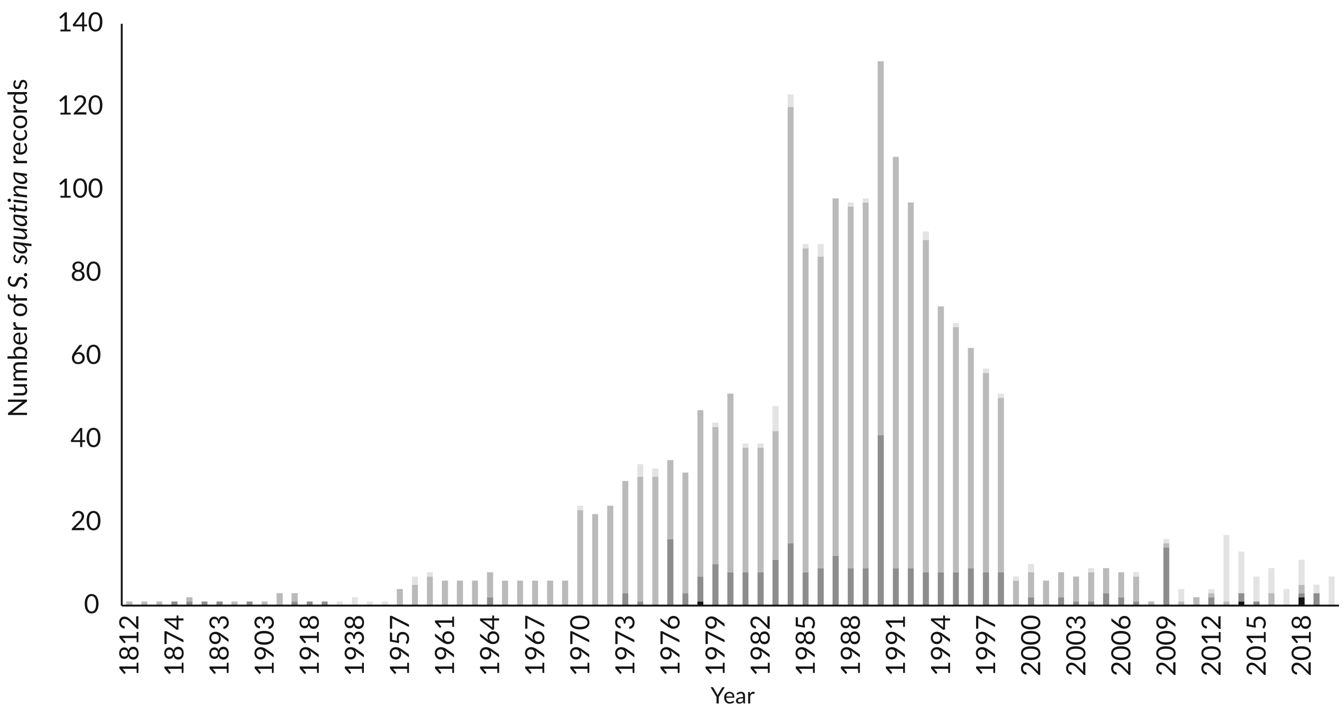

FIGURE 1 Number of *Squatina squatina* records each year, spanning a 208 year period between 1812 and 2020. Only those records where a specific year was provided are shown ($n = 2099$). Bars are stacked with different kinds of shading representing the different ID confidence levels (Supporting Information 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

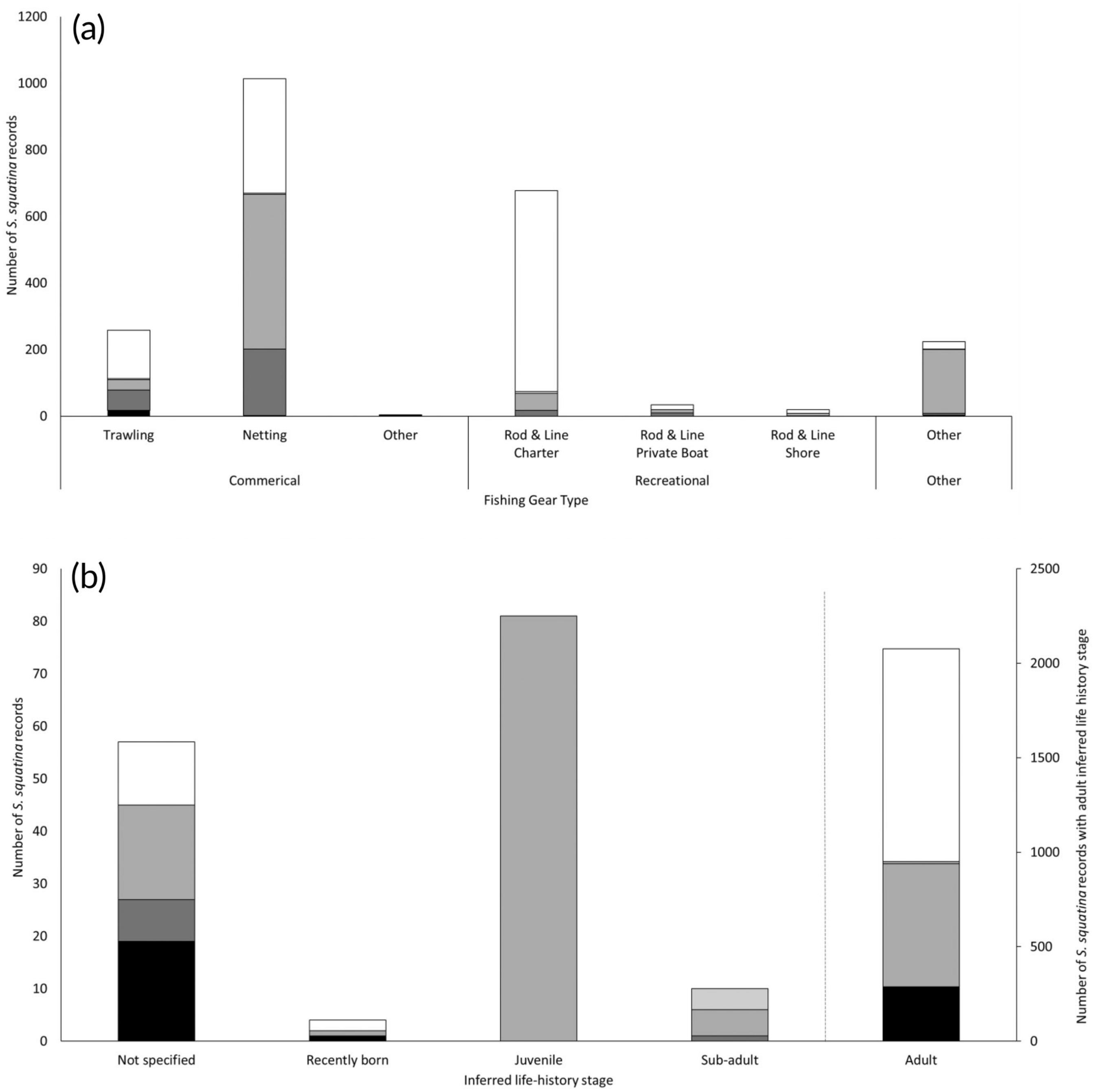

FIGURE 2 (a) Number of *Squatina squatina* records reported for each quarter by fishing gear and fishing sector. Bars are stacked with different kinds of shading representing the different quarters of the year. (b) The number of *S. squatina* records provided to the project each quarter, broken down into inferred life-history stages (recently born, juvenile, sub-adult and adult). Adult *S. squatina* records are plotted on a secondary axis as they account for 93.19% (n = 2079) of records (shown to the right of the dashed line). Bars are stacked with different kinds of shading representing the different quarters of the year. (■) Q1, (■) Q2, (■) Q3, (□) Q4, (□) specific quarter not specified

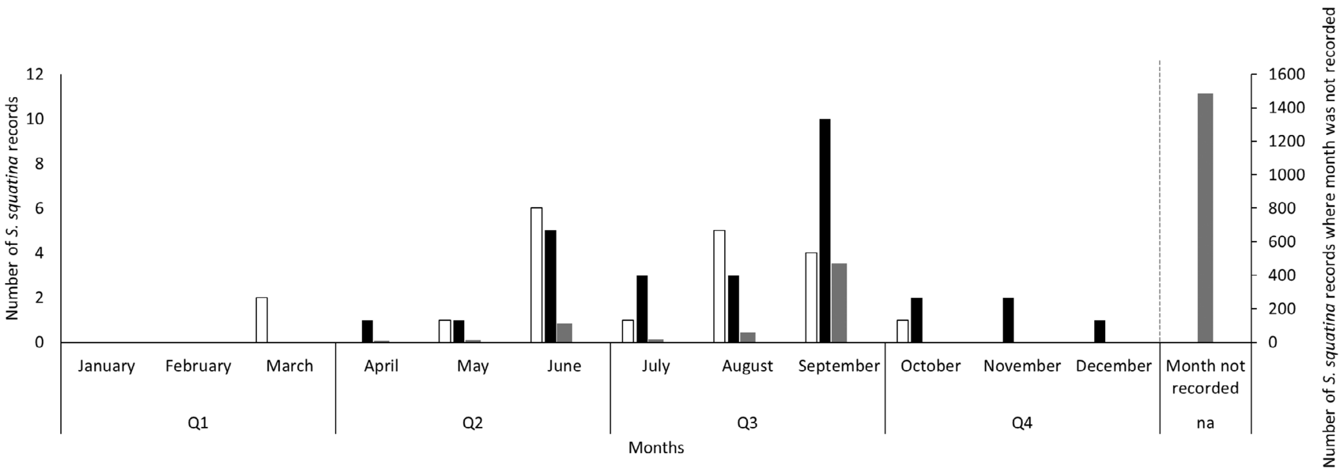

FIGURE 3 Comparison of the number of female, male and sex not recorded (nr) *Squatina squatina* records reported in each month. Specific month not recorded is plotted on a secondary axis as the majority of records spanned more than a month period (shown to the right of the dashed line). (□) Female, (■) male, (■) nr

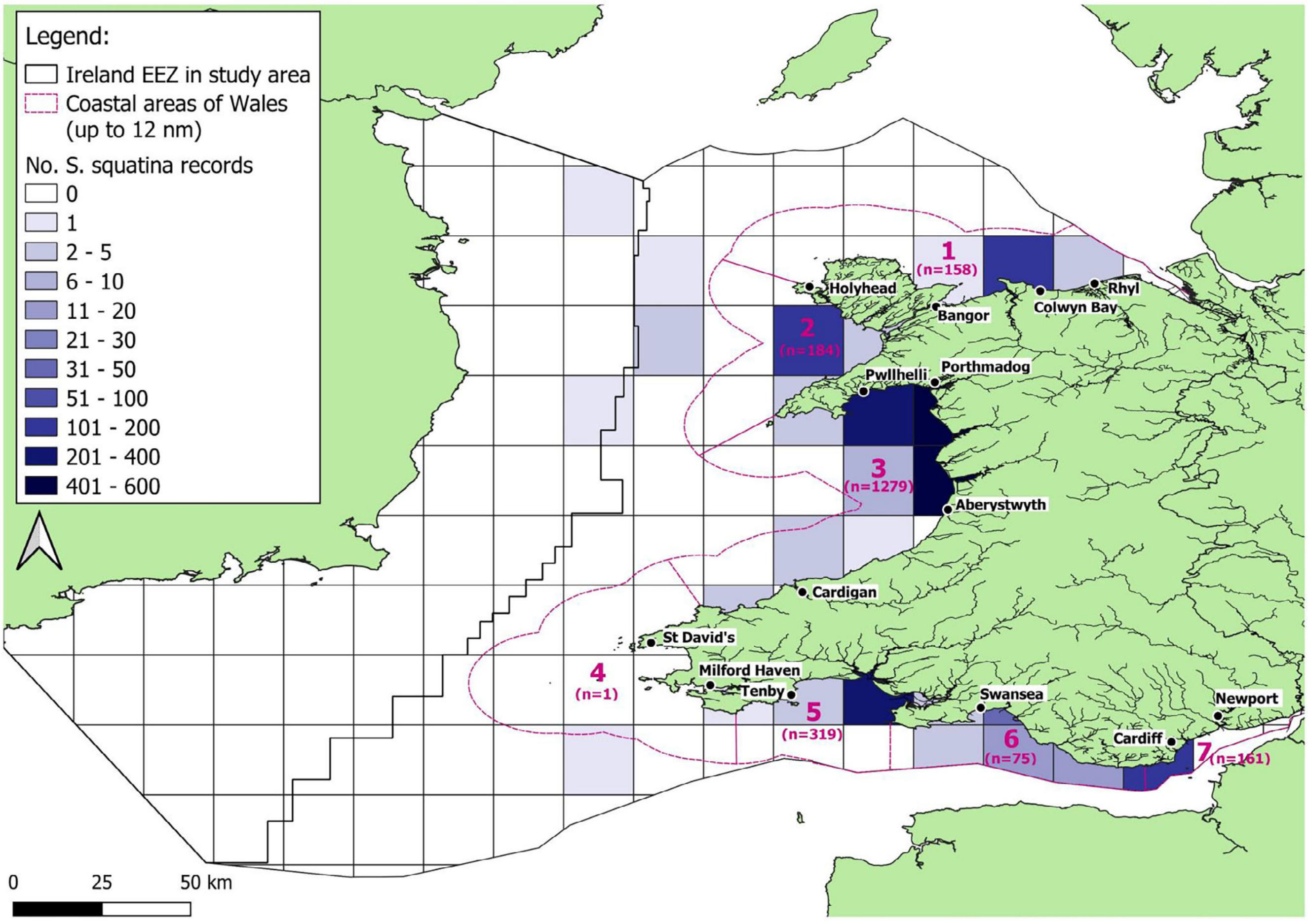

FIGURE 4 Spatial variation in *Squatina squatina* records across the UK EEZ around Wales and the central Irish Sea, shown as counts per 20 km grid squares. Coastal areas of Wales are divided using biogeography and extend out to 12 nm or the mid-line: 1, Dee Estuary to North Stack; 2, North Stack to Bardsey Island; 3, Bardsey Island to Strumble Head; 4, Strumble Head to St Govan's Head; 5, St Govan's head to Rhossilli; 6, Rhossilli 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 1812 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

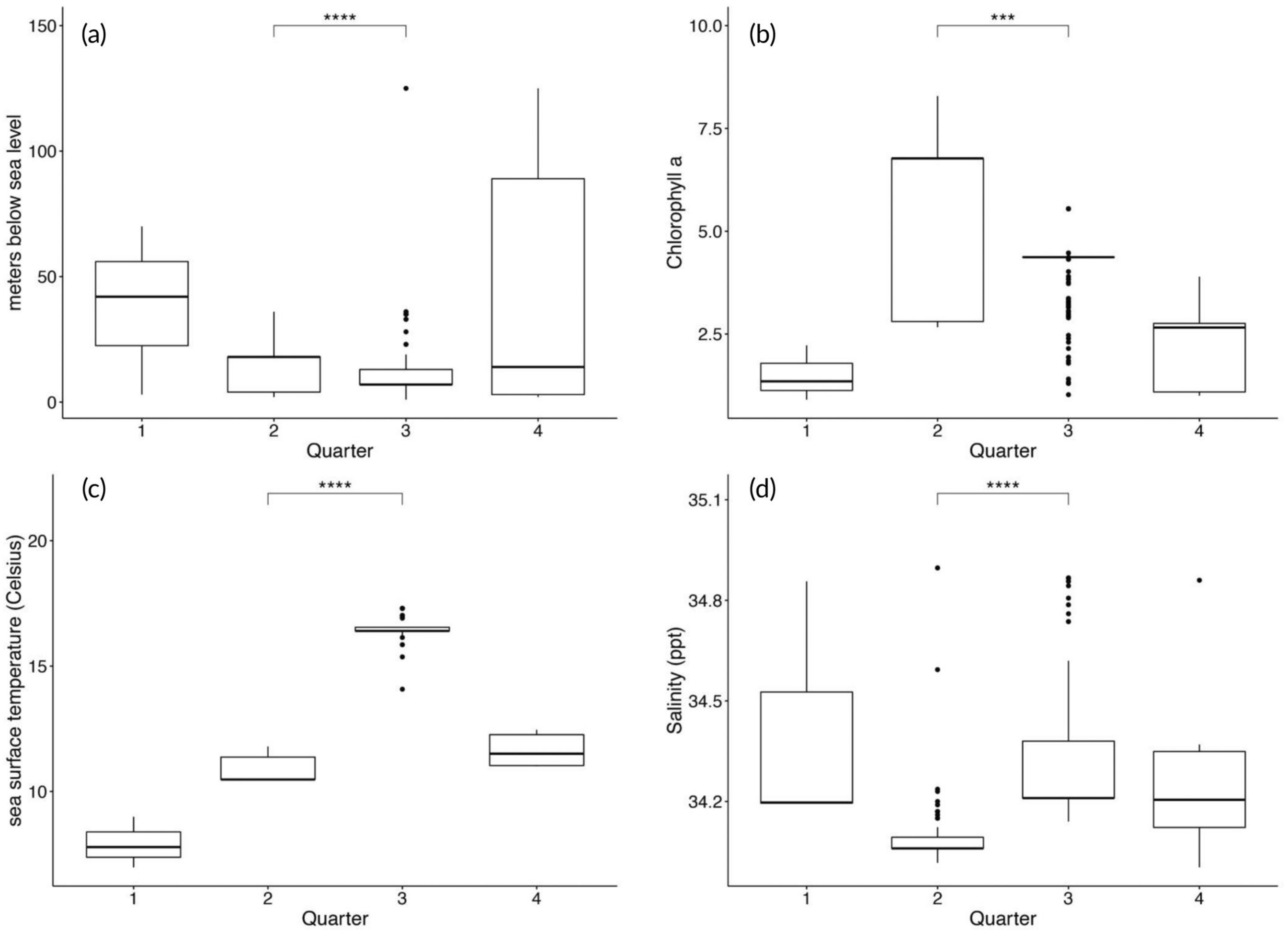

FIGURE 5 Comparison of environmental variables extracted at *Squatina squatina* records for each quarter, including depth (m) (a), chlorophyll-a (mg m^{-3}) (b), sea surface temperature (°C) (c) and salinity (ppt) (d). ***Identifies statistical significance between variables in Q2 and Q3; sample sizes were too low for statistical analysis of Q1 and Q4

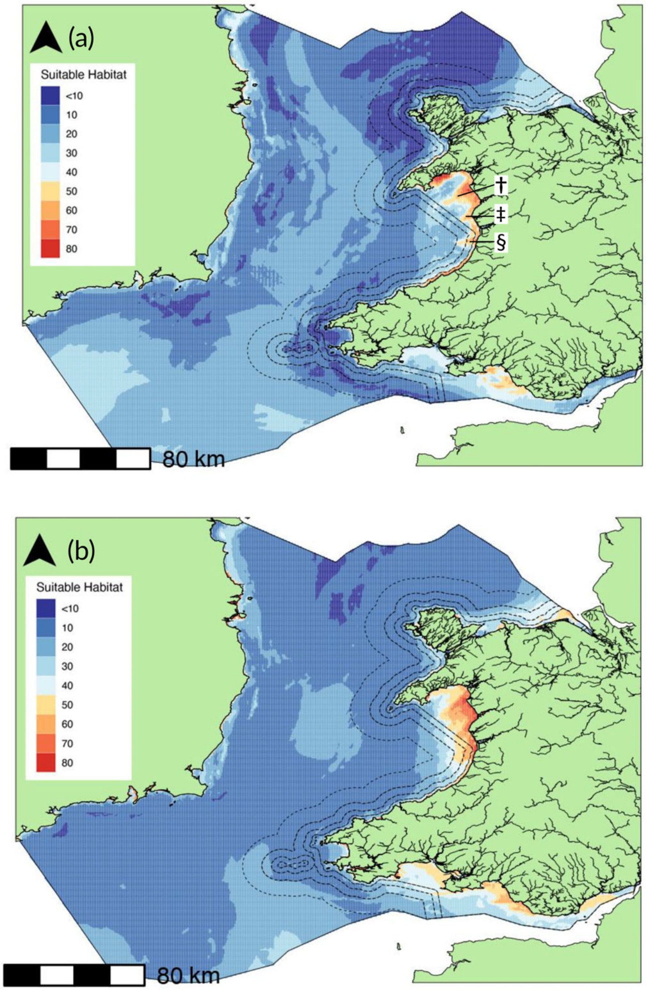

FIGURE 6 Ensemble prediction of relative habitat suitability (scaled 0–100) for *Squatina squatina* in the Welsh Exclusive Economic Zone and central Irish Sea during Q2 (a) and Q3 (b) based on species distribution model outputs. In (a) three glacial moraines are marked to aid interpretation: Sarn Badrig (†); Sarn y Bwch (‡); Sarn Cynfelyn (§)

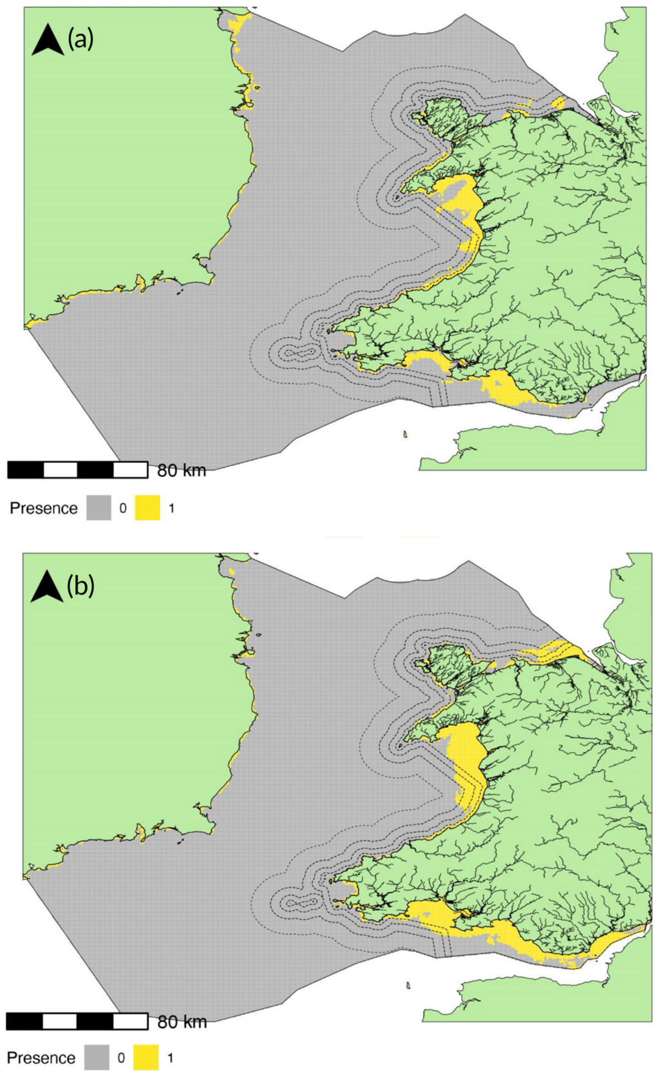

FIGURE 7 Binary model predictions of *Squatina squatina* presence in the Welsh Exclusive Economic Zone (EEZ) and central Irish Sea during Q2 (a) and Q3 (b). Yellow cells show model prediction of *S. squatina* presence and grey cells show model prediction of *S. squatina* absence

boat skippers (Q1 $X^2 = 52$, d.f. = 1, $P < 0.0001$; Q2 $X^2 = 17.8$, d.f. = 1, $P < 0.01$; Q4 $X^2 = 38.8$, 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 $X^2 = 2067$, d.f. = 1, $P < 0.0001$; subadult $X^2 = 2049.19$, d.f. = 1, $P < 0.0001$; juvenile $X^2 = 1848.15$, d.f. = 1, $P < 0.0001$) (Figure 2b). More adult *S. squatina* were reported in Q3 compared with Q1 ($X^2 = 646$, d.f. = 1, $P < 0.0001$), Q2 ($X^2 = 142$, d.f. = 1, $P < 0.0001$) or Q4 ($X^2 = 620$, d.f. = 1, $P < 0.0001$) and in Q2 compared with Q1 ($X^2 = 281$, d.f. = 1, $P < 0.0001$) or Q4 ($X^2 = 256$, d.f. = 1, $P < 0.0001$) (Figure 2b).

Only 2.73% ($n = 61$) of records provided information on sex (male = 34, female = 27), with no significant difference in the number of female *S. squatina* reported each quarter ($X^2 = 14$, d.f. = 3, $P = 0.688$), but a greater number of male *S. squatina* reported in Q3 than in Q1 ($X^2 = 19$, d.f. = 1, $P < 0.01$) (Figure 3).

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 ($X^2 = 2151$, d.f. = 1, $P < 0.0001$), 12 nm to UK EEZ around Wales

TABLE 2 Chronological timeline of historical literature that includes text on frequency of *Squatina squatina* encounters 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
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

($X^2 = 2104$, d.f. $= 1$, $P < 0.0001$) or outside of UK EEZ around Wales ($X^2 = 2166$, 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 Lleyn, 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)[a]
Magazine	*Sea Angler*	1980	June	Tope should start to feature (June)[a] 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)[a]
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)[a] 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)[a], 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)[a] 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)[a]
Magazine	*Sea Angler*	1989	July	Monkfish are not now so abundant (July)[a], 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)[a] for monkfish
Magazine	*Sea Angler*	1993	October	The migratory move of black bream and monkfish began some weeks ago (Oct)[a]

[a]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 & Benoít, 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 & Dewailly, 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 fishers providing records to the project in north Wales, where project staff are based. Replication of the data collection methods with fishers in south Wales and non-Welsh fishers 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 fishers 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 fishers 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. D.Q. collected data from the central Irish Sea and made moderate contributions to manuscript preparation. B.W. supported project conception, design, analysis and interpretation, secured funding to complete the work and made significant contributions to manuscript preparation.

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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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