

Full length article

Spatiotemporal and demographic patterns in commercial catches of tope (*Galeorhinus galeus*) and spurdog (*Squalus acanthias*)

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ABSTRACT

Tope (*Galeorhinus galeus*) and spurdog (*Squalus acanthias*) have been historically overexploited by fisheries, leading to global population declines. Despite both species having well-documented migration patterns and being known to aggregate by sex and life-stage, interactions with commercial fisheries in the Northeast Atlantic have not been assessed in relation to seasonality, sex ratio and/or life-stage. Identifying and quantifying any differences would inform fisheries management efforts to mitigate the impact of overexploitation on these populations. Using reported landings and observer programme data, interactions with United Kingdom commercial fisheries on the Northwest European shelf were investigated. Both species were vulnerable to capture in setnet and bottom trawl gears, particularly in the English Channel and Celtic Sea. Recorded tope catches in the study area peaked in August (bottom trawls) and December (setnets), with no significant sex ratio bias in hauls suggesting the region is important for both sexes. For spurdog, sex-specific seasonal differences were found in the Celtic Sea in setnets with evidence of male-dominated hauls occurring further from the coast than female-dominated hauls. These results provide insights into finer scale spatio-temporal fisheries interactions for two elasmobranch populations in the Northeast Atlantic and demonstrate the utility of landings and observer programme data to identify opportunities for spatio-temporal fisheries and conservation management measures.

1. Introduction

Many shark species are characterised by slow-growth, late maturity, and low fecundity (Stevens et al., 2000) and are susceptible to fisheries capture (Ellis et al., 2008), meaning populations are vulnerable to the effects of fishing mortality. Fisheries overexploitation has caused global shark population declines (Dulvy et al., 2014), which has in-turn led to increasing attention from conservation and fisheries managers (Ellis et al., 2008, Salomon et al., 2011). The decline of shark abundance can result in alterations to the biological components of marine ecosystems (Stevens et al., 2000), so there is a need for improved quantification of catch levels (Ellis et al., 2008) to evaluate the impact of fisheries and inform both species and fisheries management. However, the effectiveness of potential management measures can be complex for migratory species, where interactions with fisheries can vary seasonally and across areas.

Tope shark (henceforth 'tope') *Galeorhinus galeus* (Linnaeus, 1758)

and spurdog (also known as spiny dogfish) *Squalus acanthias* (Linnaeus, 1758) require international collaboration to promote stock conservation, as evidenced by the listing of these species in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS, 2010, 2020). Tope is a demersal-pelagic species that is associated primarily with continental shelf waters. Whilst it has been subject to targeted fisheries in various parts of its range (Camhi et al., 2008), tope has largely been a bycatch species in the Northeast Atlantic. To deter the development of target fisheries for this non-quota species, the United Kingdom (UK) introduced the Tope (Prohibition of Fishing) Order 2008 (henceforth Tope Order). This regulation prohibited landings of line-caught tope and introduced a 45 kg (live weight) daily trip limit for all other gears.

Spurdog is also a continental shelf-associated species. In the Northeast Atlantic, historical target fisheries were in operation from the early 1900s but catch declines since the 1980s led to Total Allowable Catch (TAC) limits being established for the North Sea part of the species'

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range in 2000. Other areas in the Northeast Atlantic have been subject to quota management since 2007 (ICES, 2024a). TAC limits for vessels operated under the European Union (EU) and UK were set to zero in 2010 and landings were prohibited in 2016. Following evidence of stock recovery, spurdog have been allocated annual TACs since 2023 (ICES, 2024a), with the 2026 TAC being set at 54.04% of the headline advice from the International Council for the Exploration of the Sea (ICES) at 10,875 t in EU and UK waters (Department for Environment, Food & Rural Affairs DEFRA, 2025).

Tope is a migratory species and, from tagging studies, have been recorded moving distances up to 2500 km in the Northeast Atlantic (Holden and Horrod, 1979) but movements of up to 5000 km have been reported between Australia and New Zealand (Camhi et al., 2008). In both hemispheres, juvenile tope often remain in, or close to, the shallow bays and nursery areas in which they were born, and do not undertake seasonal migrations until their third or fourth year (Holden and Horrod, 1979; Stevens and West, 1997). Tope have been reported to aggregate by size and sex (CMS, 2020). For example, in Anegada Bay, Argentina, juveniles and adult males both occurred in catches year-round, whilst mature females spent winter offshore (Lucifora et al., 2004). This contrasts with the wider and deeper distribution of males compared to females in the eastern English Channel (Martin et al., 2010).

Seasonal inshore to offshore movements have been reported for spurdog in the Northwest Atlantic (Garrison, 2000) and Northeast Atlantic (Pawson, 1995). Spurdog is also known to segregate by size and sex (Compagno, 1984). Around the British Isles, adult spurdog aggregate in the Celtic Sea in spring (Pawson, 1995) before utilising the North Sea in summer then aggregating in the Celtic Sea again in autumn (Vince, 1991). In Norwegian fjords, males have displayed greater aggregating behaviour than females, whose aggregations were more spatially restricted to the innermost fjords (Dahlmo et al., 2026). Males have been reported to occupy deeper water than females (Shepherd et al., 2002). In particular, Klöcker et al. (2024) reported pregnant females occupying shallow areas and displaying diel vertical migrations in Nordic waters.

Despite the diverging movement patterns exhibited by tope and spurdog, interactions with fisheries have not been evaluated in relation to seasonality, sex or life-stage. Silva and Ellis (2019) previously identified nets (including gillnets, tangle nets, and trammel nets) and otter trawls to be the main gears catching both tope and spurdog, with the relative proportions discarded increasing in line with management restrictions. Aggregating behaviours can increase vulnerability of such species to overexploitation, as fisheries may have a disproportionate effect on particular population components (i.e., mature females; Colonello et al., 2026). In the Northeast Atlantic, spurdog had a maximum landing length of 100 cm (EU, 2023) as typically only mature (reproductively active) females exceed this length (Ellis and Keable, 2008), thus limiting exploitation on this life-stage. However, the impact of the catch-and-release process could still reduce the reproductive success of the females (Ellis et al., 2017). Therefore, as segregation by sex and life-stage may lead to seasonal differences in fishery interactions, identifying and quantifying these differences could support fisheries management efforts (Cameron et al., 2025) through, for example, spatial or temporal measures to reduce interactions with vulnerable stock components.

In this paper, we used data from reported landings and national at-sea observer programmes that collect catch and bycatch data on fishes, including tope and spurdog, from commercial fisheries around the British Isles to test the following hypotheses:

- a) Seasonal changes in catches will reflect known migration timings of each species, specifically,
 - i. Tope catches in the Southwest Approaches are highest in winter, and catches in the North Sea are highest in summer,
 - ii. Spurdog catches in the Southwest Approaches are highest in winter, and catches in the North Sea and Irish Sea are highest in spring and summer,

- a) There are sex- and life-stage-specific seasonal variation in catch levels.

2. Methods

Focusing on UK continental shelf waters within the Food and Agriculture Organisation of the United Nations (FAO) Area 27 (Fig. 1), reported UK landings were extracted and analysed for the period 2000–2022 from the official national fisheries statistics, iFish database (maintained by the Marine Management Organisation; data accessed on the 5th April 2023). All landings were reported in tonnes (t; live weight) and are presented in this work to one decimal place when reporting values were < 100 t and to the whole integer when ≥ 100 t were reported.

Landings data were analysed in conjunction with at-sea observer data from the Centre for Environment, Fisheries and Aquaculture Science (Cefas, 2002–2022, accessed 24th July 2023) for English and Welsh commercial vessels. This was supplemented by data (2010–2022) from the UK Bycatch Monitoring Programme (BMP) which is managed by the Sea Mammal Research Unit (SMRU)/Scottish Oceans Institute (SOI) at the University of St Andrews and covers UK vessels. BMP data used in this study represent vessels operating setnet gears only (accessed 12th December 2023). Further details of the data collection are provided in Supporting Information, S1. For seasonal and sex-based analyses, all results refer to observed (not raised) individuals unless otherwise stated. Both the Cefas and BMP data comprised retained (landed) and discarded individuals and therefore these combined records are referred to as ‘captures’, to distinguish from the landings-only dataset (iFish data).

Data were analysed in R (version 4.3.0; R, 2023) with latitude and longitude aggregated to ICES Rectangles (i.e., a scale of 0.5° latitude by 1° longitude) using the *ices.rect* function (library *mapplots*, Gerritsen, 2018) and mapped using the *ggplot2* library (Wickham, 2016). Landing reports were analysed by month, but observer data were aggregated in quarterly (January to March etc.) or bimonthly blocks (January to February etc.) due to more limited data in some periods. Data were further analysed by gear category (for details on aggregated categories see Supporting Information, Table S2) and ICES Divisions (henceforth “Div.”) grouped by region where appropriate (i.e., Southwest Approaches Div. 7.e–h, Irish Sea Div. 7.a, Fig. 1).

Fisheries management measures (i.e., TAC changes) for each species were also considered in the analysis, as this affected what could be landed in different periods. Relevant pre-management and post-management time blocks were used, based on when management would be considered to restrict landings. For tope, this centred around the introduction of the Tope Order which was introduced during 2008, therefore data were separated into pre-management (2000–2007) and post-management periods (2008–2022). Similarly, management measures for spurdog (introduced from 2000) became more restrictive from 2008 onwards (with the introduction of TACs in all seas, 0 TAC from 2010, and prohibited listing from 2016), so data were separated into pre-management (2000–2007) and post-management periods (2008–2022). The data do not cover the period a quota was reintroduced for spurdog (2023 onwards). Comparisons between mean annual and monthly captures in pre- and post-management time blocks are presented. Inferred seasonal movements between the main divisions (Southwest Approaches: Div. 7.e–h; North Sea, Div. 4.a–c; and Irish Sea, Div. 7.a) are summarised for pre-management blocks only, as without fisheries management restrictions, these data are more likely to reflect seasonality in spatial distribution.

The Cefas Observer Programme also provided information relating to interactions by sex and length which are not reported in the official landings database. Using the length frequency data (see Supporting Information, Figure S3), two length classes were examined focusing on important demographic stock components, neonate/immature fish and fecund females. Tope ≤ 75 cm are considered immature fish (including neonates), whilst females ≥ 150 cm are considered to be largely mature,

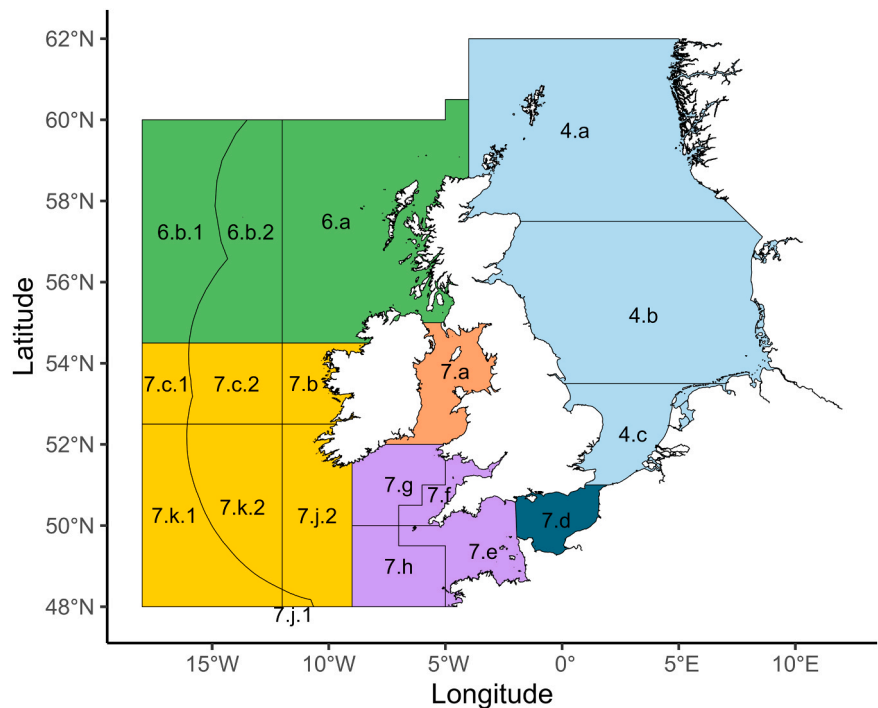


Fig. 1. ICES Divisions on the UK shelf (part of FAO Area 27). Grouped by area into the Southwest Approaches (Divisions 7.e-h, ■), eastern English Channel (Division. 7.d, ■), North Sea (Divisions 4.a-c, ■), West of Scotland (Divisions 6.a,b, ■), Irish Sea (Division 7.a, ■), and Southwest Ireland (Divisions 7.b,c,j,k, ■).

following Dureuil (2013) and Cameron et al. (2025), who assumed a length at 50% maturity of 150 cm for female tope. Spurdog length classes were chosen as ≤ 60 cm (immature and neonates) and females ≥ 100 cm (considered mature), based on Silva and Ellis (2019). All individual lengths in this study refer to total length (cm) and were recorded to the whole cm below.

Chi-square goodness of fit tests were performed on the sex ratio for hauls with the highest captures of each species. This determined whether single-sex aggregations occurred and provides evidence of sex-specific interaction with commercial gears. To identify ‘large’ hauls of each species, hauls were ordered by the number of tope or spurdog captured. The top 3% of hauls for each species were selected for analysis because the inclusion of the top 5% resulted in some hauls containing an insufficient number of tope to allow robust statistical test (≤ 10 individuals), whereas the top 1% included too few hauls ($N = 4$). Selecting the top 3% balanced the sample size of each species caught with the number of hauls available for analysis. This equated to hauls with ≥ 15 tope, and ≥ 61 spurdog. The null hypothesis was that there would be an equal sex ratio within these hauls (i.e. no evidence of sexual segregation in large shoals).

3. Results

3.1. Tope

3.1.1. Reported UK landings (2000–2022)

Reported national landings of tope (910.2 t) peaked in 2000 (110.7 t). Following the introduction of the Tope Order in 2008, landings decreased and remained low (pre: 49.4–110.7 t per annum 2000–2007; post: 12.6–23.3 t per annum 2008–2022). Based on aggregated data, about half of reported landings (450 t) were from setnets, followed by 230 t (25%) from hooks and lines (all pre-2008) and 219 t (24%) from bottom otter trawls. Reported landings were mostly

from the Southwest Approaches, Div. 7.e–h (562 t) 340 t (61%) of which, were landed from setnets.

3.1.2. Pre- and post-management restrictions

Gear: Pre-management (2000–2007; 636 t), most reported landings were from setnets (254 t, 40%), hooks and lines (216 t, 34%) and bottom otter trawls (163 t, 26%; Table 1). Post-management (2009 onwards; 274 t), the highest landings were from setnets (197 t, 72%).

Division: The majority of reported landings were from the Southwest Approaches (annual mean pre: 21.4 t, range: 8.9–30.4 t; post 6.5 t,

Table 1
UK reported landings in tonnes (t, to iFish) pre-management (2000–2007) and post-management (2008–2022) for tope (*Galeorhinus galeus*) and spurdog (*Squalus acanthias*) by gear category (see Supporting Information, Table S2). All landings rounded to 1 decimal place.

Species	Gear	Pre-management (t)	Post-management (t)
Tope	Beam trawl	1.3	0.3
	Bottom otter trawl	162.6	56.8
	Gillnets and trammel nets	253.6	196.9
	Hooks and lines	215.7	14.7
	Midwater trawl	0.7	2.2
	Seines (Danish, Scottish, Purse)	0.7	1.8
	Other	1.6	1.6
	Total	636.2	274.3
Spurdog	Beam trawl	188.7	12.7
	Bottom otter trawl	13819.8	581.9
	Gillnets and trammel nets	6995.2	557.0
	Hooks and lines	9256.5	66.0
	Midwater trawl	4679.7	50.7
	Seines (Danish, Scottish, Purse)	1660.6	133.0
	Other	140.2	5.3
	Total	36740.7	1406.6

range: 4.4–19.9 t). Pre-management, the Irish Sea (mean: 11.6, range: 1.6–47.3 t) and southern North Sea, Div. 4.c (mean: 9.6, range: 4.5–12.4 t) both had high annual contributions, reducing to < 1.0 t in the post-management period. Most reported landings from these two divisions prior to restrictions were from hook and line gears (Div. 7.a: 8.0 t, 84%; Div. 4.c: 35.9 t, 47%).

Seasonality in landings: Due to management measures introduced in 2008, average monthly landings reduced by 76.4% across all regions from 6.4 t (range: 1.3 – 19.9 t) on average per month pre-management (2000–2007) to 1.5 t (range: 0.1 – 8.7 t) post-management (2008–2022). Pre-management, 849 t (93.3%) of reported landings occurred in the Irish Sea, Southwest Approaches, eastern English Channel, and southern North Sea (Div. 4.c). In the Southwest Approaches, 76% of average annual landings pre-management were reported from November to May (Fig. 2), 60% of annual landings reported from the eastern English Channel were from April to July, and in the southern North Sea 84% of landings were reported from May to November (Fig. 2). Seasonality was less apparent in the Irish Sea but landings were highest from May to November (Fig. 2).

3.1.3. Cefas observer data

Of the 3765 observed trips conducted (2002–2022), tope was recorded on 246 trips (6.5%) with a total of 1712 individuals recorded. Annual variability in the number of tope observed captured was high ($N_{ind} = 9$ –387), with 87% of individuals captured by setnets ($N_{ind} = 1490$) followed by bottom otter trawls ($N_{ind} = 205$, 12%). Of the 1712 tope observed, 1636 (96%) occurred in the Irish sea, Southwest Approaches, southern North sea and English Channel. 1536 tope (90%) were captured in just the Southwest Approaches, with Div. 7.f alone accounting for 716 tope (47%). There was an even sex ratio across the observed individuals ($N_{ind} = 826$, 49% females; $N_{ind} = 863$, 51% males) with lengths ranging 37–185 cm (mean: 101 cm) for females and 36–189 cm (mean: 109 cm) for males. Records with sex reported as unknown ($N = 23$) were removed from analyses by sex.

Seasonality in captures: There were year-round captures in the Southwest Approaches, predominantly in November to December with an average of 34 individuals per year (range: 0–297 individuals). Outside these divisions captures were negligible, averaging < 1 individual per year.

Inferred seasonality by sex: The highest number of tope captured were from the Southwest Approaches, particularly from setnets ($N_{ind} = 643$ over 21-years). For this region and gear, monthly average captures for both males ($N_{ind} = 187$, 27%) and females ($N_{ind} = 201$, 30%) were predominantly recorded in December (Fig. 3). The lowest recorded captures for females were in August ($N_{ind} = 2$, 0.3%) and males in September ($N_{ind} = 1$, 0.1%; Fig. 3). 133 individuals were captured in bottom otter trawls in the Southwest Approaches with highest captures recorded in August for both males ($N_{ind} = 20$) and females ($N_{ind} = 15$) accounting for 30% and 23% of observed captures of each sex in this region and gear, respectively.

Sex ratio of aggregations: There were 19 large hauls of tope (determined by hauls in the top 3% in terms of number of tope captured), which comprised 15–49 individuals per haul. None of these hauls had a statistically significant bias in sex ratio, averaging 1:1 (see Supporting Information, Table S4). All 19 hauls were from the Southwest Approaches and from setnets, with one haul in January, five in May, six in November, and seven in December.

Tope ≤ 75 cm: Overall, 185 tope were observed in this length class (36–75 cm), and were captured in 121 hauls ($N_{ind} = 1$ –10 per haul). The sex ratio of females to males was 1:0.8 with similar mean lengths (females: 66 cm, ranging 37–75 cm; males: 66 cm, ranging 36–75 cm). Captures occurred every month with peaks in December ($N_{ind} = 45$) and August ($N_{ind} = 35$) when combining all years (Fig. 4). Observations were predominantly from Div. 7.e ($N_{ind} = 26$), Div. 7.f ($N_{ind} = 78$), and Div. 7.g ($N_{ind} = 28$) with most captures in setnets ($N_{ind} = 121$) followed by bottom otter trawls ($N_{ind} = 58$).

Female tope ≥ 150 cm: Between 2007 and 2022, 27 females ranging from 150 to 185 cm were recorded in 27 hauls. 85% were observed in hauls from the Southwest Approaches (with single individuals recorded in Div. 7.j: January 2020; Div. 7.d: November 2021; and Div. 4.c: May 2010; Fig. 4). Setnets were responsible for 22 (81%) of the captured individuals from this length class. Only single individuals of this length class were recorded in any one haul. Observations occurred every month except December, and peaked in May ($N_{ind} = 6$) based on data aggregated across years.

3.1.4. Additional observations from the bycatch monitoring programme

Observed captures ($N_{ind} = 429$) from the BMP database (2010–2022;

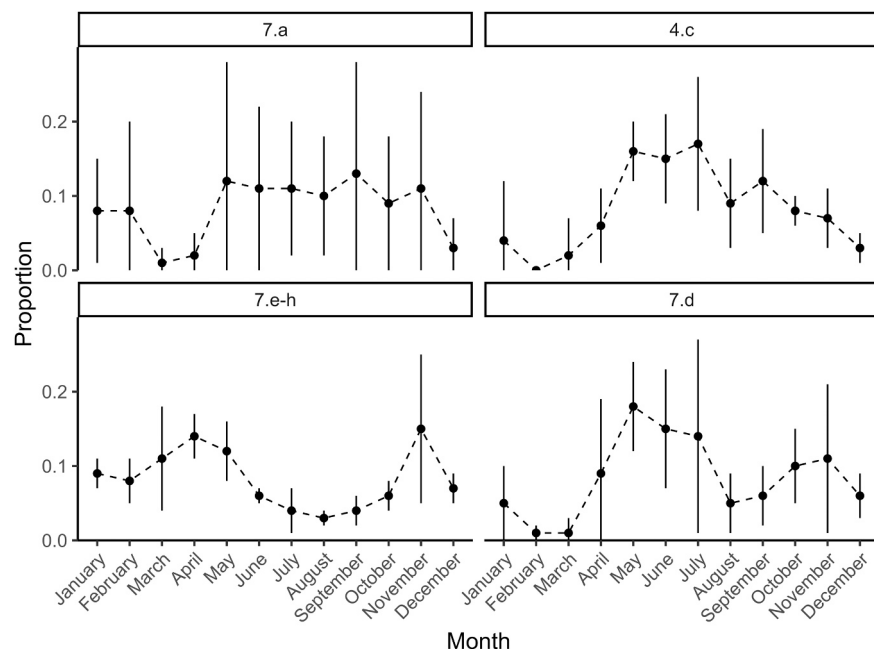


Fig. 2. Mean ($\pm$ SD) proportion of annual landings by month, pre-management (2000–2007, all gears combined) for *Galeorhinus galeus* in UK fisheries as reported to iFish.

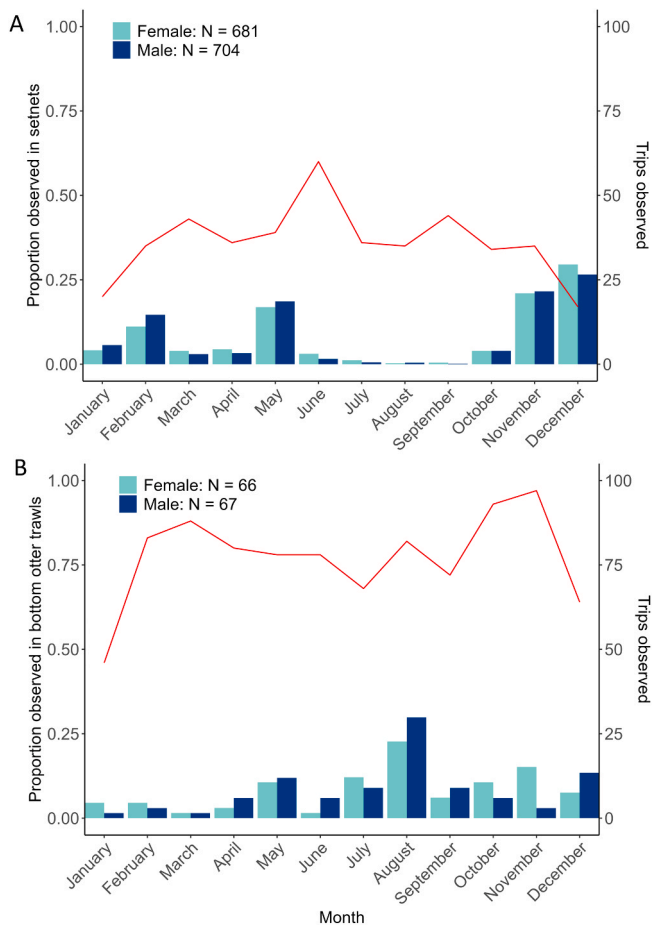


Fig. 3. Proportion of *Galeorhinus galeus* (by sex) observed caught in setnets (A) and bottom otter trawls (B) in Div. 7.e-h per month (all years combined). Red line indicates observer effort (number of trips observed) per month (all years combined).

see Supporting Information, Figure S5) were predominantly reported from 2011 ($N_{ind} = 115$; 27%). Captures were close to the coast around the British Isles but predominantly in the Southwest Approaches, particularly Div. 7.f ($N_{ind} = 102$; 23.8%) and Div. 7.g ($N_{ind} = 153$; 35.7%). Tope were captured year-round in the Southwest Approaches

but were recorded less frequently from June to September.

3.2. Spurdog

3.2.1. Reported UK landings

From 2000–2022, a total of 38,147 t of spurdog were reported ranging from 0 t (2014/15) to 7304 t (2001) per year. As expected, landings were highest before management interventions became increasingly restrictive (Table 1), decreasing steadily to zero in 2014. Following the introduction of a bycatch avoidance programme in 2016 (when selected vessels were permitted to land limited quantities of spurdog), reported UK landings increased in the Southwest Approaches between 2016 and 2022, ranging from 29.6 t to 151 t. The highest total reported landings were from Div. 6.a (12,561 t), followed by Div. 7.a (8541 t), Div. 4.a (4966 t) and Div. 7.k (3093 t). By gear, 14,402 t (38%) were landed from bottom otter trawls, of which 7526 t (52%) were caught to the West of Scotland and 4493 t (31%) from the North Sea. 9322 t (24%) were caught in hooks and lines, 3311 t (36%) from the West of Scotland and 2393 t (26%) in the Irish Sea.

3.2.2. Pre- and post-management restrictions

Gear: Pre-management (2000–2007; 36,741 t), 13,820 t (38%) were reported from bottom otter trawls followed by 9256 t (25%) from hooks and lines, and 6995 t (19%) from setnets (Table 1). Post-management (2008–2022; 1407 t), most landings were still reported from bottom otter trawls (582 t; 41%) but were closely followed by setnets (557 t; 40%). Hooks and lines landings reduced dramatically to 66.0 t (5%; Table 1).

Division: Pre-management, most spurdog landing reports were from the West of Scotland (1749 t on average per year, range: 315–3095 t) and Irish Sea (mean: 1050 t, range: 203–1869 t). However, post-management (2008–2022), most landing reports were from the Southwest Approaches (mean: 25 t, range: 0.0–104 t).

Seasonality in landings: Pre-management, the highest mean landing reports in the Southwest Approaches occurred March to June (Fig. 5), peaking in May (mean: 39.5 t, range: 4.7–134 t) and June (mean: 38.4 t, range: 2.1–106 t). In the eastern English Channel landings peaked in April (mean: 3.6, range: 1.7–6.0 t) and again in November (mean: 4.2, range: 1.3–12.7 t) and December (mean: 4.0, range: 1.2–14.1 t; Fig. 5). In the southern North Sea (Div. 4.c), average monthly landings showed a peak in June (mean: 8.6, range: 0.2–33.5 t), and another in January (mean: 10.2, range: 1.8–29.5 t) whilst landings from the central North Sea (Div. 4.b) peaked in August (mean: 38.3, range: 1.0–184 t). In the Irish Sea, landings also peaked in August (mean: 185 t,

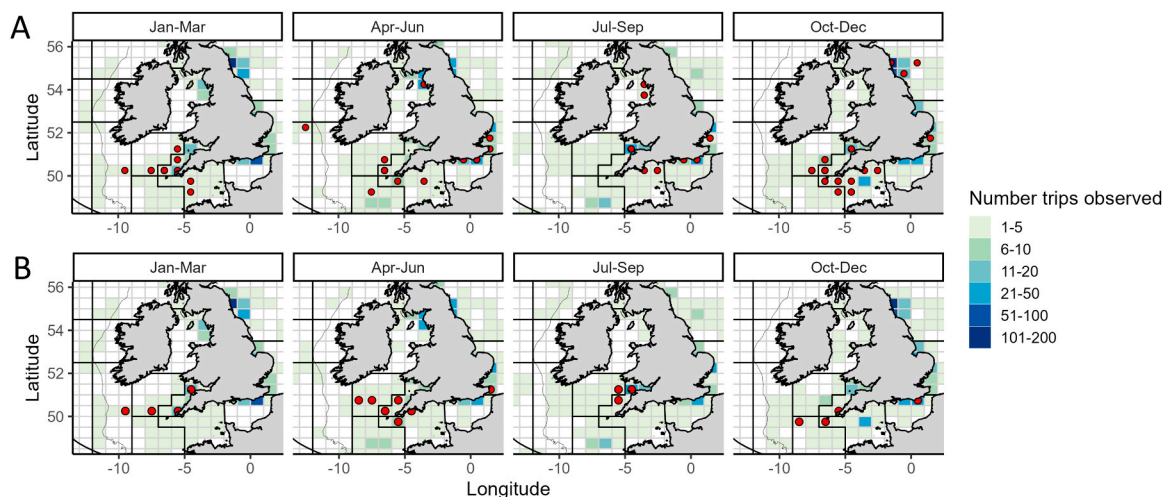


Fig. 4. Locations (aggregated to ICES Rectangle, red circles) of hauls where *Galeorhinus galeus* ≤ 75 cm (A) and females ≥ 150 cm (B) were observed (2002–2022; all gears) by quarter (Jan-Mar; Oct-Dec). Shading refers to number of trips observed as a measure of observer effort aggregated to ICES Rectangle across the time period.

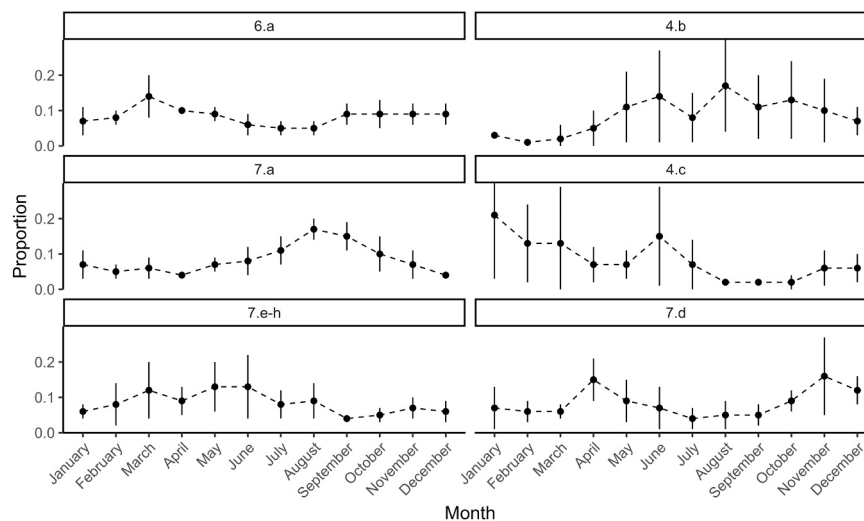


Fig. 5. Mean ($\pm$ SD) proportion of annual landings by month, pre-management (2000–2007, all gears combined) for *Squalus acanthias* in UK fisheries as reported to iFish.

range: 29.6–373 t), whilst the peak occurred in March to April and September to December in West of Scotland.

3.2.3. Cefas observer data

Cefas observers recorded 13,813 spurdog ranging annually between 71 and 2987 individuals (in 2002 and 2016, respectively). Across the time-series, most recorded captures occurred from September to December (range: 1760–4554 individuals). By region, 92% of observed spurdog captures were from the Southwest Approaches ($N_{\text{ind}} = 12,708$) with each Division having over 1300 records, peaking in Div. 7.g with 8045 individuals (63%). This was followed by the Irish Sea ($N_{\text{ind}} = 300$, 2%) and North Sea ($N_{\text{ind}} = 419$, 3%, specifically Div. 4.b $N_{\text{ind}} = 265$, 63%). Setnets ($N_{\text{ind}} = 12,072$) and bottom otter trawls ($N_{\text{ind}} = 1320$) captured spurdog year-round. The reported lengths of males ($N_{\text{ind}} = 7607$, 55%) and females ($N_{\text{ind}} = 6151$, 45%) ranged from 17 to 112 cm (mean: 75 cm) and 22–128 cm (mean: 86 cm), respectively. Records with sex reported as unknown ($N = 55$) were removed from analysis by sex.

Seasonality of captures: In the Southwest Approaches, an average of 295 (range: 1–2961) spurdog were observed captured per year in November and December with high numbers also observed in September and October (mean: 205, range: 0–1237). Average captures in the eastern English Channel and southern North Sea were negligible (<1 per year), but the central North Sea (Div. 4.b) had 10 (range: 0–116) captures on average per year in September and October. In the Irish Sea, the greatest number of captures were observed in May and June (mean: 5, range: 0–43) and July to August (mean: 7, range: 0–143), on average, with < 2 observed individuals captured per year in other months. Similarly, to the West of Scotland, < 1 spurdog was observed captured, on average, per year in all months except in July and August (mean: 5, range: 0–103).

Inferred seasonality by sex: Focusing on the métiers with highest overall interactions, spurdog captures in setnets in the Southwest Approaches ($N_{\text{ind}} = 11,780$) occurred year-round with highest proportions of males captured September to October ($N_{\text{ind}} = 3210$, 47.1%, Fig. 6) and females in November to December ($N_{\text{ind}} = 2808$, 56.8%). Bottom otter trawl captures in the Southwest Approaches ($N_{\text{ind}} = 643$) also occurred year-round with male interactions peaking in June ($N_{\text{ind}} = 42$, 17.3%), and July ($N_{\text{ind}} = 74$, 30.5%) and female interactions peaking in April ($N_{\text{ind}} = 66$, 16.5%) and December ($N_{\text{ind}} = 91$, 22.8%; Fig. 6). In bottom otter trawls in the North Sea (Div. 4.a–c; $N_{\text{ind}} = 262$), most males were captured in November ($N_{\text{ind}} = 64$, 63%) and September ($N_{\text{ind}} = 18$, 18%; Fig. 6), and most females were captured in September ($N_{\text{ind}} = 75$, 47%).

Sex ratio of aggregations: Overall, 39 hauls ($N_{\text{ind}} = 65$ –416 per haul) were in the top 3% based on number of spurdog captured. All these were from the Southwest Approaches, predominantly in setnets in Div. 7.g ($N_{\text{hauls}} = 24$). These hauls (all gears) were from September to January, mostly in December ($N_{\text{hauls}} = 17$). Of these hauls, only five had no statistically significant difference in the sex ratio (see Supporting Information, Table S6). Thirteen hauls were female-dominated ($87\% \pm 13\%$ of each haul were female) with a mean ratio of 5 females to 1 male. There were 21 male-dominated hauls ($86\% \pm 13\%$ of each haul were male) with a mean ratio of 1 female to 25 males. In the months October to December, female-dominated hauls occurred closer to the coast than balanced or male-dominated hauls (Fig. 7).

Interestingly, five hauls with a high number of mature females were all from one trip on a netting vessel operating in Div. 7.g during December 2016 to January 2017. Three of the hauls were dominated by females with ratios of 4:1, 1.7:1, and 2.3:1 ($\chi^2(1, N_{\text{ind}} = 71) = 26.04$, $p < 0.001$; $\chi^2(1, N_{\text{ind}} = 384) = 28.17$, $p < 0.001$; $\chi^2(1, N_{\text{ind}} = 416) = 64.65$, $p < 0.001$), one was dominated by males with a ratio of 0.2:1 ($\chi^2(1, N_{\text{ind}} = 402) = 145.68$, $p < 0.001$) and the fifth had a more equal sex ratio of 0.9:1 ($\chi^2(1, N_{\text{ind}} = 68) = 0.24$, $p = 0.628$). All five hauls included both sexes and covered a length range incorporating presumed juveniles, immature and mature spurdog (see Supporting Information, Table S6).

Spurdog ≤ 60 cm: Overall, 718 spurdog (17–60 cm) were reported in this length class from 220 hauls. Observations occurred each month but were predominantly in August ($N_{\text{ind}} = 104$; 14%), September ($N_{\text{ind}} = 100$; 14%) and October ($N_{\text{ind}} = 170$; 24%; Fig. 8). Setnets ($N_{\text{ind}} = 313$; 44%), bottom otter trawls ($N_{\text{ind}} = 274$; 38%) and beam trawls ($N_{\text{ind}} = 127$; 18%) were the main gears in which spurdog in this length class were captured, largely from Div. 7.e ($N_{\text{ind}} = 300$; 42%) and Div. 7.g ($N_{\text{ind}} = 168$; 23%). In May 2019, a bottom otter trawl haul off Start Point Bay, South Devon (Div. 7.e) caught 38 spurdog (19 males and 19 females) across the 21–33 cm length range (mean: 27 cm).

Female spurdog ≥ 100 cm: A total of 1430 individuals of this length class were observed across 467 hauls. Observations were made every month (all years combined), but predominantly in December ($N_{\text{ind}} = 529$; 37%). Most were captured in setnets ($N_{\text{hauls}} = 357$; $N_{\text{ind}} = 1235$, 86%) and bottom otter trawls ($N_{\text{hauls}} = 89$; $N_{\text{ind}} = 172$, 12%) in the Southwest Approaches ($N_{\text{hauls}} = 379$; $N_{\text{ind}} = 1209$, 85%), particularly in Div. 7.g ($N_{\text{hauls}} = 211$; $N_{\text{ind}} = 840$, 69%; Fig. 8).

3.2.4. Additional observations from the bycatch monitoring programme

In the BMP database (2010–2022; see Supporting Information,

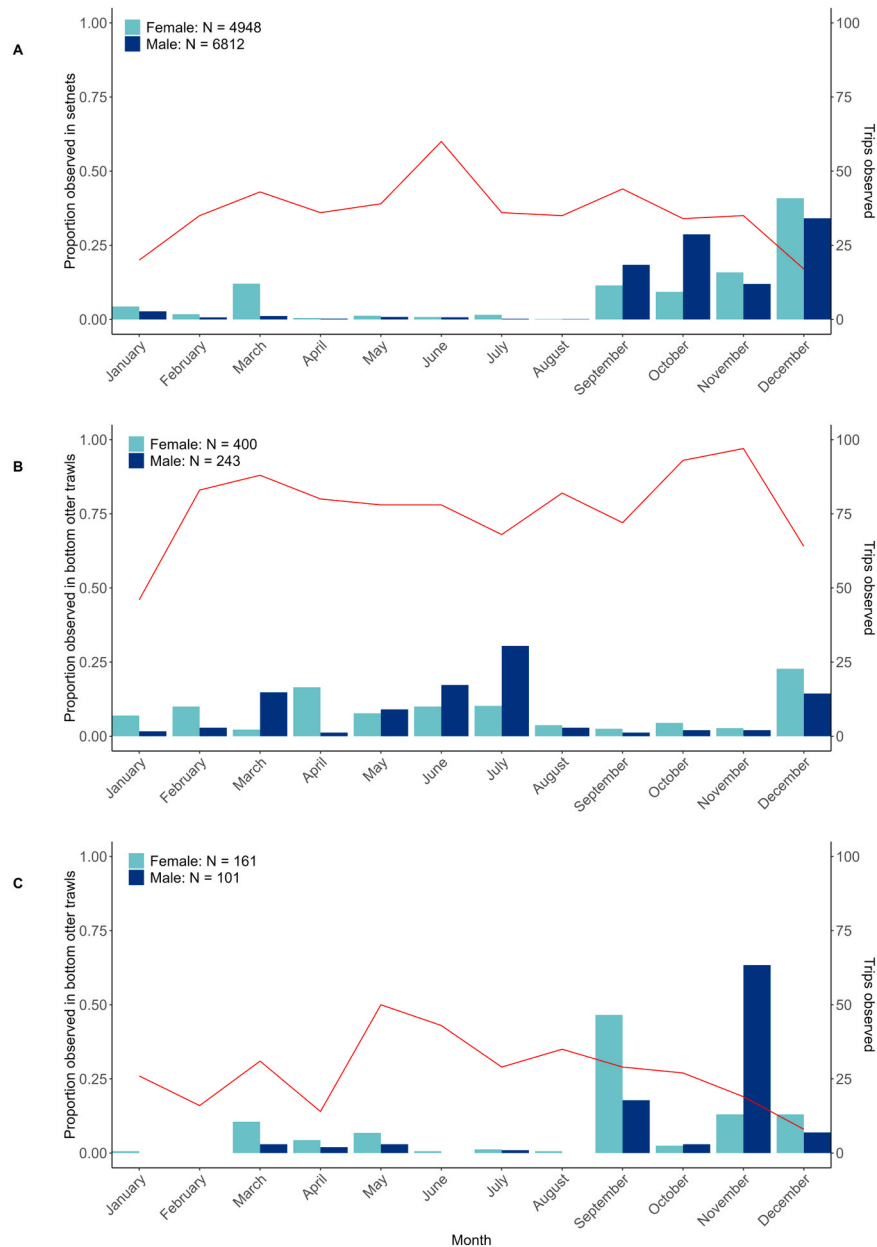


Fig. 6. Proportion of monthly (all years combined) male and female *Squalus acanthias* observed caught in (A) setnets in Div. 7.e-h; (B) bottom otter trawls in Div. 7.e-h; and (C) setnets in Div. 4.a-c. Red line indicates observer effort (number of trips observed) per month (all years combined).

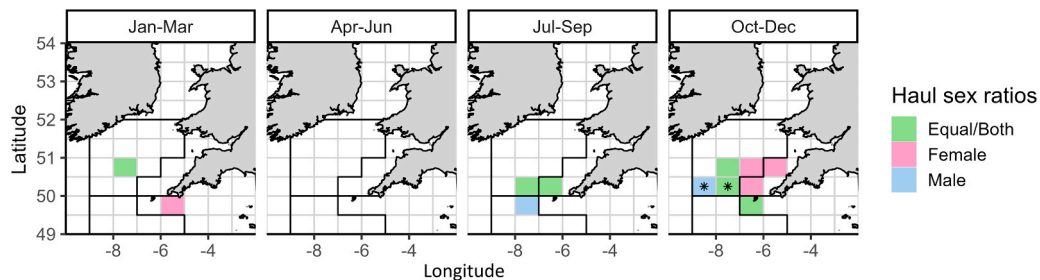


Fig. 7. Quarterly (Jan-Mar; Oct-Dec) locations aggregated to ICES Rectangle for hauls with > 60 *Squalus acanthias* observed caught based on chi-square goodness of fit test. Colours refer to: Equal/Both: no significantly dominating sex in haul or a mix of female- and male-dominated hauls; Females: significantly more females than males in haul; Males: significantly more males than females in haul. Rectangles with an asterisk denote where hauls from 2 to 4 trips in separate years occurred. Rectangles without an asterisk are where hauls occurred over 1–2 trips. Significance at $p < 0.05$.

Figure S5), 6009 spurdog were reported, with 1096 recorded in 2013 (18%) and 1014 recorded in 2014 (17%). All except 40 individuals were

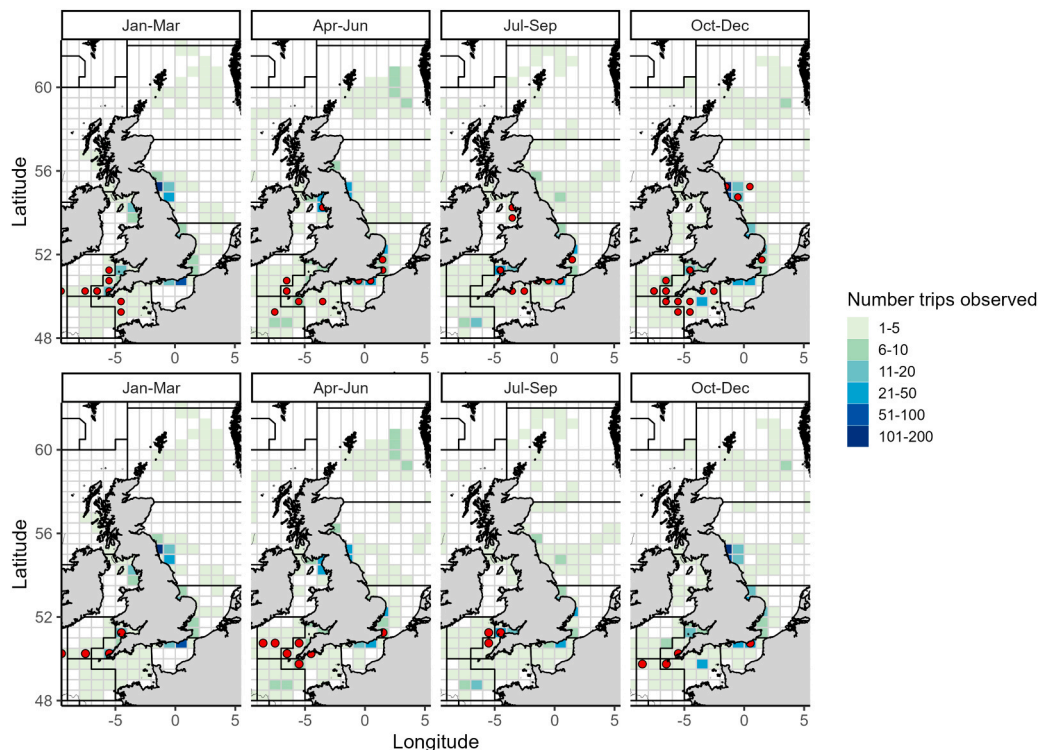


Fig. 8. Locations (aggregated to ICES Rectangle, red circles) of hauls where *Squalus acanthias* ≤ 60 cm (A) and females ≥ 100 cm (B) were observed (2002–2022; all gears) by quarter (Jan-Mar; Oct-Dec). Shading refers to number of trips observed as a measure of observer effort aggregated to ICES Rectangle across the time period.

reported in the Southwest Approaches, with 4138 (70%) from Div. 7.g. Spurdog were captured year-round in the Southwest Approaches but captures increased during October to December ($N_{ind} = 4633$, 78% of total captured).

4. Discussion

The conservation of migratory sharks requires an appropriate understanding of seasonal differences in their spatial distributions (by species, sex, and life-stage) and potential levels of interactions with fisheries. For species known to segregate by size and sex, it is important to quantify seasonality of fisheries interactions for each of these parameters, including when and where larger aggregations may occur. This study used reported landings and national observer programme data to examine spatio-temporal interactions between two migratory shark species (tope and spurdog) and commercial fisheries. There were notable interactions of both species with setnet and bottom otter trawl fisheries in the southwest UK (Div. 7.e–h), and between spurdog and bottom otter trawl fisheries in the North Sea (Subarea 4), highlighting these as important métiers to which tope and spurdog are vulnerable, supporting previous findings from [Silva and Ellis \(2019\)](#). Regional collaboration with other relevant national and administrative bodies with interest in these stocks (see [ICES, 2024b,c](#)) at appropriate spatio-temporal scales would be needed to estimate broader catch/by-catch levels. This would be of particular use for spurdog to the West of Scotland (Div. 6.a,b), as UK reported landings were highest from this region prior to restrictive management, but $< 1\%$ of Cefas Observer trips on UK (English and Welsh) vessels were in this region ($N_{trips} = 11$).

4.1. UK landings

It can be difficult to disentangle spatial and temporal patterns due to the influences of stock dynamics, changes in fisher behaviour (i.e., size selection, catchability in gears, fishing seasons operated), and evolving management actions. Landings data are more affected by management

changes than observer programme data, for which data collection relates to total catch (i.e., retained catch, plus discards). One example is the greater landings from hook and line gears prior to restrictive management. Tope and spurdog have historically been landed from longline gears ([Camhi et al., 2008; Finucci et al., 2020; ICES, 2024a](#)) accounting for their high landings reports in the pre-management part of the time-series. Management practices since 2008 for both these species restricted or prohibited landings from line fisheries. Post-management, this led to a large decline in landings records. Interaction rates could have remained the same, but had decreased reporting due to an increase in discarding of these two species. However, it also likely led to a change in fleet or fisher behaviour, depending on the proportion of the catch (income) which relied on tope and/or spurdog and other available fishing opportunities.

Discard observer trips have traditionally focused on the major fisheries, particularly those that are less selective and likely to have high discard rates such as demersal trawls. Consequently, only a limited number of hook and line trips were observed (73 trips; 2% of all observed trips), compared to other gears (bottom otter trawls: 1434 trips, 35%; and setnets: 893 trips, 24%). This was also noted by [Silva and Ellis, \(2019\)](#) who highlighted that observer programmes may have limited spatial and/or temporal overlap with vulnerable migratory species and noted the method of randomly selecting vessels to be observed as a contributing factor. Higher landings pre-management from hook and line gears, coupled with limited observed coverage, suggests the need for dedicated surveys to monitor catch and discard levels in fleets which may have greater encounter rates with migratory sharks.

The total level of landings and captures, as presented in this study, are useful for identifying fisheries with greatest overlap with fish stocks as well as investigating the distribution and movements of a species. Whilst these were the aims of the current study, fishing effort is another important and useful component of fisheries analysis, allowing catches to be compared across time periods and fishing operations ([Hoyle et al., 2024](#)). Typically, effort is quantified using measures such as number of

days at sea or number of days/hours fishing, which are used to calculate catch or landings per unit effort (CPUE/LPUE). This standardised measure of effort works well for trawl gears as, being an active gear, the swept area, tow duration, and distance are all known parameters. In the current study, most landings of tope and spurdog were from setnet gears which do not have a standardised and accurate measure of effort, as this would need to consider the number of nets in use, gear configuration (e.g., length, mesh size, number of panels), and soak duration. Additionally, net saturation has been shown to negatively impact catch rates over time, with catch rates decreasing as soak time and fish accumulation in the net increases (Li et al., 2011), complicating the interpretation of effort metrics. As such, the total landings and captures were deemed more appropriate to present in the current study given the aims of determining fish movement and vulnerability to capture by length and sex, but it is important to recognise that development of standardised effort metrics for setnets would be useful for fisheries analyses.

4.2. Observer coverage

Observer programmes provide detailed data recorded with standardised methods. However, observer programmes globally, typically have limited coverage of fleets, often due to the high costs of running the programmes (Kelleher, 2005; Roda et al., 2019), that can be problematic for species which are caught infrequently such as many chondrichthyans. As such, whilst observer programmes are incredibly useful, in some cases it can be problematic to extrapolate results for infrequently caught species (Kelleher, 2005). As the use of electronic monitoring systems to replace (or supplement) physical observer programmes continues to be developed, it has the potential to enhance sampling coverage of the fleet (Roda et al., 2019; Emery et al., 2025). In the meantime, a method to address this coverage limit for infrequently caught species is to compare observer data with fisher logbooks, landings data, and tagging data, to enhance biological and ecological information for different species. Furthermore, improved collaboration between different nations could ensure better quantification of gear interactions across the broader fishing grounds. Data sharing between observer programmes would be particularly useful for data-limited species, such as sharks, especially during periods where restrictive management reduces landings reports and individual observer programmes are limited by the practicalities of fleet coverage. At present, various ICES working groups (e.g., Working Group on Bycatch of Protected Species (WGBYC) and the Working Group on Elasmobranch Fishes (WGEF)) provide a platform for broader collaborative research. Species-specific studies incorporating this broader data across fleets would be useful to assess fishery interactions at a regional level for tope and spurdog.

4.3. Tope

Highest tope landings were reported May to November both pre- and post-management, whilst the Cefas observer programme reported tope catch year-round, supporting residency of at least part of the Northeast Atlantic stock on the UK shelf (Stevens and West, 1997; Cameron et al., 2025). In support of hypothesis a(i), seasonal shifts in reported tope landings reflected known movements between the Celtic Sea in winter and southern North Sea in summer. However, this seasonal movement was found to be the same for both sexes, contrary to the hypothesis b. It does align with previous tagging data, where tope tagged in the German Bight were found to travel to the Southwest Approaches in autumn and remain there between October and December before heading off the continental shelf (Schaber et al., 2022). This suggests the Southwest Approaches is an important area for mixed sex aggregations, supporting the findings of Cameron et al. (2025). As both sexes utilise the Southwest Approaches in winter, it is likely that the annual aggregations are due to site fidelity on mating grounds. This theory has previously been speculated by Thorburn et al., (2015) and Cameron et al. (2025) but further

research, specifically tagging of mature individuals of both sexes, is needed.

Length classes: In August, 49% of tope observations in bottom otter trawls in the Southwest Approaches (Div. 7.e–h; $N = 35$) were ≤ 75 cm ($N = 17$) suggesting an increased vulnerability of this length class to this gear type during summer. This coincides with the known parturition season as better documented in the southern hemisphere (Stevens and West, 1997; Lucifora et al., 2004; Bovcon et al., 2018). Coastal areas in the Celtic and Irish Seas are suspected nursery grounds for tope (Cameron et al., 2025) supported by most catches of tope ≤ 50 cm being close to the coast, whereas tope closer to the 75 cm threshold were caught further offshore. Overall, there were few records of tope ≤ 50 cm ($N = 19$), which may be due to limited observer coverage in these regions; limited overlap between neonates and commercial fisheries; and/or low catchability. It is also possible small-length tope are misidentified when caught with morphologically similar species such as starry smooth-hound (*Mustelus asterias*) and therefore more interactions might be occurring but not being reported. Increased observer coverage or dedicated research trips would be needed to verify the reason for the apparent limited interaction with neonate tope, alongside providing training or identification keys for observers to reduce incidents of misidentification.

There were year-round reports of female tope ≥ 150 cm, but captures were limited (a maximum of one per haul). Most mature female interactions were in setnets in the southwest of the UK shelf, predominantly in May. Increased captures during this time could be due to pregnant females moving inshore towards nursery areas for summer parturition (Stevens and West, 1997).

4.4. Spurdog

Supporting hypothesis a(i), both landings and observer data reflected movement between the Southwest Approaches in winter either northwards toward the Irish Sea, or east through the English Channel to the North Sea in spring and summer. This aligns with earlier studies (Gauld and MacDonald, 1982; Vince, 1991; Pawson, 1995) which reported more recapture records in the southern North Sea in summer and autumn, and occupancy of the Celtic Sea in winter months, with these seasonal patterns likely related to parturition and overwintering.

Peak interactions for each sex differed by season and gear in the southwest of the shelf (Div. 7.e–h) supporting hypothesis (b). The lowest interactions with females occurred in summer when females are known to occupy shallower, warmer water (Sulikowski et al., 2013; Junge et al., 2025) suggesting less overlap with commercial fisheries which do not operate close inshore. However, captures of males peaked in summer from bottom otter trawls and during autumn from setnets. Observer coverage of setnet trips in October to December covered deeper, cooler water towards the shelf edge, which has been documented as preferred environmental conditions for male spurdog in the Northwest Atlantic (Haugen, 2017). As such, the difference in capture by gear is just as likely an artefact of observer coverage than of gear vulnerability.

There were significant sex biases within the large hauls reported in the current study within the Southwest Approaches. The male-dominated catches occurred slightly further offshore than female-dominated catches in the Southwest Approaches, supporting Vince, (1991) who found males to be distributed more widely than females. A similar distribution pattern was also found in the Northwest Atlantic with females preferring shallower water of lower salinity than males (Shepherd et al., 2002). Sexual segregation in spurdog is speculated to be driven by depth and temperature with males preferring deeper, cooler water to females (Dell'Apa et al., 2014; Haugen et al., 2017), as reported for other elasmobranch species (Hopkins and Cech, 2003; Heupel et al., 2007; Matich and Heithaus, 2012; Schlaff et al., 2014). It has also been speculated mature females prefer warmer waters to maximise embryonic development (Hanchet, 1988). Thorburn et al. (2025) reported migration of spurdog in and out of Loch Etive,

Scotland, to be temperature driven with significant thermal preferences by sex. The documented seasonal residency by mature females in warmer waters of the upper basin of Loch Etive in winter coincided with the known parturition period in the Northeast Atlantic (Pawson, 1995; Albert et al., 2019), which might explain the finer-scale sexual segregation of spurdog within the Celtic Sea in winter as presented in the current study. Given the small sample sizes, dedicated observer or research trips would be needed in the Celtic Sea to confirm this potential sexual segregation.

Sexual dimorphism by length has been reported for spurdog with regional variation (Finucci et al., 2020) yet most studies indicate that only females reach lengths > 100 cm (Hanchet, 1988; Pawson and Ellis, 2005; Ebert and Stehmann, 2013; Gračan et al., 2013). Twelve males were reported with lengths 100–112 cm in the Cefas Observer data. Although included in the present analysis, these records could not be corroborated to ensure there was no misidentification of species or sex. However, 99% of male spurdog reported in the Cefas Observer Programme were ≤ 97 cm, only slightly higher than previous maximum lengths reported in the Northeast Atlantic (Pawson and Ellis, 2005: 86 cm; Ebert and Stehmann, 2013: 95 cm).

Length classes: Spurdog ≤ 60 cm represent early life-stages of spurdog (juveniles and mostly immature fish) and were captured in every month (all years combined) supporting the observations of Vince (1991) that juveniles remain on the shelf and do not migrate offshore. Length at 50% maturity for males has been reported at 60–61 cm (or ~5 years) in Norwegian waters and females at 78 cm (or ~9.5 years; Albert et al., 2019). Whilst most individuals (and all females) in this length class will likely be immature, some males at the top end of this length class could be approaching maturity. Size-at-birth estimates range from 18 to 33 cm (Albert et al., 2019; Finucci et al., 2020), but very few spurdog < 30 cm were captured (N = 46) in the current study, suggesting limited spatial overlap with commercial fisheries and/or low catchability of neonatal spurdog, compared to immature and maturing individuals. However, this low number of observed captures might be influenced by limited observer coverage, not sampling areas of highest neonate densities. For example, previous studies noted that early-stage spurdog occurred in the Irish Sea (around the Isle of Man), off southwest Ireland, and off Northwest Scotland (Ellis et al., 2005, 2012). In the current study observer coverage was limited in these areas (236 trips observed in time series, 6% of total observer effort).

Interestingly, one observed haul from a bottom otter trawl contained 38 early-stage spurdog (21–33 cm; Div. 7.e; May 2019), suggesting analysis of data from neighbouring observer programmes, or dedicated studies, could be undertaken to improve our understanding of the spatial and temporal distribution of early stages. Parturition for spurdog in the Northeast Atlantic occurs in winter (Ellis and Keable, 2008) and given size at birth ranges 18–33 cm (Albert et al., 2019; Finucci et al., 2020), the spurdog caught in this haul were likely young-of-the-year. The sediment these spurdog were captured in has been described as sand and mud substrates (Diesing et al., 2012) reaching 100 m depths with an extensive inshore area of < 50 m (Burt et al., 2013). Sulikowski et al. (2013) found neonates occurring over finer (silt-clay) substrates in the Northwest Atlantic, but the depths were ca. 40 m, suggesting that depth might be as or more important than substrate for spurdog nursery areas.

Spurdog parturition is suspected to occur in winter (Pawson, 1995) supported by Albert et al. (2019) who reported near-term females in August to January around the Norwegian coast and coinciding with highest reported catch of large females (≥100 cm) in the Southwest Approaches in the current study. All large catches of spurdog contained a range of length classes although male-dominated catches typically consisted of individuals ≥ 60 cm (likely comprising developing and mature individuals) and female-dominated catches either consisted of mostly 60–90 cm (immature/developing) individuals or ≥ 100 cm (primarily mature) individuals. This suggests aggregation by sex occurs for mature males and both immature and mature females. Such sex-based aggregations have previously attributed to female avoidance

of males and the mating and feeding behaviour of males (Dell'Apa et al., 2014).

4.5. Management implications

Improved knowledge of seasonal changes in catch of these species by area and gear will inform stock assessments (e.g. as input data to models), management options (spatial and seasonal management, technical measures), and data collection programmes. Understanding whether high fishing pressure is being exerted on important demographic components (e.g. pregnant females) would allow for consideration of more targeted management (Mucientes et al., 2009; Dahlmo et al., 2026). Such information could also be used to direct fishers to areas/periods where higher biomasses of males aggregate, where catches of mature females would be kept to a minimum, as studied in the Northwest Atlantic by Haugen et al. (2017). Interactions with commercial fisheries were species-specific suggesting the behaviour of each species, rather than fishing fleet behaviour, are the main influence on interaction patterns and levels. This emphasises the need for species-specific management where possible, and a greater understanding of seasonal differences in interaction levels for these data-limited migratory sharks.

Within the observer programmes, tope and spurdog interactions with fisheries did not fall over the 21-years despite the removal of targeted fisheries. Instead, as also reported by Silva and Ellis, (2019), the management measures resulted mainly in an increase in the discarded catch which can still result in mortality. Estimates of at-vessel and post-release (or cryptic) mortality vary considerably between studies (Ellis et al., 2017; see also estimates in Bendall et al., 2012; Bowlby et al., 2021; Garzon et al., 2025; Oliver et al., 2025, amongst others), due to differences between and within species (e.g., length, sex), fishing and handling practices (e.g., gear, cod end weight, air exposure time), and environmental conditions (e.g., temperature; Ellis et al., 2017). This reinforces the need for inclusion of robust estimates of dead discards in stock assessments for these species. Northeast Atlantic spurdog currently have discard estimates included in the stock assessment conducted by ICES (ICES, 2024a), but tope do not (ICES, 2023), as with many other elasmobranch species. To effectively include discard estimates, sample data needs to be raised to fleet level and there is currently no standardised method across nations for data-limited stocks (ICES, 2020).

It would also be useful to estimate post-release mortality rates of discards to allow fisheries impacts to be quantified more accurately. A lack of standardised methods for collecting mortality information alongside the challenges of collecting post-release mortality currently hinder advances in these areas. Spurdog discard estimates are currently assumed to have 100% mortality (ICES, 2024a), yet studies suggest at-vessel mortality in nets can range from 13.5% (Braccini et al., 2012) to 26.8% (Bendall et al., 2012). Few studies have been conducted reporting at-vessel or post-release mortality across gears and shark species (Ellis et al., 2017). Due to the high cost and resources needed to conduct mortality studies, for the most data-limited species, collection of standardised data on condition of discarded individuals (e.g., discarded dead; discarded live (poor condition); discarded live (good condition)) in observer programmes could be a useful tool for filling these data gaps.

4.6. Conclusions

This study has shown how interactions with commercial fisheries vary by season, sex, and length class for tope and spurdog around the British Isles. As hypothesised, seasonal changes in interaction levels reflected the known migration patterns based on tagging studies (hypothesis a), and there were differences by sex and length classes (hypothesis b). Knowledge of the seasonal movements of these different stock components could be used to implement targeted management if required, to help avoid aggregations of mature females or juveniles.

Collaborative studies with other fishing nations should be encouraged, to better quantify interactions across a broader region at equivalent spatial scales. Continued monitoring of catch/bycatch levels by observer programmes, increased reporting of discard condition and fate, and tagging studies to identify seasonal movements of different stock components will be vital for monitoring and evaluating the impact of fisheries on these migratory shark stocks.

CRedit authorship contribution statement

Maisie Evans: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Jim R. Ellis:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Allen Kingston:** Writing – review & editing, Data curation. **John K. Pinnegar:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Ana Ribeiro Santos:** Writing – review & editing, Methodology, Data curation. **Carol Robinson:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Ethics declaration

Not required.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Maisie Evans reports financial support was provided by Fisheries Society of the British Isles. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2026.107881](https://doi.org/10.1016/j.fishres.2026.107881).

Data availability

The authors do not have permission to share data.

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