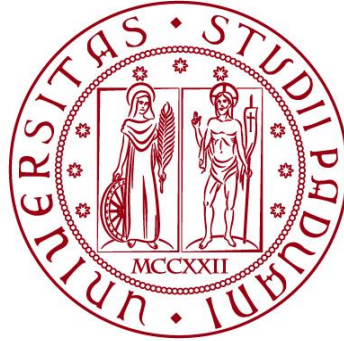


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**INVESTIGATION ON THE SPINY DOGFISH
(*SQUALUS ACANTHIAS*) SPATIAL DISTRIBUTION
AND LIFE HISTORY TRAITS: A COMPARISON
BETWEEN THE ADRIATIC AND THE NORTHEAST
ATLANTIC POPULATIONS**

Relatore: Prof.ssa Carlotta Mazzoldi

Dipartimento di Biologia

Correlatore: Dott.ssa Claudia Junge

Institute of Marine Research, Norway

Laureando:

Antonio Beggiato

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ABSTRACT

Spurdog (*Squalus acanthias*) is a widely distributed shark with a long history of exploitation. This study characterises its spatial ecology in the heavily fished Adriatic Sea using fishery-dependent data and a combination of models and mapping methodologies. The subsequent comparison with a part of the considerably more researched Northeast (NE) Atlantic population, inhabiting the coastal waters and fjords of southern Norway, allowed for the exploration of similarities and differences in this species' use of space. In the Adriatic Sea, this shark prefers northern regions, where the waters are shallower and more productive. Similar preferences for more productive locations were seen in the NE Atlantic population, which was more numerous at lower latitudes. Seasonality in one sex was then confirmed for both areas, although a different pattern was noted. While adult and pregnant females were only found in the northern Adriatic during the spring and summer months, when warmer waters and greater oxygen levels may have driven their migration to reproduce and give birth, adult females were mostly found in southern Norway throughout the winter. Males, on the other hand, appeared to remain stationary on a more local scale and were seen throughout the year in both study regions. Finally, modelling analysis revealed a decreasing trend in the Adriatic spurdog population, not detected in the NE Atlantic counterpart that instead appeared to have maintained its abundance during the investigated period. Findings of the spurdog spatial distributions, seasonality and temporal changes are expected to inform the sustainable management of this species and to develop future projects targeting the conservation of the ecosystems it inhabits (e.g., design of acoustic arrays, implementation of MPAs, etc.).

INDEX

1. INTRODUCTION.....	1
1.1. Elasmobranchs' ecology and use of space.....	1
1.2. Spurdog spatial ecology.....	2
1.3. Spurdog uses and its fishery.....	5
2. THESIS AIMS.....	9
3. MATERIALS AND METHODS.....	10
3.1. Study area: the Adriatic Sea.....	10
3.2. Adriatic data.....	11
3.3. Predictors.....	13
3.4. Statistical analysis and modelling.....	14
3.5. Adriatic spurdog maturity and sexes.....	16
3.6. Northeast Atlantic data.....	17
4. RESULTS.....	21
4.1. <i>Squalus acanthias</i> in the Adriatic waters.....	21
4.2. Maturity and sexes in the Adriatic spurdog.....	25
4.3. <i>Squalus acanthias</i> in the Northeast Atlantic.....	28
5. DISCUSSION.....	34
5.1. The northern Adriatic: a Mediterranean hotspot for spurdog.....	34
5.2. Spurdog in the deeper waters of the northern NE Atlantic.....	35
5.3. Seasonality and migrations.....	37
5.4. Temporal changes.....	39
5.5. Data and methodological limitations.....	42
5.6. Forecasts of spurdog fishery.....	45
6. CONCLUSIONS.....	46
7. SUPPORTING INFORMATION.....	48
7.1. Appendix I.....	48
8. BIBLIOGRAPHY.....	52

1. INTRODUCTION

1.1. ELASMOBRANCHS' ECOLOGY AND USE OF SPACE

Sharks are a large marine group of over 1000 species included in the subclass of Elasmobranchii (Conrath et al., 2004) within the class of cartilaginous fishes or Chondrichthyans. These predators are distributed all over the planet, occupying different habitats and ecological niches that can vary temporally and spatially (Dobson et al., 2009; FAO, 2014). Large pelagic sharks are the apex predators of the open ocean, while demersal elasmobranchs are considered the keystone meso-predators of benthic habitats (Gul et al., 2021). Despite their evolutionary success, over one-third of all chondrichthyan species are currently estimated to be threatened with extinction (Dulvy et al., 2021) because of human activities and detrimental habitat changes that are altering their environment (Cavanagh et al., 2007). These predators indeed, interact in different ways with their own environments, making the identification of this relationship a critical point for the understanding of sharks' population processes (Pattersaon et al., 2009). Peculiar behaviours observed in some elasmobranchs, such as residency¹ or philopatry² are important evidence of the presence of complex patterns of movement and space utilization (Bres et al., 1993). Alterations in abiotic factors such as temperature, salinity, dissolved oxygen, or photoperiod could greatly affect the use of space of these predators (Braccini et al., 2016) and the presence of unsuitable environmental conditions represents a severe risk for juvenile dispersal and adult movements. Many sharks are indeed considered migratory, with strong implications for their management, as the entire population or a significant proportion of its members cyclically cross one or more national jurisdictional boundaries (CMS, 2015). Around 140 species of elasmobranchs, i.e. sharks, skates and rays, show some degree of migratory behaviour (Braccini et al., 2016) ranging from short coastal to long transoceanic movements (Sims et al., 2010; Speed et al. 2010). During these displacements it is common to observe groups of individuals segregated together by size and/or sex

¹ Residency refers to an individual exhibiting a continuous occupancy of a limited area for at least 12 months (Chapman et al. 2015; Flowers et Al., 2016).

² Philopatry describes the capacity of specimens to return to their home areas or birth sites (Demian et al., 2015).

(Springer et al., 1967). Furthermore, many sharks undergo vertical daily and seasonal migrations, following changes in abiotic factors and prey availability (Bres et al., 1993).

Because of their complex interactions with surrounding space, sharks are among the most vulnerable species to fishing exploitation (Barausse et al., 2011). Furthermore, the unintentional capture of sharks in fisheries targeting other more valuable species, remains one of the major sources of anthropogenic mortality and a significant issue affecting their conservation (Bonanomi et al., 2018). This phenomenon is known as bycatch and its extent depends almost exclusively on the type of employed fishing gear (Barker et al., 2005). Shark loss not only disrupts the food chain, reducing the resilience of several trophic levels (Barausse et al., 2011), but it also promotes ecological transitions to less productive states (Coll et al., 2009). In this regard, data defining the distribution of crucial habitat and the relationships between these places and the adult populations from which juveniles recruit are urgently needed (Pawson et al., 2005). Unfortunately, documenting the movements of these predators is challenging due to their extreme vagility and the difficulty of following them in the marine environment (Demian et al., 2015). In this sense, catch data from commercial fisheries can provide general indications on elasmobranchs' spatial and temporal distribution (Pawson et al., 2005).

1.2. SPURDOG SPATIAL ECOLOGY

Squalus acanthias Linnaeus, 1758 is a widely distributed demersal shark also known under the common name of spiny dogfish or spurdog in Europe (Bigelow et al., 1953). The attribute 'spiny' is linked to the presence of a sharp spine on each of the two dorsal fins (Gallucci et al., 2011) characterized by a continuous growth throughout the entire life of the animal (Stenberg et al., 2005). The sizes of this shark can vary depending on habitat conditions, for instance: in the Northeast (NE) Atlantic average sizes range from 74cm to 84.5cm for females and from 54cm to 65.9cm for males (Fahy et al., 1988; Henderson et al., 2002; Daan et al., 2005; Albert et al., 2019; Silva et al., 2021) , whereas in the Mediterranean Sea average

sizes range from 51.5 to 87cm and from 47.5 to 66.7cm for females and males respectively (Chatzistryrou et al., 2005; Capapè et al., 2011; Gračan et al., 2013 and 2015; Bargione et al., 2019). This omnivorous opportunistic mesopredator is a long-lived species with recorded maximum age for males and females of 35 and 40 years, respectively, in the north Atlantic Ocean (Gallucci et al., 2011). This species is characterized by a low population growth rate (2–7% per year), making it extremely susceptible to overexploitation (Large et al., 2008). Nowadays, European markets still require spurdog primarily as a food resource, with females in particular being in great demand since they are bigger and hence more valuable than males (Large et al., 2008). The International Union for the Conservation of Species (IUCN) classifies the spurdog, globally, as *Vulnerable* (IUCN 2020), but the situation is more dramatic in Europe, where it is considered *Endangered* (Gračan et al., 2013; Gračan et al., 2017). Focusing on spatial ecology, this shark is considered a benthopelagic species (Stehlik et al., 2007) with a global distribution (**Figure 1**): it is found on the continental shelves of boreal and temperate zones of all oceans, and it seems to not associate with any benthic habitat (Kulka et al., 2012).



Figure 1. Global distribution of spurdog (IUCN 2020).

This shark prefers water with a temperature range between 5.6-15 degrees Celsius (°C) and its presence has been recorded in both inshore and offshore habitats and

from 0 up to 1978 m deep (Compagno et al., 1984; Jac et al. 2022). The spurdog tolerates a wide range of salinities, including estuarine waters (Lack et al., 2006). Temperature, depth, and salinity appear to be important parameters affecting its distribution with the larger specimens always inhabiting warmer, shallower, and less saline waters (Jac et al., 2022). Data outlines a north Pacific origin of the current spurdog populations with a subsequent dispersal firstly into the south Pacific, then into the north Atlantic and finally into the Mediterranean Sea passing through the Strait of Gibraltar (Verissimo et al., 2010). Interestingly population genetics shows very little mixing with low overlapping range among the stocks of these different areas, and for this reason, they are considered and managed as distinct subpopulations (IUCN 2020). In European Seas, this species can be found in most of the brackish and shelf waters from the Barents and Norwegian Seas down to the Skagerrak, North and Baltic Seas, and even further south, reaching the Irish Sea, the Celtic Sea, and the Gulf of Biscay (Kulka et al., 2012; IUCN 2020) at depths ranging from 25 m to 460 m (Jones et al., 2001; Daan 2005; Jac et al., 2022). In southern Norway, this shark is particularly abundant especially near the coast where it is denser at water temperatures ranges between 7.8–9.6°C (Jac et al., 2022). For what concerns the Mediterranean basin instead, the spurdog is one of the most abundant elasmobranchs with an estimated biomass of 6700 metric tons, and a peculiar hotspot of concentration has been detected in the Adriatic Sea where it inhabits the soft, sandy and muddy-sandy bottoms of the continental shelf up to a depth of 200 m (Serena et al., 2009). Large numbers of individuals can be found in the northern and central Adriatic between July and September at depths ranging from 30 to 55 m (Bonanomi et al., 2018). As a result, this area has been considered a possible breeding and nursery site, although little research on the distribution and migration of spurdog in the Adriatic and Mediterranean waters is currently available.

This species exhibits a complex migratory pattern and populations can for example be fragmented into residential and migratory components (Thorburn et al., 2015). Its displacements include long transoceanic migrations, seasonal regional migrations, and vertical movements through the water column (Gračan et al., 2020). Long trans-Atlantic (Templeman et al., 1976) and trans-Pacific (McFarlane et al.,

2003) migrations are known to have occurred in the past, but nowadays they are considered rare and occasional phenomena (Dobby et al., 2005). The factors driving spurdog migrations seems related to either environmental variables, prey availability or the breeding cycle (Shepherd et al. 2002; Stehlik et al., 2007). During both horizontal and vertical migrations, males and females segregate in groups of individuals of same sex and males tend to occupy areas with lower temperatures, higher depths, and higher salinities than those occupied by females (Serena et al., 2009). Females, on the contrary, seem to predilect habitats characterized by lower depths and higher productivity (Dell’Apa et al., 2016; Haugen et al., 2017). A possible explanation for this gregarious behaviour in the breeding stock is social avoidance (Sims et al., 2005): mature females try to limit mating attempts by avoiding males due to their aggressive courtship behaviour (Haugen et al., 2017). Moreover, when gravid, the active movement of females into warmer and more productive coastal waters, can maximize the survival and growth rates of embryos (Dell’Apa et al., 2016). Different is the situation of non-mature spurdogs which instead display more localised movements and a higher degree of site association (Thorburn et al., 2015). In healthy ecosystems this shark is an intermediate meso-predator often hunted by larger sharks and mammals (Compagno et al., 1984) but during the past decades, the removal of large top predators in different areas of the world, resulted in shifts to community structures that allowed spurdog to become the dominant predator and a keystone species for these regions (Morgan et al., 2015).

1.3. SPURDOG USES AND ITS FISHERY

Spurdog derived products exponentially increased in importance during the past century when, starting from 1920, the oil and meat of this shark were widely traded especially in Europe (Lack et al., 2006). In the past, the world demand for spurdog liver was much higher than the demand for its meat, because inside this organ it is contained an oil, the squalene, employed as a fundamental source of vitamin A. Nowadays vitamin A is synthetically produced, but the squalene is still employed in medical industry to treat cardiac arrests. Other peculiar applications include high-

technology industries, where it is used as high-quality lubricant and cosmetics industry where it is used as a skin rejuvenator (Walker et al., 1998). The fins of this shark are removed and sold in different parts of Asia, for the preparation of shark fin soup (Lack et al., 2006) and the cartilage is exploited to extract the chondroitin, which is used as artificial skin for burn victims (Walker et al., 1998). Globally, the spurdog is mainly taken in the industrial fisheries³ as a target or incidental catch of gillnets, longlines and trawls (Kulka et al., 2012; ICES WGEF 2021). Gillnets consists of a large wall of netting which can be set at any depth between the surface and the seafloor depending on the bathymetric profile of the fishing area (Kulka et al., 2012). In deep waters for instance, this gear tend to mainly capture spurdogs living in the water column. On the contrary, spurdogs inhabiting the bottom of continental shelves are mainly captured with otter bottom trawls (Bonanomi et al., 2018) that consist of a large fish net dragged behind a vessel along the sea bottom at an average speed of 3 knots (Kulka et al., 2012).

When analysing the history of spurdog overexploitation, a central role was undoubtedly played by Europe. France, Ireland, Norway, and the UK have historically been the main exploiters of spurdog (ICES WGEF 2021): their total catches in the NE Atlantic dramatically increased after the Second World War passing from 10000 tons in 1945 to about 60000 tons in 1961 (Aasen et al., 1964). Mature females, due to larger dimensions and closer distance to the shore, were preferentially harvested (Sagarese et al., 2015). As consequence, at the end of the 1960s the NE Atlantic stock began to decline (Dell'Apa et al., 2015) (**Figure 2**).

³ A fishery is defined as a homogeneous group of vessels with respect to gear type, season, and geographic region (Rago et al., 2009)

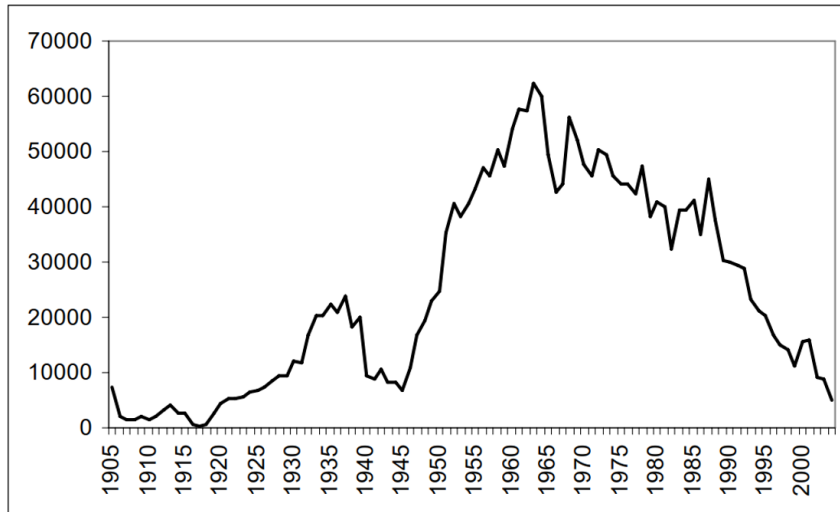


Figure 2. Total landings of NE Atlantic spurdog stock from 1905 to 2005 (Dobby et al., 2005).

Despite the signs of stock depletion, unregulated fishing activities continued until in 2005, the International Council for the Exploration of the Sea⁴ (ICES) reported that the NE Atlantic population was in danger of collapse (Lack et al., 2006). In response to this, the stock became protected and 0 total allowable catch (TAC) instituted (ICES 2019). Nowadays no commercial fishery exists for the spurdog in European Seas. Despite this, the high fishing pressure and habitat degradation typical of some basin, such as the Mediterranean Sea, resulted in the population decline of many shark species, spurdog included (Gračan et al., 2017). For instance, elasmobranch landings in the northern Adriatic Sea recorded in Chioggia market passed from 5.4% to 0.2% of total landings during the period 1945-2007 while fishing capacity continuously increased (Barousse et al., 2014). Long-time will be necessary to build up the stocks again even if no fishing took place (Aasen et al., 1964). In particular, the general increase in the adult male:female sex ratio and the decrease in average size of adult females are two problems common to many of the historically exploited stocks (Dell'Apa et al., 2015). Projections suggest that future oscillations in the female spawning stock biomass for populations of spurdog are likely to occur independently from the efficacy of fishery management measures

⁴ ICES is an intergovernmental organization with 20 member countries that develops science and advice to support the sustainable use of the seas and oceans. ICES purpose is to define the direction and priorities that fishery authorities should follow (ICES 2019).

taken (Rago et al., 2009). A successful management strategy for spurdog stocks must be based on long-term thinking (Pitchford et al., 2007) and this could not be achieved without comprehensive stock assessments and studies on spatial ecology of spurdog (Dell'Apa et al., 2015). At the present time, there is the need of research addressing the distribution and use of space of this shark, especially in the Mediterranean area, where it is still poorly studied.

2. THESIS AIMS

The goals of this study were to: (a) investigate the distribution and abundance of the spurdog in the highly exploited northern and central Adriatic Sea, (b) identify the possible environmental, temporal, and ecological drivers of its presence and abundance, (c) find similarities and differences in the use of space found in the Adriatic stock by comparing the results with a more intensively researched population of the NE Atlantic inhabiting coastal waters and fjords of southern Norway and (d) investigate how individuals of different maturities and sexes are distributed over the north and central Adriatic Sea. The findings of this study might be used to develop future management projects targeting the conservation of this shark not just in the Adriatic Sea, but also across the entire Mediterranean basin (e.g., design of acoustic arrays, implementation of MPA, etc.).

3. MATERIALS AND METHODS

3.1. STUDY AREA: ADRIATIC SEA

The Adriatic Sea, the northernmost region of the Mediterranean, is a semi-enclosed, long basin. It extends from the Gulf of Venice down to the Straits of Otranto in a northwest-southeast direction. Its volume is 35000 km³, its surface area is 138600 km², and its shape can be roughly described as a rectangle with dimensions of 800 km in length and 200 km in breadth (Cushman et al., 2001). Two distinct marine currents that dominate water circulation in the Adriatic are the West Adriatic Current (WAC) and the East Adriatic Current, which have their origins in the peculiarities of the Italian and Croatian coastlines (EAC). The first one starts in northern Italy south of the Po River and flows south along the Italian shelf, while the second one enters the Adriatic through the Otranto Sill and flows north along the Croatian coast, generating multiple recirculation cells directed by bottom topography (Artegiani et al., 1997). Because of the complicated bathymetry and various oceanographic qualities, the Adriatic Sea was evaluated and separated into three distinct geographical regions: north and mid Adriatic, where this study was entirely developed and south Adriatic, which is not considered here.

The north Adriatic is bounded by Croatia, Italy, and Slovenia, and it is constrained by 100 m isobaths. It is considered the Mediterranean's greatest shelf region, running from the Venice-Trieste seashore to the line joining Ancona on the Italian side to Zadar on the Croatian coast (Cushman et al., 2001). This area is easily distinguished from the rest of the Adriatic Sea due to its shallowness (average depth of 29 m) as well as its hydrographic and ecological characteristics. The significant nutrient loads from freshwater supplies make the northern Adriatic a zone of high marine production at multiple trophic levels (Barausse et al., 2009), distinguishing its waters from the more oligotrophic waters seen in the southern regions. Rivers coming into the north basin include the Po, Adige, Brenta, and Tagliamento. The average annual river discharge on the northern Adriatic Shelf is estimated to be around 5700 m³/s (Raicich et al., 1996), with peak flow rates occurring in spring and fall. The Po River accounts for around 28% (1585 m³ /s) of total runoff (Fonda Umani et al., 1996). This increased nitrogen intake from river runoff and human

activities produced significant eutrophication in the past, as demonstrated by hypoxia and fish deaths (Artioli et al., 2008). During the 1970s and 1980s, hypoxic events were particularly common around the mouth of the Po River (Giani et al., 2012). River flows impact not just production but also all other hydrographic and physical aspects of the northern Adriatic Sea (Russo et al., 1996). The mid and south Adriatic basins are deeper, with maximum depths of 270 and 1200 metres, respectively. They are separated by the Palagrua Sill (170 m) and have an average depth of around 140 m. (Artegiani et al., 1997a). The mid and south Adriatic have greater salinity than the northern Adriatic Shelf, but its waters are less nutrient-rich (Marini et al., 2008).

3.2. ADRIATIC DATA

All raw data on spurdog distribution were retrieved from the "BYCATCH" database, which is held at the Italian National Research Council (CNR), Institute of Marine Biological Resources and Biotechnologies (IRBIM) in Ancona, Italy (Bonanomi et al., 2022). BYCATCH is a project that assesses the accidental catch of protected species and species of conservation concern in midwater pelagic Adriatic trawling, including marine mammals, sea turtles, and elasmobranchs. Although this fishing method is considered pelagic, the net gets heavier owing to the animals caught inside and, as a result, sinks. In the shallow northern Adriatic Sea, this phenomenon enables the net to interact with the bottom, allowing it to capture species with demersal habits such as the spurdog. From July 2006 to December 2019, certified observers monitored 59 paired pelagic trawlers operating between the central and northern Adriatic Seas (FAO Division 37.2.1). The examined region covered a latitudinal range between 45.30°N and 42.30°N. For each haul, the following fishery-specific data were collected: vessel ID, date, trawl duration, latitude and longitude (in WGS84) at the beginning and end of the trawl, vessel average speed, average trawled depth, and number of spurdog caught. When feasible, sex, total length (TL) to the closest cm and total weight (TW) in kg were also recorded and catch/release conditions categorized.

A first step of the work included a comprehensive cleaning and review of the dataset as the initial operation, deleting any stations that encountered technological issues during routine fishing operations or stations placed in implausible places. A map of the study area with all of the hauls and positive captures for *S. acanthias* was created using QGIS 3.24.2. To minimise bias, the year 2014 was removed from the study due to several logistical challenges experienced during the coordination of observers' activity. The percentages of positive catch were calculated for each year by applying the formula:

$$\frac{\text{Number of bycatch events}}{\text{Number of hauls in the year}} \times 100$$

And then the abundance of sharks in each year was obtained by doing:

$$\frac{\text{Number of animals found each year}}{\text{Number of hauls in the year}}$$

Using the initial and ending coordinates as a guide, the distance (in kilometres) covered by each haul was calculated, and 0.05 - 0.95 percentiles were derived. To eliminate outliers and minimise variability in the dataset, all stations outside the specified range were excluded. The process was then replicated for the trawled time.

The fished area in midwater paired pelagic trawling varies significantly, impacting animal catchability. The main causes of these variations include elements such as the size of the deployed net, the distance between the two vessels, the speed, the period of trawling, and the covered distance. For these reasons, even if the same fishing technique was used, data standardisation was required. The size of the net in paired pelagic trawls varies according to the distance and speed of the two vessels, although the maximum length of the head rope is often correlated to the vessel's engine power. In other words, the higher the engine power, the larger the net that the vessel may utilise. The effort was standardised based on the CPUA (catch per unit area):

$$\frac{n}{a}$$

Where n corresponds to the number of sharks captured in each haul and a is the swept area in km², calculated applying the following formula:

$$a = D \times H$$

Where:

D is the distance in Km covered by each haul.

H is the length of the head-rope of the employed net which represents the horizontal opening of the net.

The distance covered (D) was estimated for each haul considering initial and final coordinates:

$$D = 6371 \times \text{acos} [\cos(\text{rad}(90 - LT1)) \times \cos(\text{rad}(90 - LT2)) \\ + \sin(\text{rad}(90 - LT1)) \times \sin(\text{rad}(90 - LT2)) \\ \times \cos(\text{rad}(LG1 - LG2))]$$

Where:

LT1 = Latitude at the beginning of the haul (degrees)

LT2 = Latitude at the end of the haul (degrees)

LG1 = Longitude at the beginning of the haul (degrees)

LG2 = Longitude at the end of the haul (degrees).

Observers ceased recording net measurements after 2015. The head-rope length of missing hauls was assumed as equal to the most recently reported measurement when considering vessels observed during the whole period. In contrast, the head-rope length of vessels spotted just after 2015 was approximated using the most recently reported length of a fishing vessel's head-rope with similar engine power as a reference value.

3.3. PREDICTORS

A variety of environmental and geographical variables were explored to find the most relevant elements impacting the existence and abundance of the target species: initial latitude and longitude, depth, temperature, salinity, and dissolved oxygen

concentration (DO). Monthly mean temperature and salinity data were retrieved from the MEDSEA MULTIYEAR PHY 006 004 model for the period 2006-2019, while DO estimates were acquired from the MEDSEA MULTIYEAR BGC 006 008 model. Both models are built on satellite-based Copernicus reanalysis (www.marine.copernicus.eu) constructed across a mesh grid with a spatial resolution of $0.042^\circ \times 0.042^\circ$. In MATLAB (version R2022a), the nearest neighbour interpolation approach was used to extract temperature, salinity, and DO at the reported location, depth, and time for each haul. Seasonality and variations in catchability over time were also investigated using temporal predictors. In this sense, for each haul, a progressive integer number indicating the chronological sequence of both months and years was assigned and the obtained predictor was named “diffmonth”.

3.4. STATISTICAL ANALYSIS AND MODELLING

All main exploratory statistical analyses were carried out in RStudio using the R packages ‘ggplot’, ‘nortest’, and ‘stats’ (RStudio, Inc., 2015). The presence of patterns in raw data was visually evaluated, taking into account each environmental predictor and the CPUA as a response. The Anderson-Darling test and QQ-plots were used to reject the hypothesis of normality in environmental predictors, and boxplots were generated to reveal the occurrence of potential outliers. The non-parametric Mann-Kendall test (Hamed et al., 1997) for multicollinearity was then performed, and the significant p-value for each pair of components was calculated. For further information see Appendix I. In case of potential collinearity, a Weight of Evidence (WOE) for the list of predictors was determined, and the matching Information Value (IV) was generated. WOE is used to turn a continuous independent variable (e.g., temperature or salinity) into a collection of groups or bins based on the similarity of the dependent variable distribution, and Information Value is then used to rank the components based on their relevance (Zeng et al., 2014). An IV greater than 0.5 indicates a factor with very strong predictive potential that should be carefully investigated.

The effect of environmental (temperature, salinity, DO), geographical (latitude, depth), and temporal (season, time) factors on the abundance of *S. acanthias* in the Adriatic Sea was investigated using a special class of generalised linear models (GLMs). Because the spurdog is a bycatch, its occurrence was far less common than that of other commercial species, and as a result, the majority of hauls contained no captures. Because of the abundance of 0, these distributions are described as zero inflated, and normal count GLM that use a Poisson or a Negative Binomial (NB) regression cannot be employed because they are unable to deal with an excess of 0, often resulting in implausible outcomes (Cindy et al., 2021; Zuur et al. 2009). The count measure of this sort of data does, in fact, contain excessive zeroes beyond what a normal count distribution can support. To suit this type of data, Zero-inflated (Lambert et al., 1992) and Hurdle models (Mullahy et al., 1986; Heilbron et al., 1994) have been developed. Both the ZI and Hurdle models assume extra zeroes to be originated by a different mechanism from the count values, and hence they are treated separately. Despite apparent similarity, these two models have significant differences. Zeroes in ZI models are thought to be produced by two distinct processes and are referred to as "true" (or structural) zeroes and "excess" (or sampling) zeroes. The first category includes zero responses from subjects whose count response will always be zero (the absence of sharks in a haul occurs because no shark was present there). The second category concerns false zeroes, which occur when a subject's count response is larger than zero but seems to be zero owing to sampling variability (e.g., the sharks, even if there, were not caught, or even if captured, the observer failed to record the observation) (Hua et al., 2014). In this sense, the zero component of a ZI model is represented by a binomial distribution with a logit link function that defines the likelihood of excess zeroes, whereas the count component is a conventional untruncated Poisson or NB distribution with a log link function that explains the distribution of counts (0, 1, 2, etc.) (Zuur et al., 2009; Payne et al., 2017). Hurdle, on the other hand, is a two-component mixture model with no distinction between structural and sampling zeroes, and the zero component is a binomial distribution with a logit function that characterises the likelihood of seeing a positive catch. Instead, the Hurdle model's count component follows a truncated count distribution, such as truncated Poisson or truncated NB

(Mullahy et al., 1986; Heilbron et al., 1994), which is used to simulate exclusively positive counts (1, 2, 3, etc.). Because of the uncertainty surrounding the origin of the zeroes, the ZI model was believed to be the best option. A likelihood ratio test was then used to determine whether a Poisson or an NB distribution should be preferred to fit positive counts. The R packages "pscl" and "countreg" were employed for model selection and validation analysis. After evaluating all potential combinations of predictors, the cAIC, AIC, and BIC of each model (Akaike, 1974; Schwarz, 1978) were extracted and used to select the most significant independent variables to include in the final model. Through the use of a variety of techniques, including the rootogram, QQ-residual plot, and Receiver Operating Characteristics (ROC) curves, the effectiveness of fitting of the chosen model was examined. R-squared and modified R-squared calculations were also made to determine the percentage of CPUA variation that the set of predictors were able to account for. To determine the environmental preferences and temporal tendencies for this species, predictions on the CPUA were carried out and graphically depicted for each significant explanatory variable.

3.5. ADRIATIC SPURDOG MATURITY AND SEXES

More investigation was then performed to ascertain how this shark is distributed in the Adriatic Sea based on its sex and stage of maturation. In this sense, sex and TL were considered for each individual. The predicted age and maturity were determined considering Bargione study of 2019 on spurdog life history traits in the Adriatic as a reference. The author took into account the reported length at maturity and the associated age at maturity for each sex (5.5 years for males and 7.5 years for females). In this sense, all males and females over the lengths of 57.5cm and 69cm were assumed to be mature. Graphs were created in RStudio to visualize distribution of maturity and of sexes during time and seasons (figure 6), while on QGIS point occurrences of adult and immature sharks at various ages were mapped (see Appendix I). GLMs were used to examine more in detail the presence of potential correlations between the distribution of adult males and females in the environment and the previously extracted predictors. A logistic regression model

with sex as response was created (0 if adult male - 1 if adult female). Significant predictors were identified by performing a backward selection based on both AIC and BIC information criterion (table 2). A confusion matrix was then constructed using the R-package 'caret,' and indexes for sensitivity⁵, specificity⁶ and misclassification rate⁷ were calculated.

3.6. NORTHEAST ATLANTIC DATA

Data on spurdog distribution in the Norwegian part of the NE Atlantic were collected from the Norwegian Coastal Reference Fleet (CRF), a programme created by the Institute of Marine Research (IMR) in 2005. Principal aim of the project concerns the recording of commercial catches in numbers per species, including size- and age composition, discards, and bycatch, as well as data on gear, capture location, depth, and effort. All vessels involved were ≤ 15 m in length (Williams et al., 2020) and carried out their fishing operations in fjords and in coastal waters (within 12 nautical miles from the shore). The contracts for the Coastal Reference Fleet last for four years (Clegg et al., 2020; Williams et al., 2020), thus, the data collected are assumed to be of good quality due to continuous training, with the scientists and the fishers (Nedreaas et al. 2006). The fishers were encouraged to record with daily basis everything they caught, including what was discarded at sea. Nowadays, spurdog is mostly landed on Norway's southern half of the western coast, particularly in statistical areas 7, 28, 8, and 9 (Albert et al., 2019). The studied region is around four to five times larger than that considered in the Adriatic Sea, it presents latitudes ranging from 57.50°N to 63.00°N and longitudes ranging from 3.50°E to 11°E. The area is distinguished by the existence of several fjords, which are long, narrow, and deep geological features carved out by glacial erosion and partly filled with seawater (Aksnes et al., 2019). They often include one or more undersea sills that define the deep basin(s) of the fjord, as well as a river that flows

⁵ Sensitivity or “true positive rate”, represents the percentage of 1 the model correctly predicted.

⁶ Specificity or “true negative rate”, represents the percentage of 0 the model correctly predicted.

⁷ Total misclassification rate is the percentage of total incorrect classifications made by the model.

into the fjord's inland endpoint (Farmer et al., 1982). Numerous fjords experience occasional periods of bottom water stagnation in basins, and the freshwater discharge/volume ratio of the recipient varies greatly with respect to the season (Wassman et al., 1995). The sill depth primarily influences basin water renewal and hence the supply of new dissolved oxygen, as the sill hinders direct horizontal connection between basin and oceanic water (Syvitski et al., 1987). Stratification of water layers happens during times of little or limited basin water renewal, and microbial oxygen consumption causes oxygen loss, which may favour the arousal of hypoxic or anoxic conditions (Aksnes et al., 2019). All of these features cause fjord ecosystems to function differently from coastal or oceanic ecosystems, influencing the ecology and space utilisation of many marine species that occupy those habitats and nearby surroundings.

The vessels in the CRF were selected from along the whole Norwegian coast, and the same period (2006 - 2019) was employed to make data comparable to those from the Adriatic Sea. As a preliminary step, the dataset was filtered to include only gillnet captures. This is because, despite the employment of various fishing techniques, the gillnet was the most often used gear in all years, and therefore provided a representative sample of spurdog occurring as bycatch in Norwegian fisheries (Albert et al. 2019; Hatlebrekke et Al. 2021). QGIS was used to build a map of the research region that included all the nets and positive captures for *S. acanthias*. The total soak time for each net was then determined, and 0.05 - 0.95 percentiles were calculated. All stations outside the defined range were eliminated from the dataset to decrease variability. The proportion of positive catch per region and during each season was then computed considering the count of bycatch events and dividing it by the total number of gillnets in each area (in the first case) and by the total number of gillnets in each season (in the second case).

Gillnets, unlike paired pelagic trawls, are not trawled by a vessel, but, once deployed, remain in the same position for a variable amount of time, requiring a different type of effort standardisation. In this study, effort (E) was estimated in terms of gillnet-days using the formula:

$$E = \frac{(\text{soaktime} \times \text{gillnets count})}{24}$$

The CPUE is therefore defined as weight of caught sharks in kg (both landed and discarded) per fishing operation using gillnets:

$$CPUE = \frac{W}{E}$$

The same temporal (seasons, diffmonth), geographical (latitude, longitude, depth), and environmental factors explored for the Adriatic were subsequently tested also on Norwegian data. The Copernicus NWSHELF_MULTIYEAR_PHY_004_009 model was used to provide monthly mean temperature and salinity reanalysis, whereas the NWSHELF_MULTIYEAR_BGC_004_011 model was used to obtain DO estimations. Both models are developed on a mesh grid with a spatial resolution of $0.111^\circ \times 0.067^\circ$, and environmental data were collected by taking into account the provided date, coordinates, and average fishing depth.

A considerable number of nets were located inside fjords or in areas particularly close to the coast where satellite coverage was not available and where, as consequence, environmental data were missing. To extract temperature, salinity and DO estimates from the missing stations, it was decided to use new sites as a reference. The initial step was to group together any missing sites with latitudinal variations less than 0.5° . In this sense, a total of 12-point groupings were discovered. A new representative coordinate was then calculated for each group. The new latitude was calculated by taking the mean of the latitudes of the points in the same group. To establish the new longitude instead, the maximum recorded depth for each group was evaluated, and the point was relocated from fjords toward coastal sea until the maximum recorded depth was available, while maintaining the value of the new latitude constant. A map showing the new extraction locations is reported in Appendix I of the supplementary material section. To study the presence and possible influence of environmental factors on the CPUE, two zero inflated models were created with the same approach employed for Adriatic data and outlined in the chapter "STATISTICAL ANALYSIS & MODELLING." The first model was created considering the complete dataset, whereas the second model was

created as an integration of the first and solely using data from non-modified sites.
The results were then analysed and compared to those of the Adriatic Sea model.

4. RESULTS

4.1. *SQUALUS ACANTHIAS* IN THE ADRIATIC WATERS

Between 2006 and 2019, 59 fishing boats were observed. Only 819 hauls (5.7 % of the total) caught spurdog among the 14354 hauls examined in 4006 fishing trips. A total of 2192 animals were captured. The geographical distribution of fishing effort and bycatch events is represented in **Figure 3**. Both hauls and bycatch events were more common in the northern Adriatic Shelf, which constitutes the major fishery site.

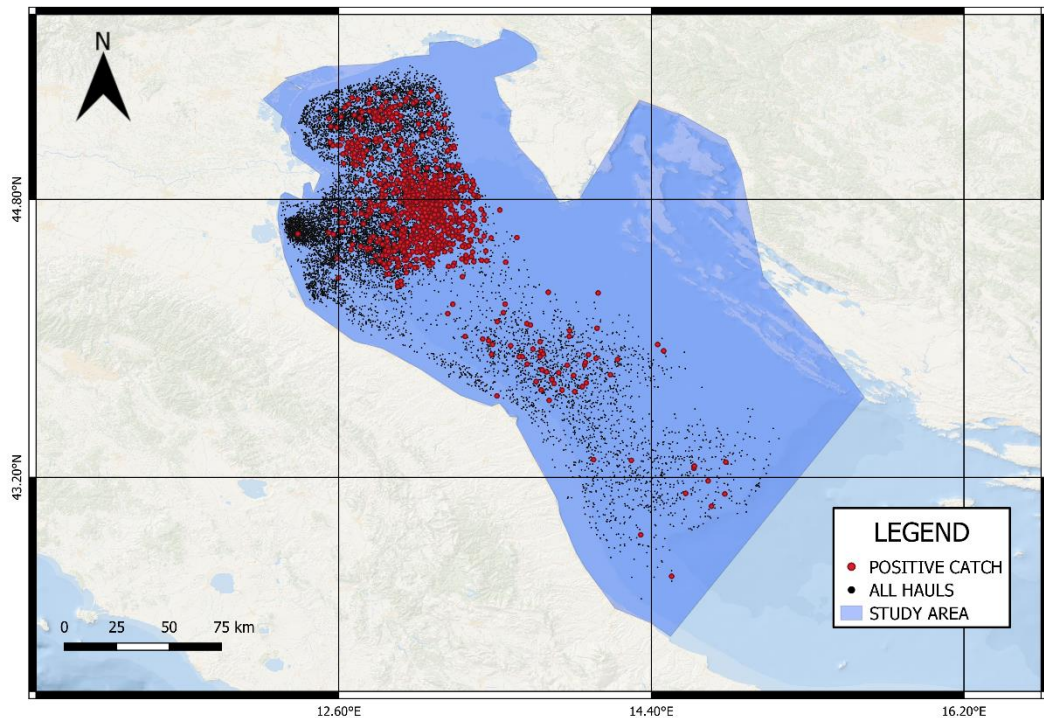


Figure 3: Distribution of hauls and of bycatch events of *S. acanthias* in the north and central Adriatic Sea from 2006 to 2019. The area where this study is focused is also represented.

Higher bycatch of this species in the northern Adriatic Sea was further verified when the relationship between bycatch occurrence and vessels' operating area was explored (see Appendix I for details). Of the 35 vessels reporting at least one positive capture indeed, the boats with the highest bycatch rates (between 10 and 20%) were all from Chioggia and only fished in the northern Adriatic. When time was taken into account, both the proportion of bycatch and the number of animals

recorded per km² varied significantly (**Figure 4a** and **4b**). The most substantial bycatch episodes occurred between 2009 and 2013, when this species was found in 7 to 10% of all hauls. After 2016, a reversal pattern was evident, with bycatch percentages declining to 2 - 2.5% (**Figure 4a**). Similar trends are observed when assessing animal catchability, with a considerable drop in abundance documented after 2015 (**Figure 4b**).

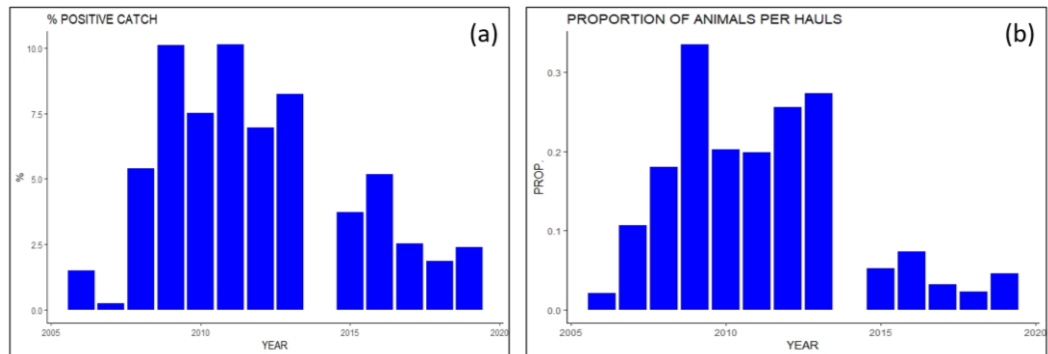


Figure 4: Barplot showing variation in: percentages of bycatch events (a) and in proportion of abundance (b) during years.

In terms of species distribution, this shark was always present in our study period throughout the seasons in the region bounded by latitudes between 44.20°N and 45.30°N (**Figure 5**).

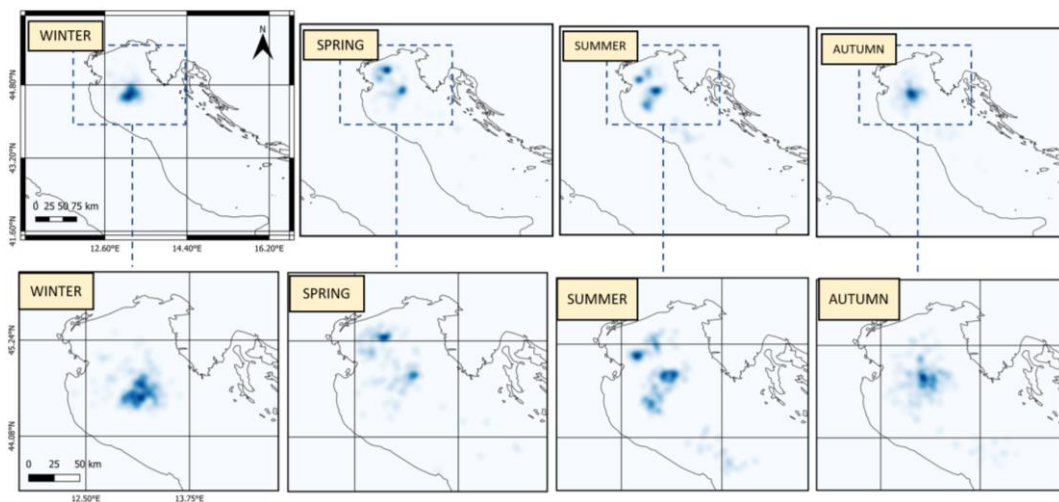


Figure 5: Presence of *S. acanthias* for included surveys from 2006 to 2019 off Italy. Bottom row shows detailed maps, reporting areas where the shark was always caught throughout seasons. Bycatch frequency is shown by colour intensity. In other words, the higher the number of spurdog-positive vessels at a certain site, the darker the region.

The situation for longitude is different, indeed longitude exhibited substantial levels of collinearity when paired with depth (0.61) and salinity (0.50), and the p-value for both indices was significant. Information Value (IV) of longitude was found to have suspiciously high predictive power (informative value coefficient >1) during WOE analysis, hence it was deleted from the list of predictors to avoid unnecessary model overfitting. When tested for overdispersion, a significant p-value ($< 2.2 \cdot 10^{-16}$) of the likelihood ratio-test indicated a better fit of negative binomial regression allowing for greater model flexibility by enabling the conditional variance of the outcome variable to be greater than its conditional mean. The best fit ZI model resulted in the removal of salinity and latitude from the count section, while the sequence of months was removed from the zero section (Table 1). This model managed to explain almost 81% of the variability present in the data ($R^2 = 0.806$).

Table 1: Summary of the best fit Zero Inflated GLM predictors on the CPOA distribution (negative binomial distribution) for *Squalus acanthias* in north and central Adriatic Sea (variables tested: latitude, depth, temperature, salinity, dissolved oxygen, season and time. The same starting variables were considered in both count and zero sections of the model)

DROP IN COUNT PART	DROP IN ZERO PART	AIC	AICc	BIC	df	logLik	Δ AIC	weight
Season, Latitude	Diffimonth	11911.4	11911.44	12040.12	17	-5938.70	0.00	0.92
-	Diffimonth	11917.10	11917.16	12068.54	20	-5938.55	5.72	0.05
-	-	11918.79	11918.85	12077.79	21	-5938.39	7.41	0.02
DO, Latitude	Diffimonth	11923.30	11923.35	12059.59	18	-5943.65	11.91	0.00
Season, DO, Latitude	Diffimonth	11929.99	11930.03	12043.57	15	-5950.00	18.58	0.00
Season, DO	-	11930.22	11930.26	12051.37	16	-5949.11	18.82	0.00
Season, DO, Latitude	Diffimonth, DO	11944.19	11944.22	12050.20	14	-5958.10	32.78	0.00

The Adriatic spurdog appears to be more common at lower depths (between 10 and 30m; **Figure 6a**) and with water salinities ranging from 38 to 39PSU (**Figure 6b**). Temperature and oxygen levels are also closely related to the abundance of this species, however, the range of preferences may vary depending on the season. Summer was by far the most common season for this shark in the study area, especially when water temperatures were between 20 and 25 °C and dissolved oxygen concentrations were greater than 270 mmol/m³ (**Figure 6c** and **6d**). The situation appears to be very different in the winter, when, despite increased water oxygenation, the drop in temperature had a detrimental effect on spurdog abundance. Regardless of season, the presence of this shark has progressively

declined over the years (**Figure 6e**). **Figures 4a** and **4b** indicate that this negative trend impacted not only the number of individuals detected, but also the frequency of positive catches.

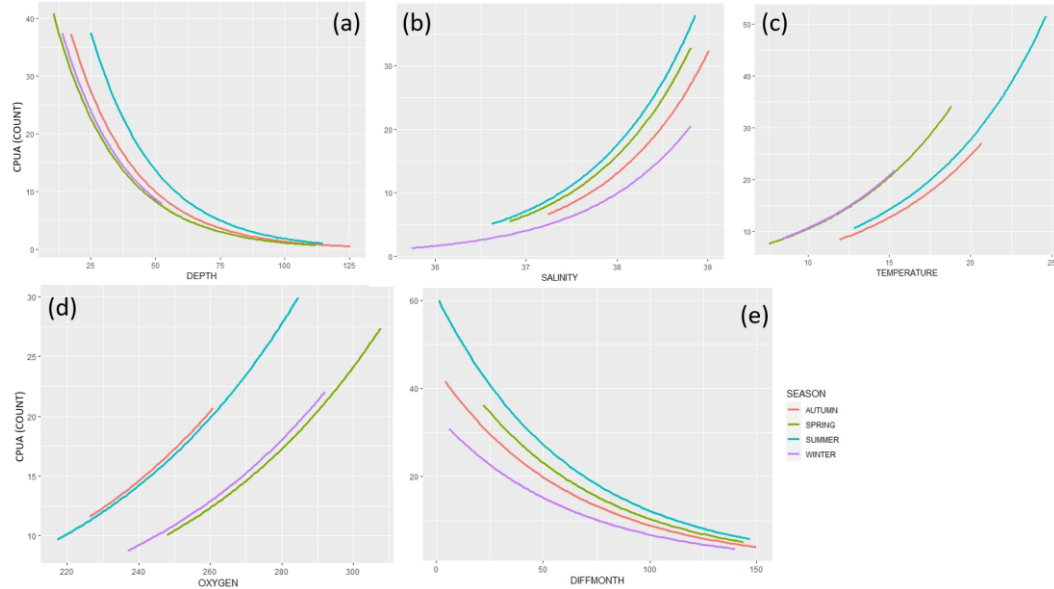


Figure 6: Model projections for *Squalus acanthias* abundance in the Adriatic Sea. Each graph takes into account a distinct predictor on the x-axis (depth (a), salinity (b), temperature (c), oxygen (d), and season=diffmonth (e)) and the CPUA as the response. Each graph forecasts the number of sharks by treating the independent predictor as variable and the others as fixed to their mean. Each graph has four lines of various colours, each of which corresponds to a distinct season.

When latitude, depth, or salinity increase, the chance of observing excess zeroes declines (**Figure 7**). In other words, when a haul occurs in the north or far from the shore (where salinity is higher and waters are deeper), the effect of sampling zeroes is reduced. On the contrary, as temperatures and oxygen levels rise, the likelihood of seeing false zeroes increases (**Figure 7**). It is important to pay close attention when analysing the zero section of the fitted model because, as is evident in Figure 5, even though they are all statistically significant, most of the predictors have modest effects and only sensibly affect the likelihood of false zeroes.

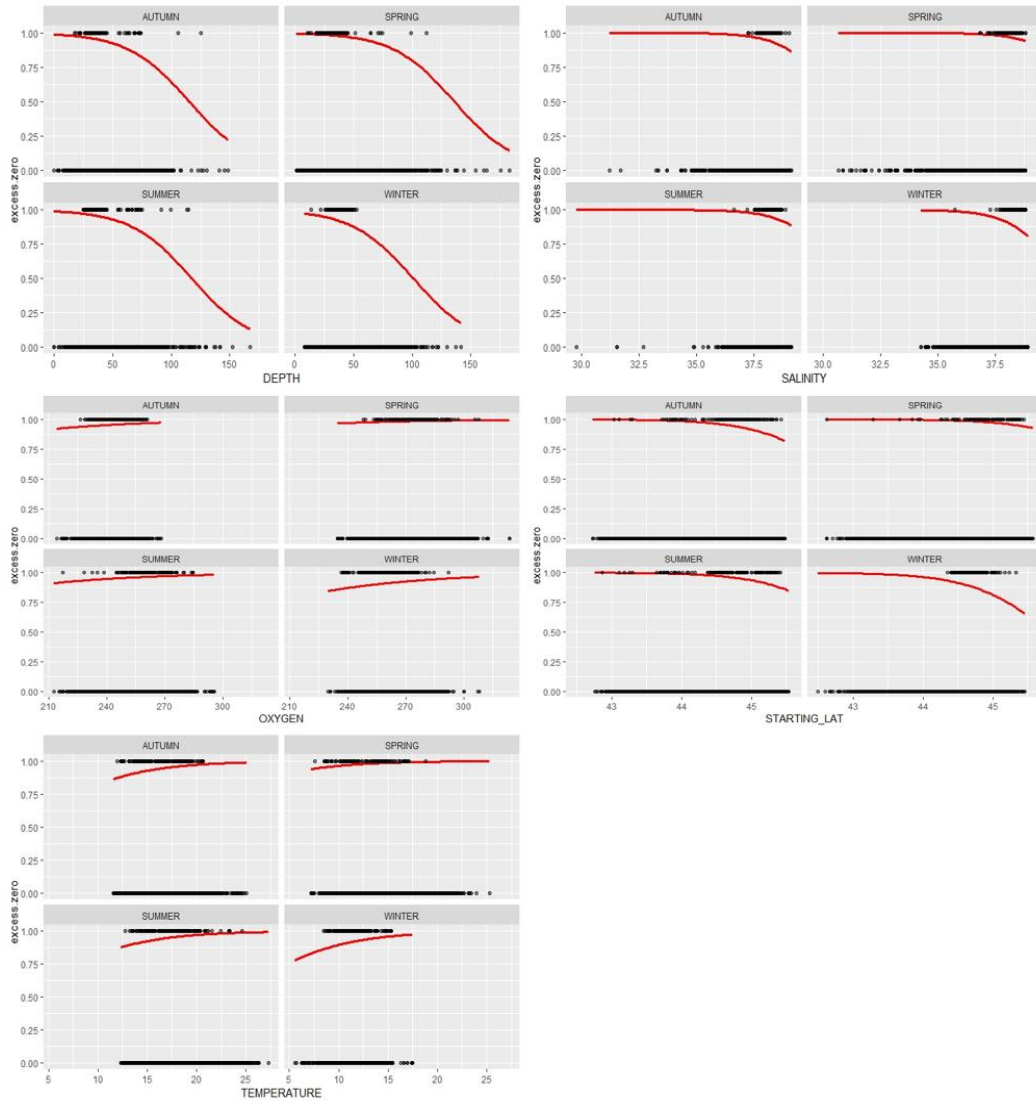


Figure 7: Likelihood of excess zeroes predicted by the best fit model. For each significant factor, the range goes from 1 (high probability to observe a false zero) to 0 (low probability to observe a false zero). The probability for each predictor, was computed by treating the independent factor as variable and the other predictors as fixed to their mean

4.2. MATURITY AND SEXES IN THE ADRIATIC SPURDOG

During the sample period, 373 females and 1137 male spurdog were examined. Females varied in size from 20 to 131 cm (mean \pm SD, 64.47 \pm 20.65 cm) and males from 20 to 120 cm (mean \pm SD, 70.77 \pm 12.15 cm). Despite reaching smaller dimensions, males appeared to have a greater mean total length than females and the Kolmogorov-Smirnov test revealed the presence of significant variations in length frequency distribution between sexes ($d = 0.357$, $p\text{-value} <$

0.001). The spurdog population examined in this study consisted of 347 immature individuals (210 females and 137 males) and 1163 mature individuals (163 females and 1000 males). The proportion of immature individuals fluctuated throughout time (**Figure 8a**), but they were generally more prevalent in the summer and fall, when they comprised around 25% of the sampled population (**Figure 8b**). For the immature component of the stock, the sex ratio in years tended to be biased towards females (**Figure 8c**), but in the mature population, the reverse trend was observed (**Figure 8d**), with a significantly larger abundance of males relatively to females. In addition to immatures sharks, adult females also appeared to exhibit some seasonality. These females were more likely to be caught in the spring and summer when they made up around 25% of the total population (**Figure 8e**).

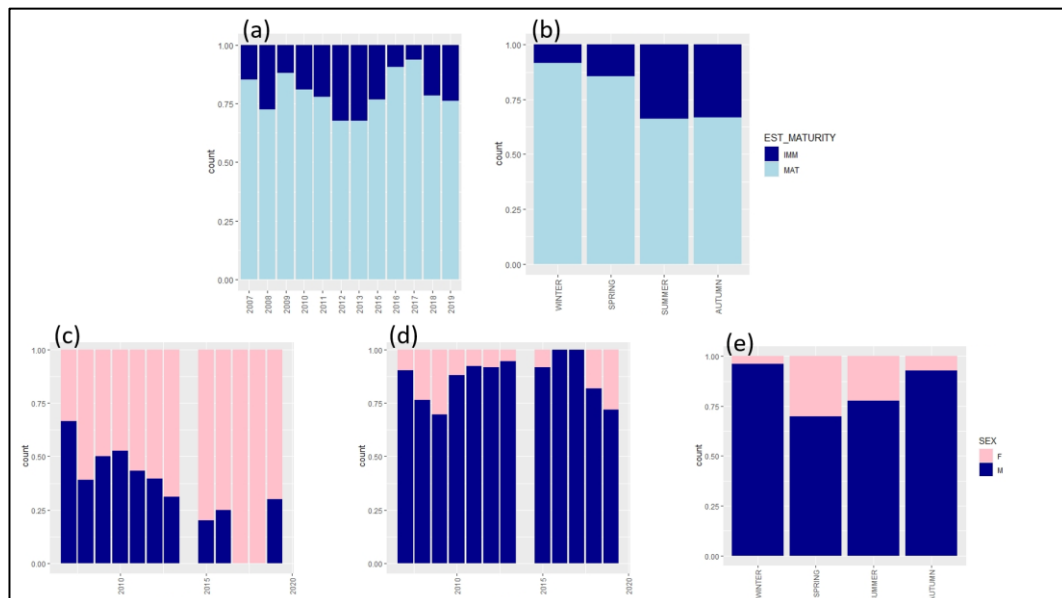


Figure 8: Representation of population composition through time and seasons. In the upper row, the proportions of adults to immatures are compared for each year (a) and for each season (b). The sex ratio in both the immature (c) and mature (d) sections of the stock is presented in the bottom row, split by years and, for adults, also by seasons (e).

Table 2 summarises the best fit GLM for environmental variables impacting adult male and female distribution. The chosen model did not take salinity and season into account as key factors. The model discovered a significant relationship between certain environmental factors and the chance of encountering an adult male or adult female. Females appeared to be more abundant when water temperatures were higher (20 - 25°C; **Figure 9a**), a situation prevalent in the Adriatic Sea from

late spring to early fall. Males, on the other hand, preferred colder water (about 10 - 15°C). Females seemed to be positively associated with water oxygenation, particularly when dissolved oxygen levels are above 280 mmol/m³ (**Figure 9b**).

Table 2: Summary of backward selection ranking the best fit GLM predictors on the sex distribution for *Squalus acanthias* in north and central Adriatic Sea (variables tested: latitude, depth, temperature, salinity, dissolved oxygen and season). Models are reported ranked by their AIC.

DROPPED VARIABLE	df	logLik	AIC	ΔAIC	weight	BIC	ΔBIC	weight
Salinity	8	-351.764	719.5	0	0.314	760.0	14.41	0.001
Season	6	-354.092	720.2	0.66	0.226	750.5	4.95	0.077
Salinity, Season	5	-355.145	720.3	0.76	0.215	745.6	0	0.922

When it comes to geographical distribution, adult females are more abundant at higher latitudes (**Figure 9c**) and further away from the shore (**Figure 9d**). As reported in **Figure 9e**, the greater quantity of adult females in the north during spring and summer, when waters are warmer, can be linked to the presence of breeding and nursery sites in the northern Adriatic Sea. This hypothesis is supported further when the distribution of juvenile spurdog between the ages of 0 and 5 years is investigated. These juveniles were indeed all mostly found in the northern Adriatic Sea (see appendix I for details and maps). Calculation of R² showed that 24.65% of variability in the data was explained by the selected model, which presented a total misclassification error rate equal to 10.15%.

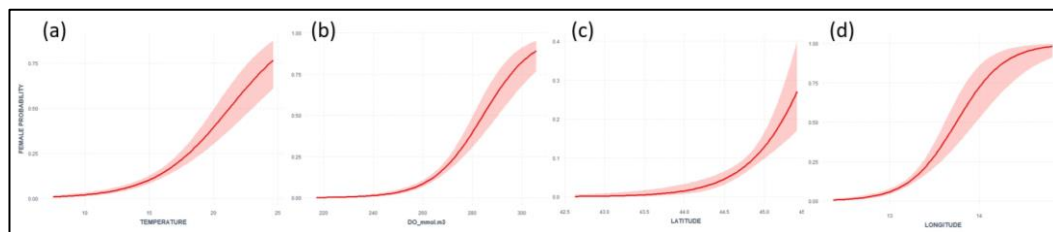


Figure 9: Model outcome on habitat preferences for adult males and females of *Squalus acanthias* in the Adriatic Sea. Each graph compares a distinct predictor on the x-axis (in order: temperature, dissolved oxygen, latitude and longitude) to the likelihood of observing an adult male (0) or an adult female (1). Model output is obtained by treating the target predictor as variable and the others as fixed to their mean. In general, all the significant environmental and spatial factors seem positively correlated with the probability of observing a female shark.

4.3. *SQUALUS ACANTHIAS* IN THE NORTHEAST ATLANTIC

Between 2006 and 2019, 64 fishing boats participated in the CRF, and 3029 of the 9028 gillnets caught spurdogs (33.5% of the total). The total biomass captured was 242 390 kg of spurdogs, which roughly equated to 89 743 animals. **Figure 10** depicts the geographical distribution of fishing effort and bycatch occurrences, as well as a comparison of the two fishing zones (Adriatic and Norwegian).

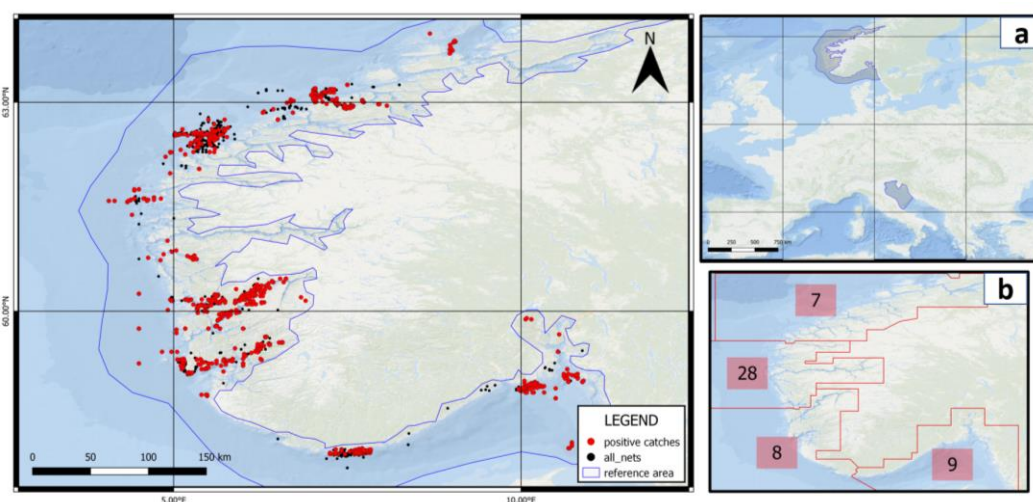


Figure 10: Distribution of nets and of bycatch events of *S. acanthias* in the southern Norwegian coast from 2006 to 2019. Norwegian fishing region (a) and the considered Norwegian statistical fishing areas (b) are also represented.

When the distribution of nets in space and season was examined, the fishing effort was found to be primarily centred in fishing area 7, which had more than twice the number of nets compared to the other regions (**Figure 11a**). Despite this, the majority of bycatch events occurred further south, in areas 28 and 8, where 30 to 50% of all deployed gillnets caught spurdog (**Figure 11b**). Gillnets were mostly deployed during the winter (2863) and spring (2510), with the summer having the fewest nets deployed (1667). This trend is also mirrored in the seasonal variation of bycatch proportion (**Figure 11c**).

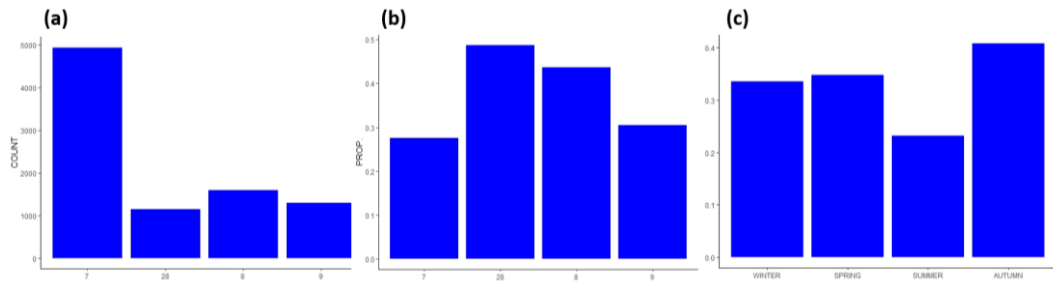


Figure 11: Barplot showing the total number of deployed gillnets (2006-2019) among the considered statistical areas (a), the proportion of bycatch events (0 to 1) among the different areas (b) and the proportion of bycatch events (0 to 1) among seasons (c).

Among all 64 vessels, 24 showed positive catch events for *S. acanthias* (37.5%). For each of these boats, **Table 3** summarizes the period when they were part of the CRF, the count of deployed nets and the count of positive nets. Asterisks are placed next to the vessels that performed the 4 highest bycatch events. In particular vessel “4354”, was by far the vessel presenting the highest overall numbers of bycatch with 893 positive nets out of 2415 nets in total, which was however also the highest number of nets. This corresponded to 37% of spurdog bycatch within its fishing area centred in the north (**Figure 12a**). When considering percentages, the highest proportions of spurdog bycatch were achieved by vessels “2191”, “9570” and “4346” with respectively 93%, 73% and 65% of positive nets. Despite its high bycatch percentage, vessel “2191” presented a low number of deployed nets (only 15) and it was part of the CRF for only one year. Different is the situation of “9570”, that presented 208 positive nets on a total of 248 deployed.

Table 3: Summary of the CRF fishing boats that between 2006-2019 recorded at least one gillnet positive for *S. acanthias*. In the table it is then reported the period each vessel took part into the CRF program, the number of nets deployed, the number of bycatch events occurred and the % of positive catch. * are placed next to the vessels that performed the 4 highest bycatch events.

VESSEL	PERIOD OF ACTIVITY	NUMBER OF YEARS	NUMBER OF NETS	NUMBER OF POSITIVE NETS	% POSITIVE CATCH
2191	2015	1	15	14	93.33
4344	2013	1	8	5	62.50
4875	2006	1	42	5	11.90
4349	2006 - 2007	2	95	40	42.11
4543	2007 - 2008	2	187	24	12.83
9258	2018 - 2019	2	124	48	38.71
9316	2016 - 2017	2	187	34	18.18
9528	2018 - 2019	2	54	22	40.74
9570	2018 - 2019	2	284	208	73.24
9701	2018 - 2019	2	82	43	52.44
3215	2013 / 2014 / 2019	3	150	32	21.33
3687	2006 - 2008	3	229	29	12.67
9379	2017 - 2019	3	108	5	4.63
1361	2009 - 2012	4	122	47	38.52
3487	2012 - 2015	4	85	12	14.12
4801	2008 - 2010 / 2012	4	88	56	63.63
4311	2006 - 2012	7	614	142	23.13
3488 *	2012 - 2019	8	678	395	58.26
4346 *	2010 - 2018	9	417	271	64.99
2668 *	2010 - 2019	10	1232	270	21.92
4299	2006 - 2015	10	538	209	38.85
4493	2006 - 2015	10	708	28	3.95
4542	2006 - 2015	10	565	197	34.87
4354 *	2006 - 2017	12	2415	893	36.98

Interestingly, in terms of species distribution, this shark proved to be significantly more abundant in statistical area 9 throughout the winter period (**Figure 11a**), rather than in northern regions, where bycatch looked to be more frequent during spring and summer. When patchiness was explored (**Figure 12b**), 50% of the total CPUE was shared by just 8.6% of all positive spurdog stations. In other words, the further north we go, the more frequently the spurdog appears to be caught by a gillnet, but the more difficult it gets to achieve a large capture.

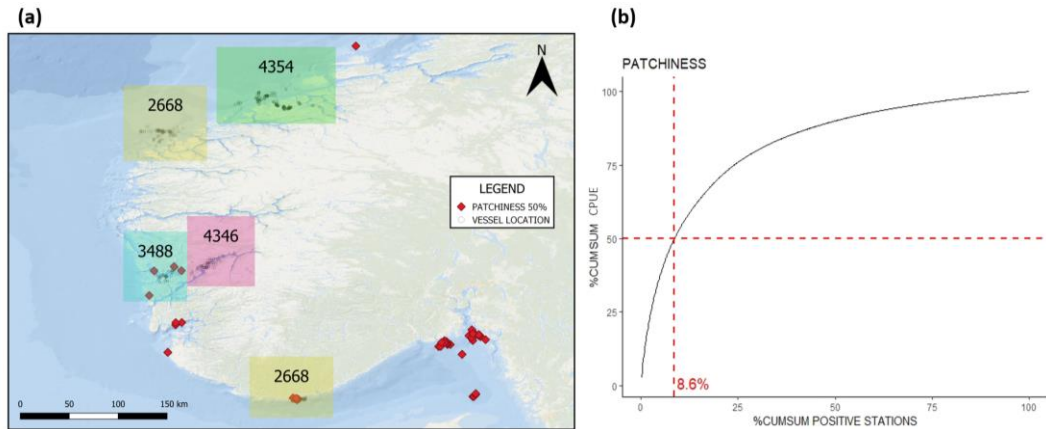


Figure 12: Map representing all areas with the highest abundance of spurdog (a). Red diamonds depict the stations accounting for the 8.6% of the CPUE reported in figure (b), while coloured squares indicate the fishing locations of the 4 vessels with the highest number of positive nets.

When modelling the distribution of the spurdog in southern Norway, no multicollinearity was observed (see Appendix I for more information), and WOE analysis revealed no uninformative variables or predictors with suspicious predictive power. In this sense, all temporal, geographical, and environmental factors were utilised in both models. When all sites were considered, the best fit ZI model resulted in the removal of the sequences of month, depth, salinity, temperature, and dissolved oxygen from the count section, and the sequences of months, longitude, and temperature from the zero section (**Table 4**). This model was able to explain 42.6% of the variance in the data ($R^2 = 0.426$). When only non-modified locations were modelled, the best fit model eliminated latitude, depth, salinity, temperature, and dissolved oxygen from the count part, whereas longitude, depth, temperature, salinity, and dissolved oxygen were removed from the zero section (Table 3). This second model described 66.7% of the observed variability ($R^2 = 0.667$).

Table 4: Summary of the two best fit Zero Inflated models and their predictors for *Squalus acanthias* CPUE (negative binomial distribution) in southern Norway (variables tested: latitude, longitude, depth, temperature, salinity, dissolved oxygen, season and time. The same starting variables were considered in both count and zero sections of the model)

MODEL	DROPPED VARIABLE IN COUNT PART	DROPPED VARIABLE IN ZERO PART	df	logLik	AIC	ΔAIC	weight	BIC	ΔBIC
All locations	Month, Depth, Salinity, Temperature and Oxygen	Months, Longitude and Temperature	15	-3370.68	6771.36	14.40	0.00013	6877.98	0
Non – modified locations	Latitude, Depth, Salinity, Temperature, and Oxygen	Longitude, Depth, Temperature, Salinity and Oxygen	13	-565.54	1157.07	22.07	1.66E-06	1237.84	0

Based on the results of both models, the NE Atlantic spurdog appears to be more numerous at higher longitudes (**Figures 13a** and **13d**) and in southern regions (**Figure 13b**), notably in the Skagerrak area. The larger concentration of patchiness at lower latitudes also supported this result. When only non-modified coordinates were considered, the model detected a decreasing abundance across time (**Figure 13c**), but this trend became statistically insignificant when all remaining locations were included. In terms of seasonality, the results of both models revealed a decrease in the number of spurdog in this region of the NE Atlantic during the warmer months (March – August). Indeed, the majority of the small but frequent captures occurred in northern areas throughout late spring and summer, whereas all large captures happened during the winter at lower latitudes. Surprisingly, no environmental element proved to have a significant influence on spurdog CPUE; only oxygen and salinity appeared to be positively related with the occurrence of an excessive zero in the model when all sites were included. Because this model used a lot of modified sites outside of fjords to extract environmental data, the outcome must be carefully interpreted.

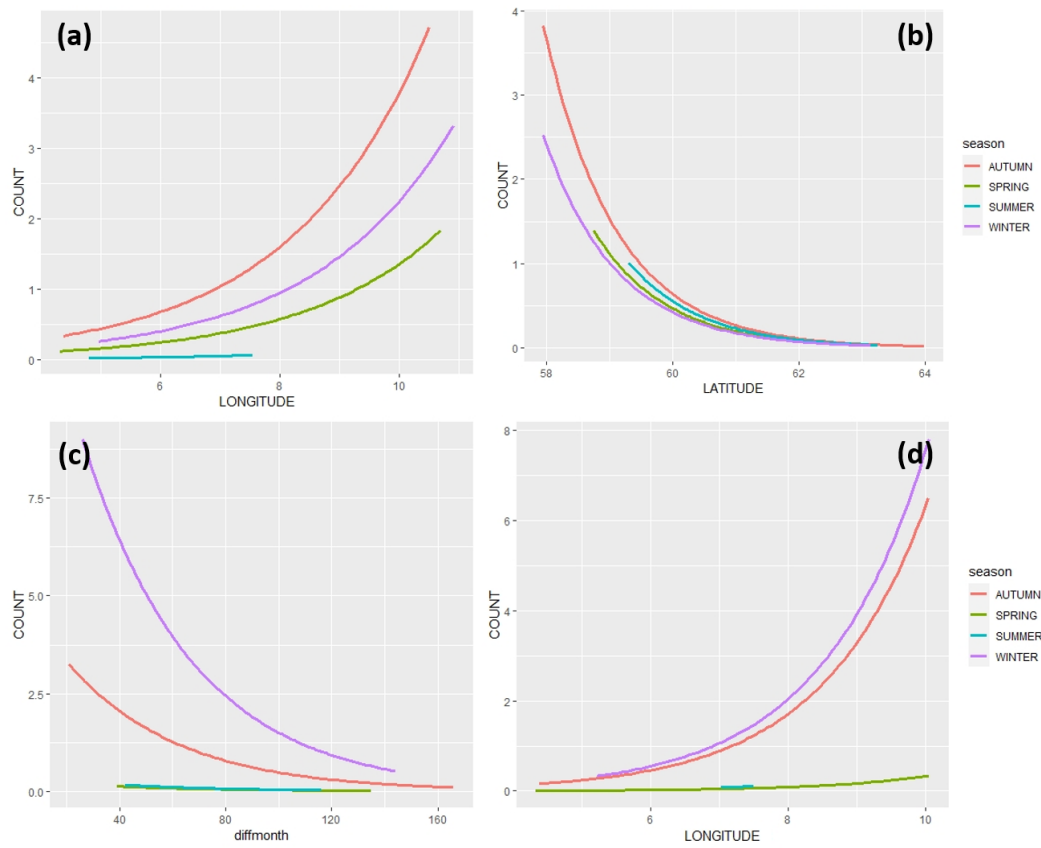


Figure 13: Count predictions for *Squalus acanthias* abundance in fjords and coastal waters of southern Norway obtained from all data (a, b) and from only non – modified locations (c, d). Each graph takes into account a distinct predictor on the x-axis and the CPUE as response. Each graph forecasts the number of sharks by treating the independent predictor as variable and the others as fixed to their mean.

5. DISCUSSION

This study offers a much-needed characterisation of spurdog spatial ecology in the heavily fished Adriatic Sea using fishery-dependent data and a combination of models and mapping approaches. Furthermore, the comparison with the considerably more researched NE Atlantic population, inhabiting coastal waters and fjords of southern Norway, allowed for the investigation of similarities and differences in this species use of space.

5.1. THE NORTHERN ADRIATIC: A MEDITERRANEAN HOTSPOT FOR SPURDOG

The results show that *S. acanthias* is prevalent throughout the year in the northern Adriatic Sea, particularly in the maritime area defined by 44.10°N to 45.25°N latitude and 12.50°E to 13.70°E longitude (**Figure 5**). The northern Adriatic is the most productive sea in the Mediterranean due to its climatic characteristics and nutrient input from river runoffs (Barausse et al., 2014; Bonanomi et al., 2018; Bonanomi et al., 2022). Favorable environmental conditions and prey availability might be two possible explanations why spurdog is so abundant in this location but scarce elsewhere in the Mediterranean basin (Serena et al., 2009). This is also congruent with the findings of MEDITS, a scientific trawl survey programme that has been running in the Mediterranean Sea since 1994, which revealed that the northern Adriatic has the highest density of spurdogs, with an average density of 116 kg/km² (Serena et al., 2009).

When environmental factors impacting spurdog distribution were examined, the observed elevated collinearity between salinity and depth can be explained by the Adriatic Sea's maritime characteristics. Both depth and salinity do, in fact, tend to rise when moving from the west to the east. For what concerns depth, while the western (Italian) coast is smooth, sandy, and regular, with no islands and a moderate shelf; the eastern (Croatian) coast is high, rocky, with a very irregular bottom and deep waters (Fonda Umani et al., 1996). Salinity can range from almost zero at the mouth of the Po Delta to around 38.4 PSU in open seas (Cushman et al., 2001). This

diminishing east-west salinity gradient is connected to freshwater discharge from rivers flowing in northern Italy (Marini et al., 2008), and this affects the distribution of numerous marine species inhabiting northern Adriatic regions (Coll et al., 2009). The influence of river freshwater inflow is so significant that the western half of the northern Adriatic Shelf is considered as a dilution basin for the whole Mediterranean Sea (Raicich et al., 1996). Spurdog is one of the species impacted by this salinity gradient, and the model in fact showed a larger number of individuals in the central part of north Adriatic, where salinity is approximately 38 PSU, significantly higher than along the shores and river mouths. Temperature and dissolved oxygen, in addition to depth and salinity, were shown to have a considerable influence on spurdog abundance. This shark appears to prefer higher temperatures and higher oxygen concentrations, two conditions commonly observed on the northern Adriatic Shelf, but which can vary significantly on a daily basis depending on weather and river runoff (Marini et al., 2008; Barausse et al., 2009).

5.2. SPURDOG IN THE DEEPER WATERS OF THE NORTHERN NE ATLANTIC

In contrast to Adriatic conditions, only two of the tested explanatory environmental variables potentially impacting spurdog distribution in southern Norway were determined to be significant: latitude and longitude. When latitude was taken into account, the model discovered greater spurdog abundance in the southern coastal area, a location that, like the northern Adriatic Shelf, is characterised by considerable primary productivity, resulting in important trophic food chains (Artioli et al., 2008). Aside from southern Norway, two additional regions at similar latitudes are characterised by high spurdog abundances: one on the southern Swedish coast and one in north of Scotland (Stenberg et al., 2005). The high abundance of individuals in these places is due to gregarious behaviour, which is typical in *S. acanthias* (Finucci et al., 2018).

The model output revealed that greater abundances of this species were found in fjords and, more particularly, in locations east of 9.00°E of longitude. It is unclear how and why fjord environments are so crucial for this species, however Hjertenes et al. (1980) reported that spurdogs inhabiting Norwegian fjords are isolated from the rest of the NE Atlantic population and appear to perform seasonal migrations inside and outside these peculiar habitats. Temperature, in particular, proved to have a significant impact on the ecology and distribution of fish groups in fjord ecosystems (Shepherd et al., 2002). During the cold season, for example, the stagnation of water in the upper basin creates a different thermal environment than that of adjacent water bodies (Edwards et al., 1977), establishing a thermal niche that spurdog may use during winter. Furthermore, fluctuations in oxygen and salinity recently reported (Aksnes et al., 2019) and ascribed to climate change may influence spurdog habitat preferences and, as consequence, its future distribution in fjords.

Unlike the shallow Adriatic waters, Norwegian fjords and coastal regions have large depth variability (from a few metres to more than 400m), and gillnets were deployed at all depth intervals where spurdog is usually found. The fact that the model did not find this predictor significant is intriguing and might be interpreted in two ways: either no depth preference is demonstrated from this data or sex-specific depth preferences, if existent, were masked by merging and analysing both sexes together. Not only was depth omitted from both models, but so were all of the other examined environmental factors. In this context, another plausible cause might be linked to the nonlinear relationship that exists between each environmental predictor and the CPUE. If this is the case, the zero-inflated GLM cannot discover any link, meaning that all of the specified predictors are considered insignificant and then removed. On the other hand, previous research in other parts of the NE Atlantic has revealed a significant effect of environmental conditions, particularly temperature, on spurdog distribution (Daan et al., 2005; Thorburn et al., 2015; Jac et al., 2022). All of these studies revealed a preference for shallower, warmer waters where the temperature stays between 10°C and 11°C. It is interesting to note that this temperature range is totally different from that described in the Adriatic, where

larger spurdog abundances appear to occur at temperatures over 15°C throughout the year.

5.3. SEASONALITY AND MIGRATIONS

For the Adriatic, the model not only identified significant environmental parameters influencing spurdog distribution, but also demonstrated an increase in the number of individuals throughout the spring and summer months, when water temperatures can exceed 25°C. The monthly temperature maximum occurs in August, especially along the coast, when wind force is reduced, and a significant stratification of the water column forms. During the winter months, however, vertical homogeneity of temperature and salinity throughout the entire water column occurs (Cushman et al., 2001), and a significant reduction in spurdog abundance is observed, particularly with respect to adult females (**Figure 8b**), which almost disappear from the northern and central Adriatic. This persistent presence of males and lack of females during fall and winter suggests that females may migrate into and out of the studied area on a seasonal basis (Gracan et al., 2015).

Migrations have already been documented for this species in earlier studies (Gracan et al., 2020; Templeman et al., 1976; McFarlane et al., 2003; Serena et al., 2009), but no research has been conducted in the Adriatic Sea. The seasonality of females suggests that the northern Adriatic Shelf in particular might be used for reproductive and parturition purposes. When examining the distribution of spurdogs between the ages of 0 and 5 years indeed (see Appendix I), a hotspot of juvenile abundance is found in this area. Furthermore, the GLM output confirmed female spurdog's preference for warmer waters and greater oxygen levels (**Figure 9a** and **9b**), circumstances that occur mostly between April and September in the northern Adriatic Sea (Fonda Umani et al., 1996). All of these findings are consistent with the observations of Bargione et al., 2019 who discovered pregnant females with nearly full-term embryos in this same area between late spring and summer. During this period indeed temperatures are higher and melting ice from the Alps increases runoff of the Po and adjacent rivers, which bring more oxygen and nutrients to the northern Adriatic (Marini et al., 2008; Raicich et al., 1996).

Spurdog females, even in other zones, tend to actively look for similar environmental conditions (IUCN 2020; Dell'Apa et al., 2017) because such habitats can maximise embryo development rates (Sagarese et al., 2014). Based on the findings of this study, it is possible to hypothesize that, while male population is randomly distributed across the Adriatic Sea throughout the year, mature females cluster in northern locations of the Italian side during warmer months to reproduce and give birth. Then, in the fall and winter, they may migrate to the eastern parts, closer to the Croatian coast, where the waters are deeper and can provide a refuge from the temperature drops typical of the shallow north-west Adriatic. (Gracan et al., 2015; Fonda Umani et al., 1996).

Some degree of seasonality was also detected in spurdog population inhabiting fjords and coastal waters of southern Norway. During the spring and summer, for example, low bycatch of a few individuals was observed at lower latitudes and frequent bycatch of a few individuals at higher latitudes. On the other hand, large captures of spurdog were common during fall and winter months in fishing areas 8 and 9 which are included in ICES subareas 4a and 3a. This peculiar pattern in bycatch might imply that migratory activities are taking place in at least a part of the population. Previous study in the ICES area indicated that this species has a complicated migratory pattern. Norwegian and British tagging programmes on individuals captured in the northern North Sea in the 1950s and 1960s discovered, for instance, that the areas north of Scotland were primarily inhabited by the spurdog population during the summer, and that there was an extensive migration to the Norwegian coast during the late autumn and winter (Aasen et al., 1960; Holden et al., 1962). This larger abundance of animals throughout the winter also corresponds with the reproductive season, which, unlike in the Adriatic Sea, is reported to occur between December and February in the NE Atlantic (Stenberg et al., 2005; Jones et al., 2001). Furthermore, according to additional research by Albert et al., 2019, female-dominated captures are mostly seen in these southern locations during the winter, with male-dominated catches happening the rest of the year. In this sense, it is possible that *S. acanthias* may utilise coastal regions of Norwegian fishing areas 8 and 9, as breeding and nursery grounds. However, the lack of accurate data regarding the magnitude and frequency of spurdog migrations

in both the NE Atlantic and the Adriatic Sea, as well as the uncertainties around the location of nursery grounds precludes spatial management for this species.

The findings of this study revealed that the diverse oceanographic and environmental variables that characterise Norwegian and Adriatic maritime environments influenced spurdog seasonality and distribution in very distinct ways. Females migrate to southern Norway in the NE Atlantic mostly throughout the winter months to breed and give birth, whereas females move and reproduce in the Adriatic Sea in late spring and summer. This difference in seasonality between the two locations might be attributed to the long isolation that characterized the Adriatic population. In fact, even though the Adriatic spurdog directly derives from the NE Atlantic population (Verissimo et al., 2010), the distance, the geographic isolation, and the restricted gene flow from the Atlantic population might have profoundly impacted spurdog ecology in the Adriatic Sea, affecting its genetics, seasonality, and habitat preferences. This speculation is supported by Gracan et al., 2020, who detected 12 distinct haplotypes in the mitochondrial DNA of the Adriatic spurdog, suggesting that this population should be considered isolated.

5.4. TEMPORAL CHANGES

Throughout the entire study period in the Adriatic Sea, the model showed a significant decline in spurdog abundance over time, particularly in the north. The same pattern was also reported for other elasmobranch species such as the smooth hound (*Mustelus spp.*), the small spotted catshark (*Scyliorhinus canicula*), the nursehound (*S. stellaris*), the thornback ray (*Raja clavata*) and the Mediterranean starry ray (*R. asterias*), which inhabit northern Adriatic waters and are considered bycatch, similar to spurdog (Barausse et al., 2014; Bonanomi et al., 2018). The main cause of this reduction in landings and CPOA might be attributed to overexploitation of marine resources associated with extensive fishing operations taking place in the small, landlocked region of the northern Adriatic Shelf (Barausse et al., 2014). This overfishing effect is also confirmed when comparing the sex ratio in immature and adult populations (**Figure 8c** and **8d**). While the sex ratio among immature individuals is around 1:1, the adult population was found to

be significantly skewed toward males, with very low occurrence of females between 2010 and 2017. If on one side the skewed sex ratio is partly due to seasonality in females, which disappear from the study area during colder months, on the other side their lower abundance compared to males also throughout spring and summer must be linked to other variables as well. Females are easier to catch than males because they are bigger and, in this sense, their rarity is likely also the result of fishing operations conducted in past decades when market demand for large adult females was particularly high (Large et al., 2008). This imbalance in adult sex ratio (Stevens et al., 2000) is known to lead to low recruitment and reproductive potential (Prince et al., 2005), which likely resulted in the observed decrease of population abundance.

Despite the fact that bycatch has been identified as the primary cause, there may be additional and less investigated reasons contributing to spurdog reduction in the Adriatic Sea. One example is the capture and subsequent depletion of small pelagic fish, which are the principal food of spurdog (Gracan et al., 2017). The main targets of pelagic and midwater trawl fisheries in the Adriatic Sea are anchovies (*Engraulis encrasicolus*) and sardines (*Sardina pilchardus*) (Bonanomi et al., 2018), and it has been shown that the spurdog diet (particularly that of adults) is nearly entirely composed of these two teleost species (Jusufovski et al., 2010; Gracan et al., 2017). However, heavy fishing pressure on anchovies and sardines has resulted in considerable decreases in landings since the 1980s (Azzali et al., 2002; Santojanni et al., 2003), severely influencing the foraging success of *S. acanthias*, increasing its vulnerability and contributing to the abundance reduction outlined by the model.

Climate change is another key element that may be promoting spurdog reduction in combination with fishing pressure (Barausse et al., 2014). Regardless of the fact that the Adriatic is considered a temperate warm sea because the bottom layers are generally always over 10°C (Marini et al., 2008), hydroclimatic time-series suggest a warming environment with considerable fluctuations in yearly temperature and atmospheric precipitations (Giani et al., 2012). In this sense, the spurdog's vulnerability might be indirectly related to habitat changes that resulted from the Po River's recent low water discharge, which was caused by a decrease in rainfalls (Coll et al., 2009). Po is of critical importance for Adriatic ecosystem and the

change in precipitation and in Po River flow impacted the natural conditions and productivity of this habitat utilised as a nursery ground by the spurdog, increasing the fragility of this shark and decreasing its abundance. Runoff from the Po River has also been connected to anchovy landings, and the reduced freshwater intake into the Adriatic Sea (Revelante et al., 1977; Santojanni et al., 2006; Coll et al., 2009) contributed to the fall in anchovy abundance, reducing the major food supply for adult spurdogs.

Furthermore, the Adriatic Sea is significantly impacted by two main winds that pass across its waters: the Bora and Sirocco (Marini et al., 2008). Bora is a katabatic wind that blows from November to March, bringing cold continental air from the northeast. This wind causes coastal upwelling along the eastern coast, and intense bora episodes (up to 50 m/s) cause significant heat loss in the northern Adriatic and the creation of the so-called Northern Adriatic Deep Water (NAdDW). Sirocco, on the other hand, is a warm, humid breeze that sweeps across the whole Adriatic Sea in fall and winter, occasionally producing flooding events in the shallow lagoons along the western shore (Marini et al., 2008). It can be speculated that strong fluctuations in the incidence and severity of these winds as a result of climate change might cause unexpected anomalies in water temperature, salinity, dissolved oxygen, and nutrient content, hence influencing spurdog ecology, seasonality, and abundance.

Completely different is the situation in southern Norway, where the model that considered all bycatch data did not find any significant temporal trend in spurdog abundance. After decades of overfishing, the NE Atlantic population size touched a historic low in the early 2000s, causing stricter management measures to be implemented, and the population has since been rebuilding (ICES WGEF 2021). The main steps made to ensure its preservation were the introduction of a 100 cm maximum landing length in EU waters in 2009, a 90% reduction in the TAC in 2010, and the setting of the TAC to zero starting in 2011 as the last step, and in Norway, the catch prohibition in 2007 (Albert et al., 2019). Spurdog in the NE Atlantic had been less exploited as a result of these initiatives. Similar laws specifically designed for this species are instead very scarce in the heavily exploited Adriatic Sea and monitoring programmes assessing the impact of sharks' bycatch

in this area are just in their early stages of development (Bonanomi et al., 2018). It is plausible to believe that the implementation of stringent species-specific conservation measures in the NE Atlantic was the prime reason explaining why the model on NE Atlantic spurdog and that of Adriatic indicated two opposing temporal trends in population abundances. Obviously, the NE Atlantic population covers a considerably larger range than just the Norwegian fishing areas 7, 8, 9, and 28 (Dobby et al., 2005), therefore extending the study with data from other regions would be useful to determine whether the temporal abundance of this population is consistent.

In addition to management and rebuilding plans, modifications in water temperature linked to climate change appear to have contributed to the NE Atlantic spurdog's recovery and maintenance. In their model simulations, Kjesbu et al., 2021 did in fact demonstrate an increasing sea surface temperature, particularly in the North, the Barents, and the Norwegian Seas. While cold-temperate species are approaching the top limit of their temperature adaptation, resulting in continued decline and local extinction, there are populations that are well-adapted to temperatures exceeding those generally experienced (Barcelo et al., 2016; Gullestad et al., 2020). One of these populations include the spurdog which was assessed to have extended its distributions towards the northeast and to potentially become more abundant in the future.

5.5. DATA AND METHODOLOGICAL LIMITATIONS

Both Adriatic and Norwegian data are fisheries dependent, hence caution must be exercised when interpreting results, since both data have significant limitations. To begin, fishing places are not chosen at random, but all vessels prefer to conduct their operations in areas where there is a known higher concentration of target species. As a result, a complete representation of the whole research region is not feasible, as evidenced by the distribution of fishing operations on Adriatic and Norwegian maps (**Figure 3** and **10**). Second, all the considered fishing vessels were of different dimension, had different engine powers and not always technical data on fishing gear was reported and available for standardization, thus forcing the

estimation of the missing data. Third, since fishing operations did not occur during the entire day, it was not possible to analyse if spurdog undergoes daily vertical migrations following its preys and the changes in abiotic conditions as observed in other studies (Carlson et al., 2014; Sulikowski et al., 2010; Thorburn et al., 2015). Depth is indeed a crucial factor to take into account: in both areas the average depth was considered (between 10 – 125m in Adriatic Sea and between 12.5 – 440m in southern Norway). While in southern Norway, the measured depths roughly correlate to the depth ranges of *S. acanthias* (Jones et al., 2001; Jac et al., 2022); in the Adriatic Sea, paired pelagic trawlers tend to fish mostly in the first layers of the water columns, leaving deeper layers with minimal to no coverage, especially in the central Adriatic where seafloor can reach depths higher than 200m. Finally, depending on the applied fishing technique, spurdog catchability changes. It's important to remember that all individuals referred in this study are only a portion of the entire bycatch. More specifically, to allow for comparisons, the author selected in both areas only the fishing technique responsible for the highest spurdog bycatch, which was trawl in the Adriatic Sea and gillnets for the coastal fishery in the south of Norway.

Different types of model-based techniques exist in spatial ecology today, and the type of model used has implications for the interpretability of results and the efficiency of analysis (Warton et al., 2015). The adoption of GLM (Nelder et al., 1972) was justified in this study for two reasons: the response variable does not have a normal distribution, and the interactions between predictors and responses are nonlinear, making a standard linear model incapable of dealing with such data (McCullagh et al., 1983). In GLM, the response variable does not have to be normally distributed, but it must be from an exponential family (e.g., binomial, Poisson, multinomial, normal). Furthermore, even though the underlying relationship between the predictors and the response could be nonlinear, this advanced statistical modelling method allows for the construction of linear correlations (Zuur et al., 2009). This is accomplished by employing a link function, which connects the response variable to a linear model (Wood et al., 2006). In other words, the original response variable does not need to be linearly dependent on the

independent variables, but the transformed response variable, as a result of the link function, must be (McCullagh et al., 1983; Ziegel et al., 2002).

While GLM are simple to interpret and can handle a variety of response/target distributions, they do have some significant limitations: they cannot directly identify nonlinearity, they are sensitive to outliers, predictor variables must be uncorrelated, and they often have low predictive power (Ziegel et al., 2002). Most of the constraints described above were detected in the fishery-dependent data used in this study, thus, partially affecting the interpretability of the results. The existence of these limitations can be confirmed further by examining the different R^2 found in the two models generated for the NE Atlantic. While the model based only on coastal sites explained 66.7% of the observed variability, the model based on both coastal and fjord locations had an R^2 lower than 43%. This considerable decrease in model explanatory power is most likely due to strong nonlinear correlations between the selected predictors and the abundance of spurdogs in fjords. Future study on this species might use more complicated modelling tools to strengthen the robustness of the results. Generalized Addictive Models (GAMs) and Generalized Linear Mixed Effect Models (GLMMs) are two methodologies that might be explored.

GAMs are an extension of linear models that consist of a GLM with a linear predictor comprising a sum of smooth functions of covariates (Wood et al., 2006). When there are potential nonlinear correlations between several predictors and the response variable, their usage is warranted (Hastie et al., 1986). Nonlinearities are common features in ecology that underpin fundamental phenomena such as the effects of temperature on species distribution and growth (Brett et al., 1971), the effects of prey abundance on predation rates (Holling et al., 1965), and the effects of population density on population growth (Ricker et al., 1954). Nonlinearities are important in species and ecosystems management because they identify goals or strategies where management actions may be disproportionately helpful. GLMMs instead, also known as hierarchical or multilevel generalised linear models, are another extension of GLMs in which the linear predictor adds random effects in addition to the normal fixed effects (Zuur et al., 2009). Such models are especially useful when the data is clustered in some way (Zuur et al., 2009), and a classic

example of clustering in fishery-dependent data regards catches, which are typically nested in boats. With GLMMs, the differences among the groups are investigated and modelled as a random effect.

5.6. FORECASTS OF SPURDOG FISHERY

A new reality for spurdog fishery is emerging with new east European countries that recently entered the market, increasing the demand for this shark. Among them are Poland, Czech Republic, Bulgaria, Romania, Russia, and all Baltic countries from Lithuania to Estonia, which are now playing the role of main importers of spurdog products (Dell'Apa et al., 2013). In the next future, this eastern European market demand might also result in the development of new spurdog fisheries in countries and coastal areas that do not present a strict regulation for the sustainable management of this resource (Dell'Apa et al., 2015). Populations present in the Black Sea, in Africa, in south America and in Asia are not protected by any EU or Norwegian regulation or TAC regulation and an increase in spurdog exploitation could negatively affect the conservation status of this species (Dell'Apa et al., 2013; Dell'Apa et al., 2015). Even before any laws are enacted, it is critical to determine which linkages exist between this shark and the specific environmental factors existing in the aforementioned new fishing zones. In this sense, the findings of this study could be utilised as a template for future research in these locations, assisting in the establishment of conservation measures for this shark and the peculiar ecosystems it inhabits.

6. CONCLUSIONS

The study aims to give crucial information for understanding the distribution of *S. acanthias* in the intensively exploited Adriatic Sea, as well as the potential geographical, environmental, and temporal forces affecting its dispersal. This knowledge is critical for detecting spatio-temporal changes in spurdog populations as a result of major stressors such as fishing, habitat loss, or climate change (Espinoza et al., 2020). Despite all the limitations previously discussed, landings data collected from commercial fisheries offered a unique opportunity to document the general spatial and temporal patterns in the distribution of this shark of conservation concern. Latitude, depth, temperature, salinity, and dissolved oxygen were found to be significant drivers affecting its distribution in the Adriatic Sea, and the northern Adriatic Shelf was revealed to be a hotspot for spurdog concentration, particularly for mature females that migrate in these shallow, warm waters to reproduce during the warmer months. The modelling technique utilised in this study explained much of the variability found in the data and overcame the challenge provided by an excess of zero observations, showing to be a helpful tool that might be used to extend the investigations of spurdog distribution to other, less studied, fishing locations. The findings of this study can be used to inform species-focused approaches to fisheries management and to guide long-term monitoring programmes (Espinoza et al., 2016; Williams et al., 2018).

When the Adriatic results were compared to what was found in the population inhabiting the fjords and coastal waters of southern Norway, significant differences in the spatial ecology and seasonality were discovered. While in the Adriatic Sea modelling analysis revealed the presence of multiple environmental drivers affecting spurdog distribution, in coastal waters and fjords of southern Norway, only latitude and longitude appeared to have an impact. Not only were the environmental drivers different in the NE Atlantic population, but so was the seasonality, with significant concentrations of this shark at lower latitudes, especially during late autumn and winter when the mating season should begin. Furthermore, the existence of spurdog-specific measures in the NE Atlantic was at the heart of this species' recovery and of the documented long-term abundance

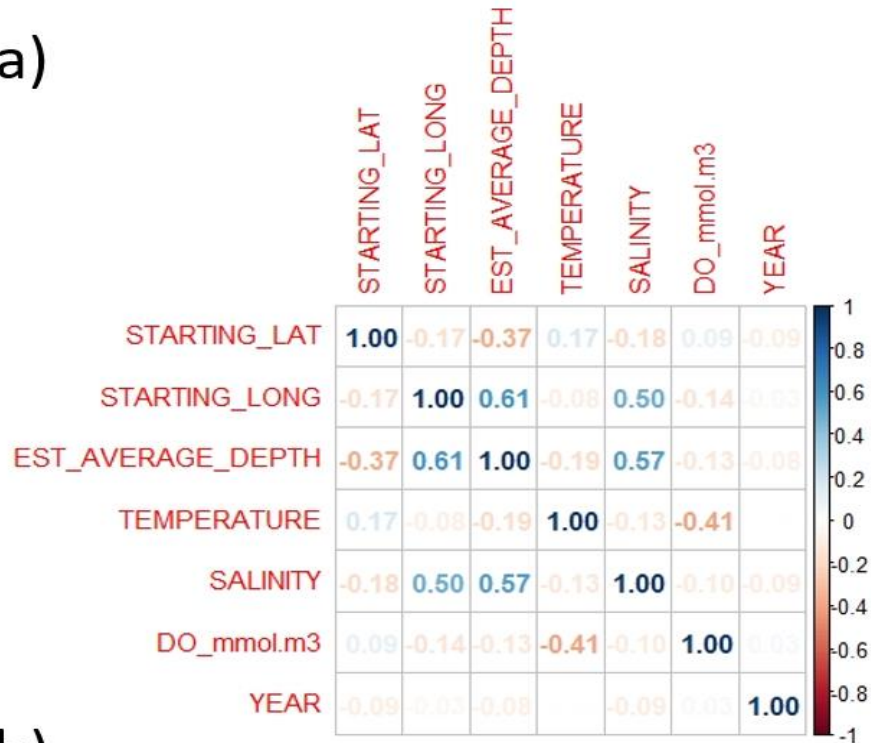
maintenance. Similar conservation actions are urgently needed in the Adriatic Sea, where spurdog abundances are decreasing significantly and continuously. Future research should be conducted in both the Adriatic Sea and the NE Atlantic Ocean to identify the links between spurdog nursery regions and the adult populations to which the juveniles later recruit, that are usually inferred based on geographical location. Understanding this link is critical for fisheries management because, when populations are exploited more intensively, juveniles tend to form a large and somewhat unpredictable part of the harvest. Furthermore, knowledge of the relative abundance of young fish is frequently the greatest indicator of population status (e.g., breeding success). All of this demonstrates that effective management is dependent on prior knowledge on the spatial ecology of the different maturity stages within a species.

7. SUPPLEMENTARY MATERIALS

7.1. APPENDIX I

Figure A1: tables reporting for each pair of considered variables in the Adriatic Sea: the calculated non-parametric Mann-Kendall test for multicollinearity (a), and the corresponding p-value (b).

(a)



(b)

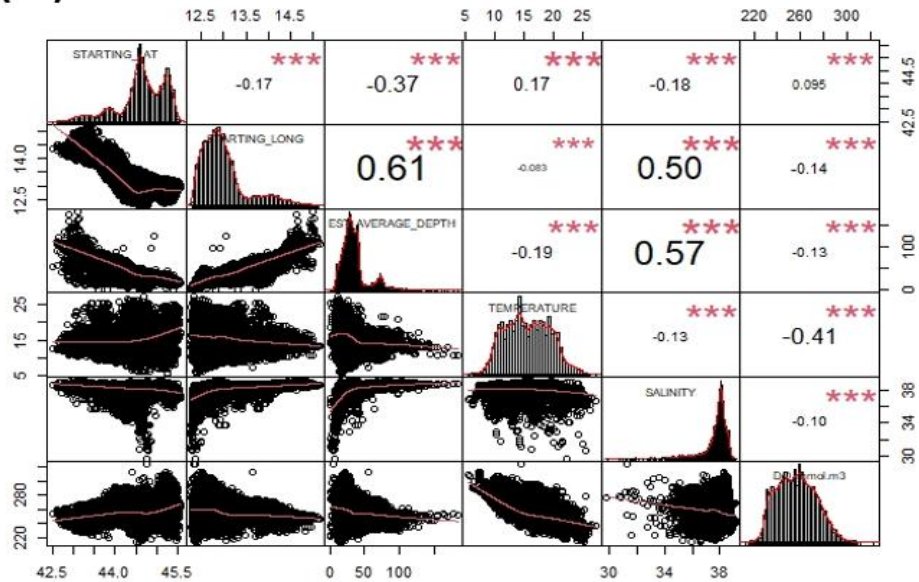


Figure A2: maps reporting point occurrences of immature sharks in the Adriatic Sea at various ages.

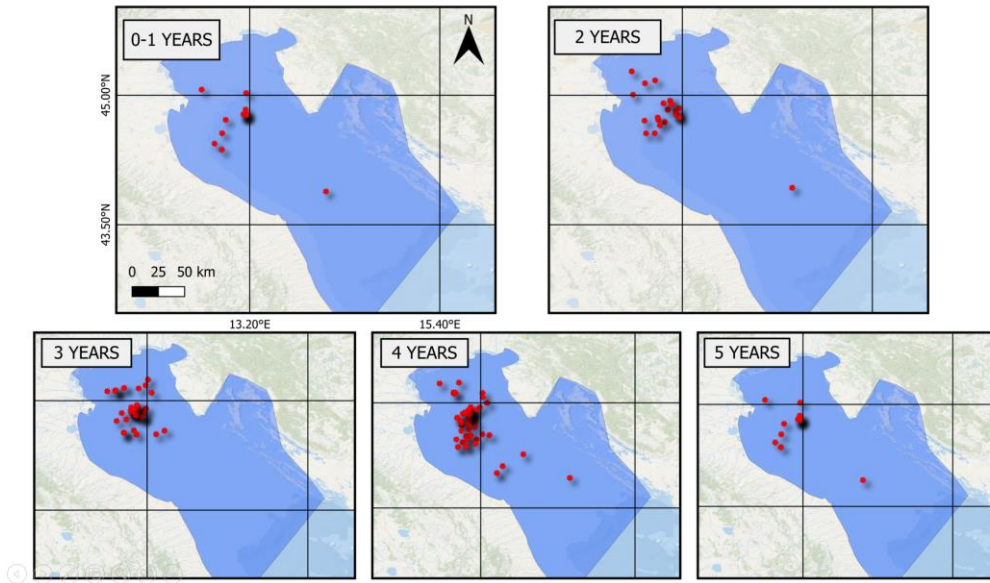


Figure A3: map showing the new coordinates (red stars) assigned to gillnets (black triangles) deployed out of Copernicus reading grid. These new points were used to extract environmental data.

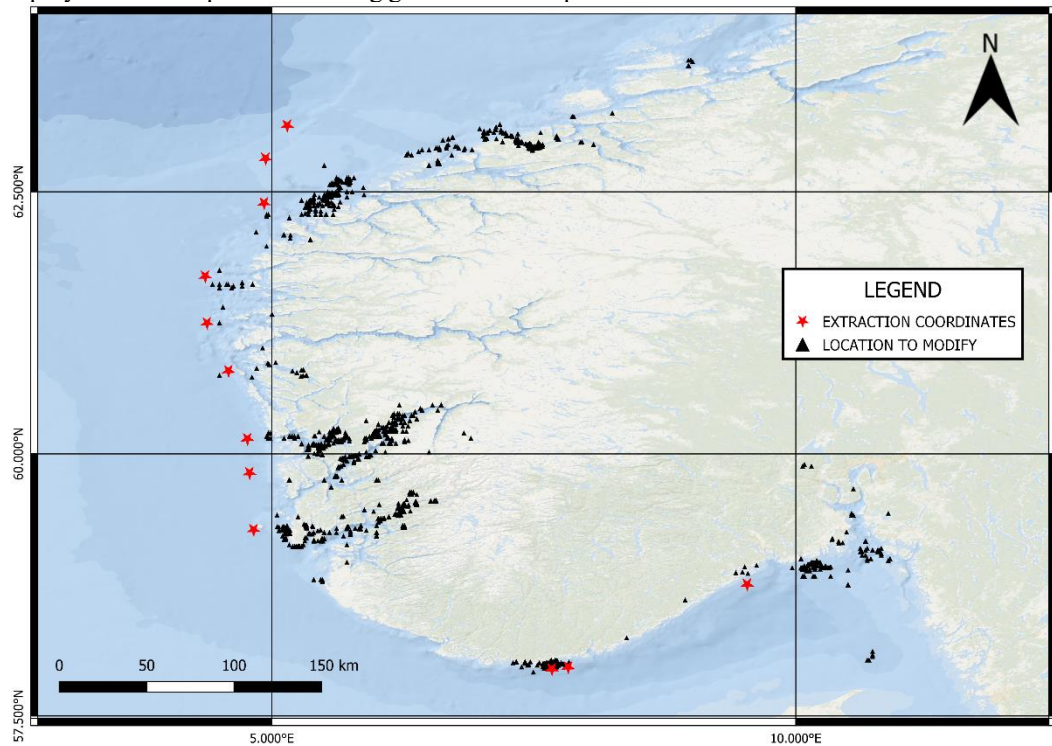


Figure A4: graph representing the relationship between bycatch occurrence and vessels operating in the Adriatic Sea. Orange bars indicate the total number of bycatch events reported by each fishing vessel. On the other hand, the black line indicates for each vessel the percentage of hauls positive for spurdog.

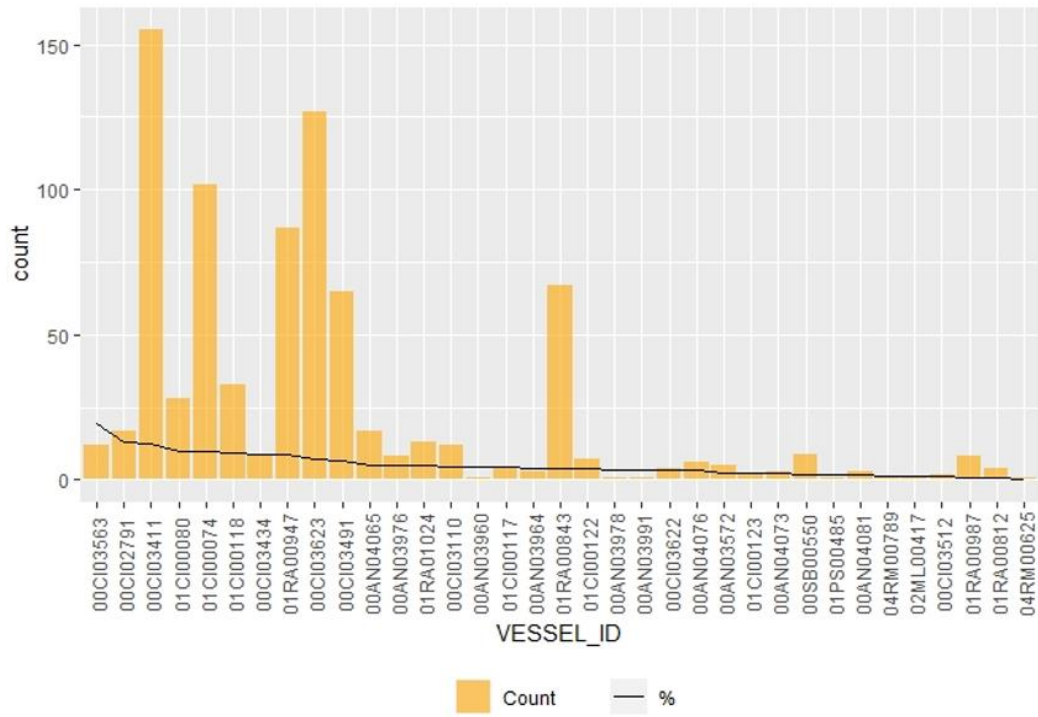
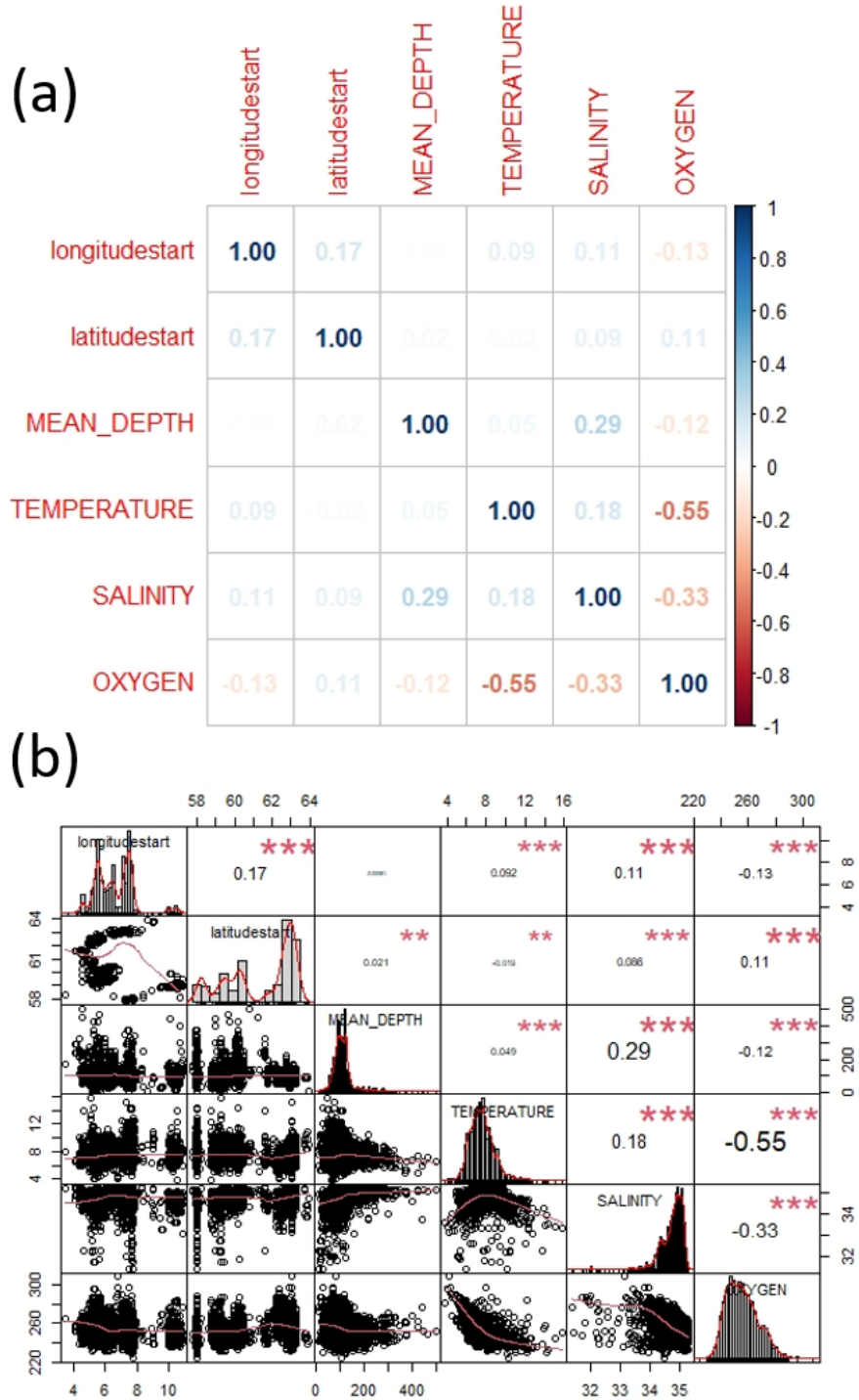


Figure A5: tables reporting for each pair of considered variables in southern Norway: the calculated non-parametric Mann-Kendall test for multicollinearity (a), and the corresponding p-value (b).



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