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Identifying the Genetic Population Structure Knowledge Gaps Hindering an Improved Management of the Spurdog (*Squalus acanthias*) stock in the Northeast Atlantic: A Systematic Review

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Abstract

Despite its long history of exploitation, there is limited information about the spurdog. Therefore, it is important to identify which general and genetic information is available for the species and what is missing to resolve stock structure and advice future management schemes. The goal of this study was to identify the knowledge gaps, in terms of genetic population structure and diversity, which could inform an improved fisheries management for the spurdog in the Northeast Atlantic Ocean and Mediterranean Sea. To achieve this, a systematic review and a series of phylogenetic analyses using the NADH2 marker were done. Results from the review showed there is very limited general information about the species in the study regions, with only 38 documents found out of over 6000 hits. Only 3 studies were found concerning its genetic structure and diversity, with high diversity found for all studies but no genetic differentiation, except for the subpopulation in the Adriatic Sea. No genetic structure was found for the species in the Northeast Atlantic, but fine structuring was found for the Mediterranean Sea, indicating different stocks. The phylogenetic trees showed complex taxonomical relationships within the *Squalus* genus and no clear formation of monophyletic clades according to the location in which the samples were taken for sequences of *S. acanthias*. Major conclusions indicate the need for collecting more information, particularly with less invasive methods, given the zero TAC in the areas and the limitations of fisheries surveys, as well as more sampling efforts in regions different from Norway, the United Kingdom, and the Adriatic Sea. Furthermore, given that the phylogenetic analysis of the species with the NADH2 marker was inconclusive, the use of more efficient genetic markers, such as microsatellites or single nucleotide polymorphisms, is recommended for identifying fine genetic structuring in the populations.

Key words: spurdog, Northeast Atlantic Ocean, Mediterranean Sea, genetic structure and diversity, systematic review, phylogenetic analysis, fisheries management

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GLOSSARY

Allele- One of two or more versions of DNA sequence at a given genomic location (National Human Genome Research Institute, 2022a).

Aplacental viviparity- Type of reproduction in which eggs are fertilized and hatched inside the mother but the embryos lack a connection to the oviduct or uterus and, therefore, they do not feed from the mother but from the egg yolk (Fishbase, 2022b).

Capture-mark-recapture models- Animal survey method in which the count statistics is the total number of animals caught, and the associated detection probability is the probability of capture. The method involves capturing a number of animals, marking them, releasing them back into the population, recapturing them, and then determining the ratio of marked to unmarked animals in the population. This method is often used to estimate population size (Eastern Ecological Science Center, 2018).

Chromosome- Threadlike structures made of protein and a single molecule of DNA that serve to carry the genomic information from cell to cell (National Human Genome Research Institute, 2022b).

Cryptic species- Phenotypically highly similar species with pronounced genetic divergence (Struck & Cerca, 2019).

Demersal- Refers to a species which inhabits the column of water close to the bottom.

DNA replication- Process by which the genome's DNA is copied in cells (National Human Genome Research Institute, 2022c).

DNA- Abbreviation of deoxyribonucleic acid. Organic chemical of complex molecular structure that is found in all prokaryotic and eukaryotic cells, coding the genetic information for the transmission of inherited traits (Britannica, 2022).

Exploitation rate- In fisheries, the exploitation rate is the proportion of the numbers or biomass removed by fishing (United Nations Economic and Social Commission for Western Asia, 2022).

Fisheries management- The integrated process of information gathering, analysis, planning, consultation, decision-making, allocation of resources and formulation and implementation, with necessary law enforcement to ensure environmental compliance, of regulations or rules which govern fisheries activities to ensure the continued productivity of the resources and the accomplishment of other fisheries objectives (FAO, 1997).

Fixation index (F_{ST})- Measure of population differentiation due to genetic structure. It is frequently estimated from genetic polymorphism data, such as single-nucleotide polymorphisms or microsatellites (Holsinger & Weir, 2009).

Food security- The UN defines it as: “Food security exists when all people at all times have physical and economic access to sufficient, safe food for an adequate diet that meets their nutritional needs and preferences, and which form the basis for an active and healthy life” (Regjeringen, 2015).

Founder effect- Refers to the reduction in genomic variability that occurs when a small group of individuals become separated from a larger population. Over time, the resulting new subpopulation will have genotypes and physical traits resembling the initial small, separated group, and these may be very different from the original larger population (National Human Genome Research Institute, 2022d).

Gene flow- Movement of genes into or out of a population (Andrews, 2010).

Gene frequency- Relative frequency of an allele (variant of a gene) at a particular locus in a population (Gillespie, 2004).

Genetic drift- Describes random fluctuations in the numbers of gene variants in a population (Nature Education, 2022).

Genetic markers- DNA sequence with a known physical location on a chromosome (National Human Genome Research Institute, 2022e).

Genetics- The study of heredity and gene action (Duke University, 2022).

Genome- Complete set of genetic material in an organism (Nature Education, 2014).

Genomics- Interdisciplinary field of biology focusing on the structure, function, evolution, mapping, and editing of genomes (WHO, 2022).

Genotype- Complete set of genetic material in an organism. The term can also be used to describe the scoring of the type of variant present at a given location (locus) in the genome (National Human Genome Research Institute, 2022f).

ICES- International Council for the Exploration of the Sea. It is an intergovernmental marine science organization dedicated to advance and share scientific understanding of marine ecosystems and the services they provide. This knowledge is used to generate state-of-the-art advice for meeting conservation, management, and sustainability goals. ICES is conformed by nearly 6000 scientists from over 700 marine institutes in their 20 member countries, and their work is focused on the Atlantic Ocean, although it extends to the Mediterranean Sea, the Arctic, the Black Sea, and the North Pacific Ocean (ICES, no year).

Inbreeding index (F_{IS}): Index used to measure the proportion by which the heterozygosity of an individual is reduced by inbreeding. This index served as the base for Wright's F statistics, in which the fixation index is included (Crow, 2007).

Maximum likelihood- Statistical method for estimating the parameters of an assumed probability distribution given some observed data (Hendry & Nielsen, 2007).

Maximum sustainable yield (MSY)- Represents the highest possible annual catch that can be sustained over time, by keeping the stock at the level producing maximum growth. It refers to a hypothetical equilibrium state between the exploited population and the fishing activity (WWF, 2011). For bodies such as ICES, MSY is defined as the largest average catch or yield that can continuously be taken from a stock under existing environmental conditions (ICES, 2012).

Microsatellites- Short sequences of nucleotides that are tandemly repeated (Verma & Singh, 2020).

Mortality- Refers to a parameter used in population dynamics to account for the loss of individuals in a population. In fisheries, total mortality is the sum of both natural mortality and fishing mortality (Mannini *et al.*, 2020).

Otoliths- Calcium carbonate structure present in the inner ear, responsible for the perception of linear acceleration; in most bony fish, these structures can be used to estimate the age of the individual (NOAA Fisheries, 2022).

Outgroup- Refers to a distantly related group of organisms which serve as a reference group when determining the evolutionary relationships of the ingroup (the set of organisms under study) (Farris, 1982).

Panmictic populations- Refers to panmixia, random mating in a population (Cardon & Palmer, 2003).

Phylogenetic tree- Diagrams representing evolutionary relationships of organisms (McLennan, 2010).

Population bottleneck- Event that drastically reduces the size of a population. It produces a decrease in the gene pool of the population because many alleles that were present in the original population are lost. The remaining population after one of these events faces a higher level of genetic drift. Due to the loss of genetic variation, the new population can become genetically distinct from the original (Nature Education, 2022b).

Rebound rate- Refers to the demographic measure of a fish population's productivity that sustains a given mortality. It is directly related to a species' resiliency, and it is useful for the understanding of the status of exploited populations (Au *et al.*, 2015).

Single nucleotide polymorphisms (SNPs)- Most common type of genetic variation among organisms. Represent a difference in a single nucleotide (MedlinePlus, 2022).

Spawning ground- Geographic area where shedding and fertilization of eggs take place (Fishbase, 2022). In the particular case of elasmobranchs, a spawning ground refers to the area in which oviposition (for egg-laying elasmobranchs) and/or parturition (for live-bearing species) occurs (Ellis *et al.*, 2012).

Spawning stock biomass- An indicator of the status of the stock and its reproductive capacity. It can be defined as the combined weight of all individuals in a fish stock that have reached sexual maturity and are capable of reproducing (International Seafood Sustainability Foundation, 2022).

Stock assessment- The process of collecting, analyzing, and reporting demographic information to determine changes in the abundance of fishery stocks in response to fishing and, to the extent possible, predict future trends of stock abundance (NOAA Fisheries, 2012).

Stock structure- Arises because of deviations from random mating in a population; involves the emergence of systematic differences in allele frequencies, which as a result form subpopulations with a defined genetic structure. It is usually the result of physical barriers to dispersal, gene flow, founder effects, population bottlenecks, etc. (Ovenden *et al.*, 2013).

Tamura-Nei substitution model- The Tamura-Nei model corrects for multiple hits, taking into account the differences in substitution rate between nucleotides and the inequality of nucleotide frequencies. It distinguishes between transitional substitution rates between purines and transversional substitution rates between pyrimidines, while assuming an equality of substitution rates among sites (MEGA Software, no year).

Taxonomy- In biology, it is the scientific study of naming, defining, and classifying groups of biological organisms based on shared characteristics (Judd *et al.*, 2007).

Telemetry- In situ collection of measurements or other data at remote points and their automatic transmission to receiving equipment for the monitoring of wildlife species (Hay, 2012).

Top-down forces- In trophic ecology, top-down forces means that the species occupying the highest trophic level apply controlling influences over the species at a lower trophic level (Lynam *et al.*, 2017).

Trophic network- A set of interconnected food chains within an ecosystem (Université de Liège, 2014).

1 Introduction

1.1 A Background on Shark Fisheries Management

1.1.1 The status of sharks in fisheries

Sharks are commercially valuable for several products such as their fins, meat, liver oil, and jaws, while at the same time they represent an important source of food security for coastal communities (Stevens *et al.*, 2005). The rising demand and price of their products, particularly in the Asian market, and the decline of other valuable fisheries (FAO, 2020), caused an increase on their catch and retention during the last four decades (Clarke *et al.*, 2006). This increase, coupled with their inherent vulnerability to overfishing due to their relatively slow growth and reproductive rates, resulted in the progressive depletion of populations around the world (Worm *et al.*, 2013). Consequently, one-third of the global species of sharks are now threatened with extinction (Dulvy *et al.*, 2021). Additionally, the total annual mortality of these animals is estimated to be 97 million individuals per year (range: 63-273 million) (Worm *et al.*, 2013; Baker-Médard & Faber, 2020), with European fisheries accounting for approximately 15% of said value (Hareide *et al.*, 2007). Finally, exploitation rates for sharks as a group exceed by at least 2.5% the rebound rate for many of their populations, explaining their constant decline (Worm *et al.*, 2013).

1.1.2 Shark fisheries management and its importance

Ecologically, sharks play key roles in maintaining the functionality and productivity of ocean ecosystems by exerting strong top-down forces in the trophic networks in which they participate (Ferretti *et al.*, 2010). This has the ability to regulate the growth of other species, keep the habitats healthy, and shape marine communities at a variable temporal and spatial scale (Ferretti *et al.*, 2010; Heupel *et al.*, 2014; Booth *et al.*, 2019). As a marine resource, these animals amass over 1 billion USD per year, considering fisheries, trade, and tourism (Cisneros-Montemayor *et al.*, 2013; Dent & Clarke, 2015). Socially, sharks contribute towards the food security and well-being of several coastal communities, and in some cases, they even form an important part of their cultural identity (Leeney & Poncelet, 2015; Glaus *et al.*, 2019; Hari *et al.*, 2021). Despite their importance, sharks remain undermanaged, given the limited political and economic incentives for better management, as well as insufficient data and policy complexity (Barker & Schluessel, 2005; Dulvy *et al.*, 2017; Booth *et al.*, 2019). Multi-lateral/international agreements (e.g., Convention on International Trade in Endangered Species of Wild Fauna and Flora

CITES) and international bodies (e.g., Regional Fisheries Management Organizations RFMOs), together with robust fisheries management from hyper-developed nations and regions (e.g., Australia, New Zealand, USA, Northeast Atlantic) have improved both the catching and trade of these species, aiding towards their conservation (Booth *et al.*, 2019; ICES, 2020; Walls & Dulvy, 2021). However, fisheries in many lower-income nations, which contribute to most of the global shark production, remain poorly managed, and consequently, sharks keep getting overfished in most parts of the world (Davidson *et al.*, 2016; Simpfendorfer & Dulvy, 2017; Booth *et al.*, 2019).

1.1.3 Fundamental units of fisheries management

Fisheries management comprises two key units: the biological unit (BU) and the management unit (MU). On one hand, the BU (also called production unit) is represented by the stock. This term is often switched indiscriminately with the term population, which is why it is important to define them and recognize their differences. In this context, a population refers to a “group of fish of one species which shares common ecological and genetic features” (ICES, 2012), while a stock can be defined as “part of a fish population with a particular migration pattern, specific spawning grounds, and subject to a distinct fishery; it is assumed stocks are somewhat self-contained, meaning very little emigration or immigration from or to the stock occurs” (Cochrane, 2002). Therefore, in simpler terms, a stock comprises a sub-population, and not often do they check all the boxes to constitute a population, particularly when talking about marine species (Booke, 1999). Consequentially, both terms should not be confused, and stock should be used in the context of fisheries management. On the other hand, the MU (also called operational unit) does not have a set definition, with it being usually context-dependent according to a nation’s or body’s interests or management purposes. Frequently, it can refer to the set of fishing fleets exploiting a common pool of fish (Uriarte *et al.*, 2014), specific delimited areas destined for fishing (Reiss *et al.*, 2009; Kerr *et al.*, 2014), management bodies in charge of regulating fishing activities (Tubman *et al.*, 2021), amongst others.

The stock and MU concepts have been central to the management of marine living resources since its earliest days. However, a search throughout the literature available has shown them to be quite elusive, with their definition depending on the discipline or body dealing with them (Pita *et al.*, 2016). An example of this variability can be seen when comparing the definitions for stock according to the Common Fisheries Policy (CFP), which regulates fisheries in the

European Union (EU): “a stock is a marine biological resource that occurs in a given management area” (Article 4.14, E.U., 2013), versus the one given by the International Council for the Exploration of the Sea (ICES), which operates in the same area: “a part of a fish population usually with a particular migration pattern, specific spawning grounds, and subject to a distinct fishery” (Cochrane, 2002; ICES, 2012). Another example, but referred to the MU, can be seen through the comparison of working regions established by ICES and the OSPAR Commission, as seen in Figure 1, in which, although working in the same area, do not coincide.

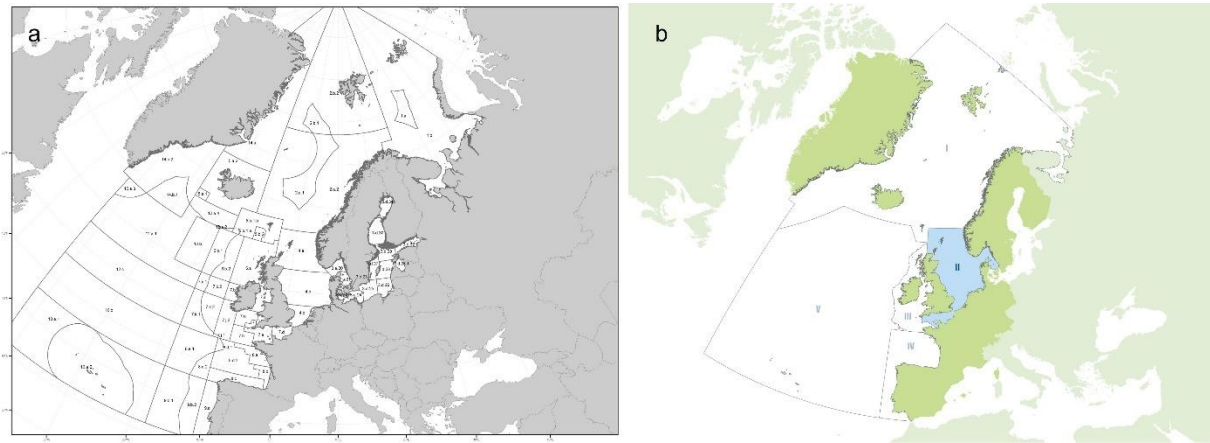


Figure 1. Comparison of MUs between ICES (a; ICES, 2016) and OSPAR Commission (b; OSPAR Commission, 2022a)

Discrepancies between the definition and delineation of both BUs and MUs can lead to issues preventing the correct fulfillment of management plans, which in turn can cause overexploitation or sub-exploitation. Therefore, now it is encouraged to establish these two through a multidisciplinary and collaborative approach, accommodating major disciplines such as those related to biology (genetics, parasitology, ecology), oceanography (physics, hydrography, microchemistry, geographic information systems, and remote sensing), and management (economics, politics, assessments) (Pita *et al.*, 2016).

1.2 The Use of Genetics to Delineate Stocks and Advise Shark Fisheries Management

1.2.1 Genetic tools to advise fisheries management

Rapid advances in the fields of genetics have provided the opportunity to integrate the results from several analyses into fisheries management schemes, supplying additional information that was hardly obtained by traditional methods (e.g., stock assessments) (Reiss *et al.*, 2009;

Doyle *et al.*, 2017). The following collection represents the most common uses of genetics within the fisheries management context. Since most of them are not the main focus of the present work, they will be briefly explained based on Ovenden *et al.* (2013), with the exception of stock structure and diversity, which will be explained later on.

- Species identification, product provenance, and fisheries surveillance: Using DNA analysis, a species can be assigned to a particular specimen, provided that the species has been taxonomically described and regions of its DNA have been characterized. It is particularly useful for specimens whose characteristics impede the traditional taxonomical identification (e.g., fish that have already been processed and filleted), species whose morphological characters are poorly defined, and cryptic species (Ovenden *et al.*, 2013). Additionally, this identification can aid towards the enforcement of accurate labeling of seafood, especially when illegal substitution from a more valuable product towards a less valuable one is highly common in some markets (Rasmussen *et al.*, 2009; Aranceta-Garza *et al.*, 2011; Ovenden *et al.*, 2013)
- Resolving mixed-stock fisheries through population genetics: It is often that two or more different stocks overlap in the same fishing area. Mixed-stock analysis quantifies the contribution of these different stocks in a fishery. Genetics can resolve this issue by comparing baseline gene frequencies from the component stocks, which are collected through the description of the genetic stock structure of the species. Simulations are then run to determine whether there is enough genetic differentiation between the stocks, and if there is, individuals are genotyped, and relative proportions of each component stock are estimated (Ovenden *et al.*, 2013)
- Age estimations: Although growth and age estimates in fish can be obtained by counting growth rings in otoliths, scales or vertebrae, some groups such as crustaceans and mollusks do not possess structures to carry on with the estimations. In these cases, telomeric DNA has proven to be useful to estimate age. Telomeres protect chromosomes against physical damage and buffer the ends of chromosomes against shortening, which happens during each cycle of DNA replication. The shortening process is related to the number of cell replications, with this process being proportional to the age of the tissue. As long as the rate in which telomeric DNA shortens with age is known, it is possible to estimate this parameter (Ovenden *et al.*, 2013)

- Ecosystem monitoring: The applications of genetics towards ecosystem monitoring include dietary analysis for food web construction, detecting the impact from stressors on the ecosystem, and monitoring evolutionary effects of climate change on harvested species. The first one involves simple DNA-barcoding from gut and fecal samples to construct food webs without the need of morphological analyses. The second one deals with monitoring responses towards stressors at a genomic level in harvested species, recognizing how these affect at a cellular and molecular level. Additionally, it allows to monitor environmental quality and predict potential risks to the fishery with the introduction of new environmental stressors (Snape *et al.*, 2004; Cossins & Crawford, 2005). Finally, by tracking genetic variants through time, evolutionary change can be detected, which in turn can help identifying the capacity of species to adapt genetically to selective forces introduced by climate change (Nielsen *et al.*, 2009; Ovenden *et al.*, 2013)
- Estimating harvest rates and abundance: Harvest rates and abundance can be estimated via gene-tagging. This process involves collecting samples from organisms (e.g., biopsies, feces, skin) and assaying variable DNA markers such as microsatellites. Given the variability of these markers, with repeat sampling, genotypes function as unique identifiers. Afterwards, this technique can be paired with conventional capture-mark-recapture modelling (CRM) to estimate said parameters (Saillant *et al.*, 2009; Harrison *et al.*, 2012; Ovenden *et al.*, 2013)

1.2.2 Achieving pressing management goals with genetics

While the different stocks in the Northeast Atlantic Ocean and Mediterranean Sea are managed by an array of bodies and policies (e.g., national management plans, the Common Fisheries Policy of the European Union; advised by ICES, OSPAR), they all have the common goal of preserving species and maintain the stocks above levels that can produce the maximum sustainable yield (MSY) (Casey *et al.*, 2016; Directorate of Fisheries Norway, 2017; ICES, 2021; Government of Iceland, 2022; OSPAR, 2022b). To attain this, fundamental information needed to advice fisheries management in the area include knowledge of stock status and the associated exploitation rates (Casey *et al.*, 2016). This is by no means an easy task, given the number of stocks and variable management units present in the area (Reiss *et al.*, 2009; Pita *et al.*, 2013; Milano *et al.*, 2014; Casey *et al.*, 2016; Jardim *et al.*, 2016). However, the outcome from genetic analyses can help provide information on both stock status and exploitation rates.

First, by identifying stock structure and diversity, stock delineation and the resolution of mismatches between the BU and the MU can be achieved. At the same time, this can provide answers to the conflicts brought up by mixed-stock fisheries, by estimating the percentage each stock contributes to the fishery. With the prior resolved, a second priority is to use this information as a baseline to then estimate harvest rates and abundance via gene-tagging and CRM models (Ovenden *et al.*, 2013; Bravington *et al.*, 2016; Casey *et al.*, 2016). By working on these two priorities, the results can be used to calculate levels of exploitation corresponding to the MSY and aid towards achieving the common management goals for the areas.

1.2.3 Genetic population structure and its aid towards stock delineation

As mentioned in the previous section, one of the first priorities concerning the use of genetic analyses to aid fisheries management schemes involves determining genetic population structure and diversity of commercially important species, to then advise towards stock delineation (Casey *et al.*, 2016). Before elaborating more on how these two concepts aid towards fisheries management, it is important to define and explain them.

Within a species, variations in a DNA sequence can be found between individuals, giving way to genetic polymorphisms, which in turn generate what is called genetic diversity (Ellegren & Galtier, 2016). Genetic population structure arises because of deviations from random mating in a population. When a population is panmictic, allele frequencies are expected to be roughly the same between groups or individuals. However, if the groups reproduce in a non-randomly way, systematic differences in allele frequencies appear, subpopulations are formed, and a genetic structure ('genetic differentiation', 'genetic stratification') emerges. This structuring, also called stratification, can be the product of physical barriers to dispersal between groups of one species, gene flow brought by migrations, founder effects, population bottlenecks, amongst others (see Glossary for definitions of these concepts), which impede random mating (Cardon & Palmer, 2003; Waples & Gaggiotti, 2006; Ovenden *et al.*, 2013), allowing the genetic differentiation of groups within a species.

Genetic structure and diversity can be measured using genetic markers. Nowadays, the most prominent ones are simple sequence repeats or microsatellites and single-nucleotide polymorphisms (SNPs) (Tsykun *et al.*, 2017). Sample sizes often vary depending on the marker employed and the type of analysis. For example, SNPs give good results with small sample

sizes (6-8 is enough) and give accurate genetic estimates when a large number of SNPs are used (Nazareno *et al.*, 2017), while microsatellites require a larger sample size (20-30) (Pruett & Winker, 2008). Studies such as profile testing require few individuals (8-10), while stock delineation requires between 25-30 individuals per location (Foster *et al.*, 2021). Therefore, a careful design of the sampling must be created to obtain accurate results. Following the sampling process of the alleged subpopulations, genetic diversity is characterized and then tested to see whether it is distributed randomly with respect to the group boundaries or throughout the region of investigation. Where genetic structure is found, it is a strong indication of limits to dispersal, and this result is usually accepted as an accurate basis for delineating different stocks (Carvalho & Hauser, 1994; Ovenden *et al.*, 2013). The importance of stock delineation relies on the fact that different stocks may possess different characteristics when it comes to population dynamics and demography, which may render them less or more susceptible to overexploitation (Ying *et al.*, 2011).

Finally, it is important to mention that the outcome of genetic structure analyses can be used to make recommendations towards management schemes and may be implemented if these findings are demographically significant within the context of a particular management objective (Palsbøll *et al.*, 2007; Lowe & Allendorf 2010; Ovenden *et al.*, 2013).

1.3 The Spurdog (*Squalus acanthias*) and its Status in the Northeast Atlantic

1.3.1 Biological characteristics

The spurdog, also called spiny or piked dogfish, is a small demersal shark belonging to the Squalidae family. It has an antitropical worldwide distribution, ranging from Northern Norway and all the way to Morocco, including the Mediterranean and Black Seas, in the Northeast Atlantic (Compagno, 1984). It occurs throughout the water column along the continental shelf, and while it has been recorded to depths of 900 m, it is most common between 10-200 m (McEachran & Branstetter, 1986). The maximum total lengths reported for the Northeast Atlantic are approximately 83 cm and 128 cm for males and females respectively, with a maximum lifespan of around 40 years for the species (Vince, 1991). In terms of reproduction, the species is aplacentally viviparous, giving birth to live young which depend on yolk reserves during their embryonic development; females typically mature between 69-77 cm, while males mature around 55-64 cm (ICES WGEF, 2021). Uterine fecundity is said to increase with their

size, ranging between 1-19 pups normally, although there are records of 1-32 pups, while the gestation period is said to last nearly two years (22-24 months), and the size at birth averages 24 cm (Hisaw & Albert, 1947; Holden & Meadows, 1964; Gauld, 1979; Albert *et al.*, 2019; ICES WGEF, 2021). It is an opportunistic feeder with a wide range of pelagic prey: herring (*Clupea harengus*), sprat (*Sprattus sprattus*), small gadoids (family Gadidae), sandeel (*Ammodytes marinus*), mackerels (*Scomber scombrus*), crustaceans, squid and ctenophores (Ellis *et al.*, 1996). As of now, it is considered the spurdog represents one unique stock throughout its whole distribution in the Northeast Atlantic (ICES WGEF, 2021).

1.3.2 Spurdog fisheries and its status in the Northeast Atlantic

Spurdog has had a long history of exploitation in the North Sea and adjacent areas (Pawson *et al.*, 2009), with it being once one of the most frequently caught sharks in the area. Major fishing nations included France, United Kingdom, and Norway. Historically, its landings peaked in the 1950s/1960s, from which the stock was reduced gradually until restrictive management was introduced in the mid-2000s, given that the biomass of the stock was estimated to be 20% of the virgin stock (Albert *et al.*, 2019; ICES WGEF, 2021). Since then, no directed fishery has targeted the stock and a total allowable catch (TAC) of 0 is still in effect for all EU regulated areas (ICES WGEF, 2021), although in 2016 a small TAC of 270 t was introduced for Union and international waters of subareas 1, 5-8, 10, and 12 (ICES WGEF, 2021). Nationally, Norway allows a limited fishery for small coastal vessels, as well as bycatch, which should not exceed 15% of total landings on a half-calendar year basis. Additionally, live specimens are to be released, whereas dead ones must be landed, and the minimum landing size in this country is 70 cm (ICES WGEF, 2021). In Sweden, fishing for spurdog with nets and longlines is forbidden; trawl fisheries must have a minimum mesh size of 120 mm, and the species may only be taken as bycatch. Additionally, when using hand-held gear, only one spurdog can be retained in a lapse of 24 hours (ICES WGEF, 2021). Finally, many of the mixed fisheries in the North Sea, West of Scotland, and the Irish Sea, where catching of spurdog was abundant, are subject to effort restrictions through the cod long-term plan (ICES WGEF, 2021). According to the latest assessment by ICES, the stock has not been overfished since 2005 and it is on an increasing path, with current estimates putting the spurdog stock at 24% of the virgin stock (Albert *et al.*, 2019; ICES WGEF, 2021).

1.4 Rationale of this Study

Despite its long history of exploitation in the area and its status as a vulnerable species (IUCN, 2019), there is limited information about the species in the Northeast Atlantic Ocean and Mediterranean Sea, particularly about its genetic population structure and diversity, which hinders management efforts (Albert *et al.*, 2019). With the slow increase of its population, it is projected that a directed fishery upon the spurdog might be reinstated once again in the areas. Therefore, it is important to identify (1) which genetic information is available for fisheries management purposes (Rodrigues-Domingues *et al.*, 2018), and (2) what is so far missing in order to resolve the stock structure and the level of genetic diversity of this species in the areas to advice future management schemes.

2 Objectives

2.1 General

Identify the knowledge gaps, in terms of genetic population structure and diversity, which could inform an improved fisheries management for the spurdog (*Squalus acanthias*) in the Northeast Atlantic Ocean and Mediterranean Sea, through a systematic review, to provide a baseline in which future studies could focus to achieve a sustainable harvest of this species.

2.2 Specific

- Identify the available information regarding the spurdog and its stock in the Northeast Atlantic Ocean and Mediterranean Sea, through a systematic review.
- Identify the available information concerning the spurdog's and similar species' genetic population structure and diversity in the Northeast Atlantic Ocean and Mediterranean Sea, through a systematic review.
- Based on the information obtained from the review, analyze published sequences from the most promising genetic marker(s) of the spurdog and build a phylogenetic tree to inform about current genetic structure of the species.
- Determine which additional information regarding the spurdog's population genetics is needed to inform fisheries management of the species in the areas.

3 Method

3.1 Systematic Review

A systematic review concerning the information available for the spurdog and its stock in the Northeast Atlantic Ocean and Mediterranean Sea was performed. This review consisted of peer-reviewed journal articles, official research reports from governmental and non-governmental agencies, and a few doctoral theses, dating up to April 2022 (Parton *et al.*, 2019). Google Scholar was the primary search engine used to perform this review. The search strings used for the review were as follow: 1a. (“squalus acanthias”) AND (“Northeast Atlantic” OR “North East Atlantic” OR “North-East Atlantic”); 2a. (“spurdog”) AND (“Northeast Atlantic” OR “North East Atlantic” OR “North-East Atlantic”); 3a. (“piked dogfish”) AND (“Northeast Atlantic” OR “North East Atlantic” OR “North-East Atlantic”); 4a. (“squalus acanthias”) AND (“Mediterranean Sea”); 5a. (“spurdog”) AND (“Mediterranean Sea”); 6a. (“piked dogfish”) AND (“Mediterranean Sea”). After the search, an initial screening of the title, abstract, and key words was done to exclude non-relevant items based on whether the topic researched matched this study’s goals or not, if it was mainly focused on the species of interest, and whether it pertained the area of study. Afterwards, the remaining items were read in completion, and a second exclusion was performed (eligibility step) for those that were not relevant for this study. Finally, data from the remaining items was extracted and considered in the synthesis, including citation information, research topic, type of data, location of the study, and main conclusions (Dudgeon, 2012).

A second systematic review concerning the information available for the genetic population structure and diversity of the spurdog and other members of the Squalidae family in the Northeast Atlantic Ocean and Mediterranean Sea was performed. The search engine, process, and exclusion criteria used were the same as for the first review, with the search strings for this case being as follow: 1b. (“squalus acanthias”) AND (“genetic structure”); 2b. (“spurdog”) AND (“genetic structure”); 3b. (“piked dogfish”) AND (“genetic structure”); 4b. (“squalus acanthias”) AND (“genetic diversity”); 5b. (“spurdog”) AND (“genetic diversity”); 6b. (“piked dogfish”) AND (“genetic diversity”); 7b. (“squalidae”) AND (“genetic structure”); 8b. (“squalidae”) AND (“genetic diversity”); 9b. (“squaloid”) AND (“genetic structure”); 10b. (“squaloid”) AND (“genetic diversity”). Data from the selected items was extracted, including

citation information, sample location, sample size, sequenced marker(s), genetic structure found, diversity estimators, and main conclusions (Dudgeon, 2012).

The process for both systematic reviews is summarized in figures 2 and 3.

3.2 Phylogenetic Analyses

Based on the second systematic review, the most promising genetic marker was selected, given the number of sequences available, with it being the mtDNA NADH2 gene. This gene codes for the protein which enables the activity of NADH dehydrogenase, involved in mitochondrial electron transport and its respiratory chain (Beckert *et al.*, 2001). It has been widely used in sharks for population genetics, phylogenetic analyses, and phylogeography studies (Gračan *et al.*, 2020), given its high conservation, slow sequence evolution, maternal inheritance, high mutation rate, and ability to provide fine resolution information about species identification and phylogenetic relationships within populations of the same species (Beckert *et al.*, 2001). Sequences for every species belonging to the *Squalus* genus were downloaded from Genbank and then imported to MEGA v.7 (Hall, 2013). Once there, they were aligned with the MUSCLE algorithm and the correct amino acidic translation was verified to avoid the presence of incomplete amino acids (Song *et al.*, 2008; Ferrari *et al.*, 2021). Before constructing the phylogenetic tree, a test was run to find the best DNA/protein models, due to MEGA offering different methods for estimating phylogenetic tress such as Neighbor Joining, UPGMA Maximum Parsimony, Bayesian Inference, Maximum Likelihood, amongst others (Hall, 2013). With this done, a phylogenetic tree was constructed to explore taxonomical relationships amongst every species in the genus (Hall, 2013).

Next, as a pre-requisite for the construction of the *S. acanthias* tree, a second analysis was performed using sequences from this species (Appendix Table I states the reference from which the sequences were obtained), with *Squalus blainville*, *Squalus cubensis*, *Squalus mitsukurii*, and *Squalus clarkae* as outgroups. For this one, sequences were aligned with MUSCLE and ran with the same settings as the previous tree. This pre-requisite was done to make sure there was a clean dataset of only *S. acanthias* sequences, without inconsistencies or the formation of multispecies clades. Once it was confirmed the sequences belonging to the outgroups formed a separate cluster from the *S. acanthias* sequences, a third and final phylogenetic tree was constructed for the *S. acanthias* sequences, applying the same method and settings as the

previous trees. For this one, sequences' names were modified to show the location where the samples were collected.

4 Results

4.1 Systematic Review

4.1.1 The spurdog and its stock in the Northeast Atlantic Ocean and the Mediterranean Sea

The systematic review concerning the spurdog and its stock in the Northeast Atlantic Ocean and Mediterranean Sea showed the following number of peer-reviewed journal articles, governmental and non-governmental reports, and doctoral theses available for each search string (Table I).

Table I. Search strings employed for the systematic review concerning the spurdog in the areas of study and number of hits obtained

Search string	Number of hits obtained
1a. (“squalus acanthias”) AND (“Northeast Atlantic” OR “North East Atlantic” OR “North-East Atlantic”)	n=1670
2a. (“spurdog”) AND (“Northeast Atlantic” OR “North East Atlantic” OR “North-East Atlantic”)	n=770
3a. (“piked dogfish”) AND (“Northeast Atlantic” OR “North East Atlantic” OR “North-East Atlantic”)	n=1240
4a. (“squalus acanthias”) AND (“Mediterranean Sea”)	n=1910
5a. (“spurdog”) AND (“Mediterranean Sea”)	n=591
6a. (“piked dogfish”) AND (“Mediterranean Sea”)	n=163
TOTAL: n=6344	

Out of the 1670 documents available for string 1a, 1638 were excluded after the initial screening. The most common reasons for exclusion were the article not being related to the species or the study not being carried out in the areas of interest. For string 2a, 768 documents were excluded, either because they didn't meet the selection criteria or because they were repeated items from the previous search string. All the documents from search string 3a were excluded due to the previous reasons. 1907 documents were excluded from search string 4a, while all from search strings 5a and 6a did not pass the initial screening, mostly due to repetition. In total, 38 peer-reviewed journal articles, governmental and non-governmental reports, and doctoral theses went onto the eligibility process, in which the full-text was read. In the end, all 38 documents that went through the eligibility process were included in the synthesis (Figure 2).

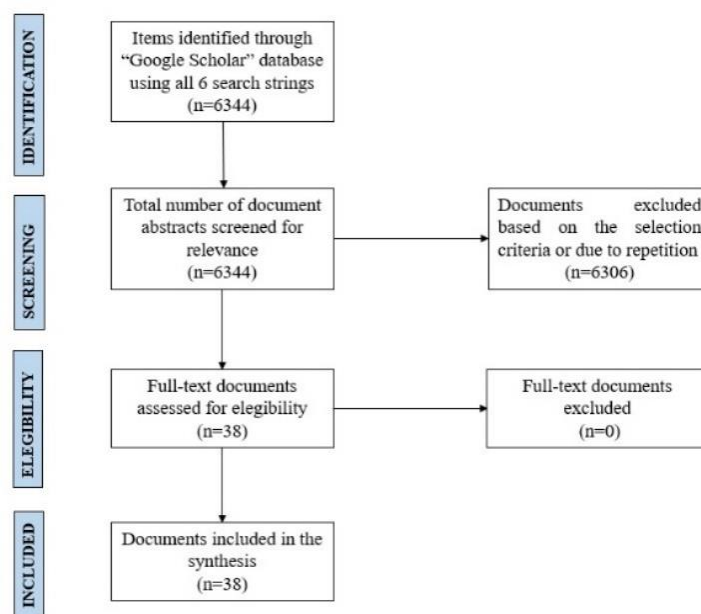


Figure 2. Conceptual map showing the process of the systematic review concerning the spurdog and its stock in the Northeast Atlantic Ocean and the Mediterranean Sea.

In general, half of the literature included was at least a decade old. The literature included in this synthesis dwelled on the fisheries (7), reproductive biology (6), trophic ecology (5), movements (4), distribution (2), conservation (2), contaminants (2), demography (1), taxonomy (1), habitat preference (1), and ethology (1) of the species, or included multiple topics focused on the species at once (6). Out of the 38 documents, 29 referred to the Northeast Atlantic area,

with most studies being done in either the United Kingdom or Norway, while 9 of them referred to the Mediterranean Sea, with the majority corresponding to the Adriatic Sea area. Although not found with the search strings used for the review, the latest report from the ICES “Working Group on Elasmobranch Fishes (WGEF)” (ICES WGEF, 2021) was included, serving as a compendium of most of the information available for the spurdog in the Northeast Atlantic Ocean. Finally, most of the data used for these studies was collected directly from commercial fisheries or fisheries surveys (Table II).

Table II. Synthesis of documents included after the systematic review of the spurdog (*S. acanthias*) and its stock in the Northeast Atlantic Ocean and Mediterranean Sea.

Literature was ordered according to the year in which it was published.

Citation Information	Research Topic	Type of Data	Location	Main Conclusions
Templeman, W. 1976. Transatlantic Migrations of Spiny Dogfish (<i>Squalus acanthias</i>). <i>Journal of the Fisheries Board of Canada</i> , 33(11):2605-2609	Movements	Tagging	Northwest Atlantic, Northeast Atlantic	First record of transatlantic migration of spurdog, corresponding to a specimen tagged and released in St. Pierre Bank, Canada, and recaptured 11 years later in the Shetland Isles-northern North Sea area. Conclusions point towards low levels of transatlantic migrations but probably not highly unusual.
Gauld, J.A. & MacDonals, W.S. 1982. The Results of Tagging Experiments on Spurdogs <i>Squalus acanthias</i> L. around Scotland. <i>ICES CM Doc, H:51</i>	Movements	Tagging	Scotland	This tagging study showed spurdogs have a tendency to disperse widely throughout the area, although they did detect an annual trend in movement from the north of Scotland into the North Sea during the summer with a corresponding movement out of the North Sea during the winter. Additionally, they found some evidence for mixing between the

				Northeast Atlantic and Northwest Atlantic stocks.
Vince, M.R. 1991. Stock identity in spurdog (<i>Squalus acanthias</i> L.) around the British Isles. <i>Fisheries Research</i> , 12(4):341-354	Movements	Tagging	United Kingdom	This tagging project, together with the CRM model, suggests juvenile and maturing spurdog move throughout the whole range of the Northeast Atlantic, indicating the stock should be treated as one management unit in the area.
Ellis, J.R., Pawson, M.G. & Shackley, S.E. 1996. The Comparative Feeding Ecology of Six Species of Shark and Four Species of Ray (Elasmobranchii) In The Northeast Atlantic. <i>Journal of the Marine Biological Association of the United Kingdom</i> , 76(1):89-106	Trophic ecology	Fisheries-dependent	Northeast Atlantic	Particularly for spurdog, it was found its diet is highly piscivorous (80.8%), supplemented with crustaceans (12%), ctenophores (3.5%), and mollusks (2.8%). Size differences in diet were observed, with smaller specimens (below 60 cm TL) consuming more crustaceans than teleosts, while larger specimens consumed primarily teleosts and very few crustaceans.
Jones, T.S. & Uglund, K.J. 2001. Reproduction of female spiny dogfish <i>Squalus acanthias</i> , in the	Reproductive biology	Fisheries-dependent	Oslofjord, Norway	Growth, age, length at maturity, fecundity, reproductive cycle, and embryonic growth were determined for the species in the Oslofjord, with

Oslofjord. <i>Fisheries Bulletin</i> , 99:685-690				a historical account given both samplings were carried out within a one-decade span.
Piñeiro, C.G., Casas, M. & Bañón, R. 2001. The deep-water fisheries exploited by Spanish fleets in the Northeast Atlantic: a review of the current status. <i>Fisheries Research</i> , 51(2-3):311-320	Fisheries	Fisheries-dependent	Northeast Atlantic	This work reviews the status of deep-water fisheries exploited by the Spanish fleet in the Northeast Atlantic. It includes fishing areas, fishing technologies, target species, and landings. For spurdog, the Spanish fleet landed around 170 thousand tons between 1996-1997.
Henderson, A.C., Flannery, K. & Dunne, J. 2002. Growth and Reproduction in Spiny Dogfish <i>Squalus acanthias</i> L. (Elasmobranchii: Squalidae), from the West Coast of Ireland. <i>Sarsia</i> , 87(5):350-361	Reproductive biology	Fisheries-dependent	West coast of Ireland	Specimens ranged in age from 4 to 30 years, with asymptotic lengths of 79 cm TL and 112 cm TL estimated for males and females, respectively. Lower age range reported in this study was attributed to fishing pressure. Length at maturity was estimated at 57.5 cm TL in males and 78.2 cm TL for females, with fecundity being positively correlated to female size. Parturition occurred mainly from August to January. Minimum fecundity was 4 while maximum was 16 embryos. Sex ratio was 1:1. Result show neither growth rate, size at

				maturity, nor fecundity have changed significantly due to fishing pressure.
Henderson, A.C., Dunne, J. & Flannery, K. 2002. Stomach contents of spiny dogfish <i>Squalus acanthias</i> L. off the West Coast of Ireland. <i>The Irish Naturalists' Journal</i> , 27(3):101-105	Trophic ecology	Fisheries-dependent	West coast of Ireland	Fish formed the main diet of the spurdog, with a total of 8 species recorded in the stomach contents. Main preys included mackerel and common dab (<i>Limanda limanda</i>). Cephalopods (<i>Octopus vulgaris</i> and <i>Eledone cirrhosa</i>) were the only other prey recorded. Results indicate the spurdog feeds throughout the water column, as well as the bottom, and in different type of substrates.
Fowler, S., Raymakers, C. & Grimm, U. 2004. <i>Trade in and Conservation of two Shark Species, Porbeagle (Lamna nasus) and Spiny Dogfish (Squalus acanthias)</i> . BfN-Skripten 118, Germany. 59pp	Biology, ecology, reproductive biology, stock assessment, fisheries management	Multiple, including fisheries-dependent and independent, literature available, economic and political traits	Northeast Atlantic, Northwest Atlantic, Northeast Pacific	Compendium of biological and ecological traits of spurdog, together with stock assessments, trade, and management.
Chatzisprou, A. & Megalofonou, P. 2005. Sexual maturity, fecundity and embryonic development of the	Reproductive biology	Fisheries-dependent	Eastern Mediterranean Sea	Minimum size of mature females was 51.5 cm TL and 47 cm TL for males, corresponding to smaller sizes of sexual maturity if compared to

<p>spiny dogfish, <i>Squalus acanthias</i>, in the eastern Mediterranean Sea. <i>Journal of the Marine Biological Association of the United Kingdom</i>, 85(5):1155-1161</p>				<p>other studies. Uterine fecundity ranged from 1-6 embryos and the size of pups varied between 7-22 cm TL. Conclusions indicate smaller sizes at maturity for both sexes, as well as lower fecundity than female fish in other areas.</p>
<p>Domi, N., Bouquegneau, J.M. & Das, K. 2005. Feeding ecology of five commercial shark species of the Celtic Sea through stable isotope and trace metal analysis. <i>Marine Environmental Research</i>, 60(5):551-569</p>	<p>Trophic ecology</p>	<p>Stable isotopes</p>	<p>Celtic Sea</p>	<p>The low values from stable isotopes of nitrogen and carbon in spurdog may be a reflection of its migratory behavior or preference towards preys from lower trophic levels, in comparison with other sharks. Additionally, levels of cadmium and mercury were shown to be diet-related, whereas zinc, iron, and copper were more linked with the species metabolism.</p>
<p>Hammond, T.R. & Ellis, J.R. 2005. Bayesian Assessment of Northeast Atlantic Spurdog Using a Stock Production Model, with Prior for Intrinsic Population Growth Rate Set by Demographic Methods. <i>J. Northw. Atl. Fish. Sci.</i>, 35:299-308</p>	<p>Fisheries</p>	<p>Fisheries-dependent</p>	<p>Northeast Atlantic</p>	<p>The authors of this study used demographic techniques to convert prior distributions for age-specific fecundity and natural mortality rate to prior distributions for the intrinsic rate of population growth. The priors for this rate were used in a Bayesian, Schaefer-model assessment, fitted to bottom trawl survey CPUE data; main</p>

				results suggested spurdog stock in the area is depleted to approximately 5% of virgin biomass.
Campana, S.E., Jones, C., McFarlane, G.A. & Myklevoll, S. 2006. Bomb dating and age validation using the spines of spiny dogfish (<i>Squalus acanthias</i>). <i>Environmental Biology of Fish</i> , 77:327-336	Demography	Fisheries-dependent	Northeast Atlantic, Northwest Atlantic, Northeast Pacific	Represents the first study to apply bomb radiocarbon as an age validation method using spine enamel from spurdogs. They confirmed the validity of spine enamel growth bands as an accurate age indicator, with individuals from the species reaching an age of at least 45 years. Additionally, hypothesis suggesting Pacific spurdog lives longer and grows more slowly in comparison to Atlantic spurdog was confirmed.
Kousteni, V., Megalofonou, P., Dassenakis, M. & Stathopolou, E. 2006. Total mercury concentrations in edible tissues of two elasmobranch species from Crete (eastern Mediterranean Sea). <i>Cybium</i> , 30(4):119-123	Contaminants	Fisheries-dependent	Crete (eastern Mediterranean Sea)	Highest concentrations of mercury were found in the muscle tissue of spurdog (5.79 mg/kg). Additionally, 81% of the muscle samples of spurdog presented concentrations of total mercury above the maximum permitted by law.

<p>Ellis, J.R. & Keable, J. 2008. Fecundity of Northeast Atlantic spurdog (<i>Squalus acanthias</i>). <i>ICES Journal of Marine Science</i>, 65:979-981</p>	<p>Reproductive biology</p>	<p>Fisheries-dependent</p>	<p>Irish Sea</p>	<p>Largest fecundity reported to date for the species (up to 21 pups). Results reenforce the idea of fecundity increasing with maternal size. This highlights the importance of big females for the recovery of the stock.</p>
<p>Williams, T., Helle, K. & Aschan, M. 2008. The distribution of chondrychthyans along the northern coast of Norway. <i>ICES Journal of Marine Science</i>, 65:1161-1174</p>	<p>Distribution</p>	<p>Fisheries-dependent</p>	<p>Norway</p>	<p>Spurdog was most abundant in the southern coast of Norway. Neither its distribution nor its abundance seemed to change significantly during the period comprising 1992-2005.</p>
<p>Serena, F., Papaconstantinou, C., Relini, G., De Sola, L.G. & Bertrand, J.A. 2009. Distribution and Abundance of Spiny Dogfish in the Mediterranean Sea Based on the Mediterranean International Trawl Survey Program. <i>Biology and Management of Dogfish Sharks</i>:139-149</p>	<p>Distribution, fisheries</p>	<p>Fisheries survey</p>	<p>Mediterranean Sea</p>	<p>Spurdog was one of the most abundant elasmobranchs in the survey, accounting for 6700 tons. Mean density of spurdog was significantly different between the Mediterranean eastern basin and the western basin, with the last one having lower values. Abundance indexes suggest a major presence of this species in coastal areas, primarily in shallow waters of the Adriatic Sea.</p>

<p>Capapé, C. & Reynaud, C. 2011. Maturity, reproductive cycle and fecundity of the spiny dogfish <i>Squalus acanthias</i> (Chondrychthyes: Squalidae) off the Languedocian coast (southern France, northern Mediterranean). <i>Journal of the Marine Biological Association of the United Kingdom</i>, 91(8):1627-1635</p>	<p>Reproductive biology</p>	<p>Fisheries survey</p>	<p>Northern Mediterranean Sea</p>	<p>Male and female sexually matured between 63.5-70 cm TL and 86-88 cm TL, respectively. Near-term embryos ranged from 24.5 cm to 27.1 cm TL. Uterine fecundity varied between 4-12, with fecundity being positively correlated with female size. While parturition and mating periods were not possible to determine, results support the hypothesis of the reproductive cycle lasting between 18-24 months.</p>
<p>De Oliveira, J.A.A., Ellis, J.R. & Dobby, H. 2013. Incorporating density dependence in pup production in a stock assessment of NE Atlantic spurdog <i>Squalus acanthias</i>. <i>ICES Journal of Marine Science</i>, 70(7):1341-1353</p>	<p>Fisheries</p>	<p>Fisheries-dependent</p>	<p>Scotland and North Sea</p>	<p>The resulting model estimated 2010 stock levels to be 23% and 19% the size of the ones in 1955 and 1905, respectively. This indicates the stock is depleted in the area but not as much as previously thought, supporting the IUCN listing of endangered and not critically endangered. Additionally, the model showed a total allowable catch (TAC) of 1422 tons/year to allow future population growth.</p>

<p>Gračan, R., Lazar, B., Posavec, I., Gregorović & Lacković, G. 2013. Maturation, fecundity and reproductive cycle of spiny dogfish, <i>Squalus acanthias</i>, in the Adriatic Sea. <i>Marine Biology Research</i>, 9(2):198-207</p>	<p>Reproductive biology</p>	<p>Fisheries survey</p>	<p>Adriatic Sea</p>	<p>Length at maturity was attained at 50.4 cm TL and 72.5 cm TL for males and females, respectively. Uterine fecundity ranged from 6 to 18 embryos; full-term embryos size ranged between 20-21.5 cm TL. Mating in the Adriatic occurs in June, November, and December, while ovulation and parturition occur during the summer. Spurdog in the Adriatic seems to attain sexual maturity at smaller sizes compared to other areas, as well as higher fecundity values.</p>
<p>McCully, S.R., Scott, F., Ellis, J.R. & Pilling, G.M. 2013. Productivity and susceptibility analysis: Application and suitability for data poor assessment of elasmobranchs in Northern European seas. <i>Collect. Vol. Sci. Pap. ICCAT</i>, 69(4):1679-1698</p>	<p>Conservation</p>	<p>Available literature</p>	<p>Northern Europe</p>	<p>A productivity and sensitivity analysis based on biological sensitivity and fisheries susceptibility was performed for data poor shark in Northern Europe. Spurdog was the most sensitive shark in the demersal ecosystem for both bottom trawls and set net fisheries.</p>
<p>Dell'Apa, A., Bangle, C.W. & Rulifson, R.A. 2015. Who let the</p>	<p>Fisheries management, socio-</p>	<p>Available literature</p>	<p>Northwestern Atlantic and</p>	<p>Integrates the biology, life history, and ecology of the species with information concerning</p>

dogfish out? A review of management and socio-economic aspects of spiny dogfish fisheries. <i>Reviews in Fish Biology</i> , 25:273-295	economic traits of fishery		European waters, including Northeast Atlantic	commercial trade, socio-economic, and political aspects of the fishery.
Gračan, R., Heppell, S.A., Lacković, G. & Lazar, B. 2015. Age and growth dynamics of spiny dogfish, <i>Squalus acanthias</i> , in the Adriatic Sea (Eastern Mediterranean Sea). <i>Marine and Freshwater Research</i> , 67(3):357-367	Demography, reproductive biology	Fisheries survey	Adriatic Sea	A Gompertz growth model estimated k values for males and females on 0.09 and 0.04 year ⁻¹ , respectively. Size at birth ranged from 22.9 cm TL to 24.1 cm TL, with a theoretical asymptotic length of 103.3 cm TL for males and 173.3 cm TL for females. Maturity age was estimated at 10.5 years for males and 20.1 years for females, while maximum age was calculated at 23 years for males and 36 years for females. Finally, natural mortality was estimated as 0.12 for males and 0.07 for females. These demographic parameters are useful for accurate stock assessments of the stock in the Adriatic Sea.
Thorburn, J., Neat, F., Bailey, D.M., Noble, L.R. & Jones, C.S.	Movements	Acoustic and satellite telemetry	Loch Etive, Scotland	Females overwintered in the loch, restricted their movements to the upper basin, and

<p>2015. Winter residency and site association in the Critically Endangered spurdog <i>Squalus acanthias</i>. <i>Marine Ecology Progress Series</i>, 526:113-124</p>				<p>remained in the area for the rest of the year. Some of the movements may be related to breeding or parturition, highlighting the importance of protecting this area for the conservation of different age and classes of the species.</p>
<p>Quaack, K. 2017. Stable isotope analysis of fish eye lenses: reconstruction of ontogenetic trends in spatial and trophic ecology of elamosbranchs and deep-water teleosts. <i>University of Southampton, Doctoral Thesis</i>, 209pp</p>	<p>Spatial and trophic ecology</p>	<p>Stable isotopes</p>	<p>Northeast Atlantic</p>	<p>This study explores the suitability of fish lenses to recover ontogenetic chemical information, reflecting foraging patterns and behavior. Main results suggest that the southern and central North Sea represent important foraging areas for maturing spurdogs, while the northern North Sea is more important during gestation, pupping, and early life history.</p>
<p>Albert, O.T., Junge, C. & Myrland, M.K. 2019. Young mums are rebuilding the spurdog stock (<i>Squalus acanthias</i>) in Norwegian waters. <i>ICES Journal of Marine Science</i>, 76(7):2193-2204</p>	<p>Reproductive biology, demography, selectivity, distribution</p>	<p>Fisheries survey</p>	<p>Norway</p>	<p>Results show spurdogs utilize Norwegian waters year-round and for their whole life cycle. Size and sex segregation was identified, but in general, proportion of males and females was similar. Population trends and reproductive potential of the species in Norwegian waters</p>

				were determined, indicating the stock increase in the area is mostly dependent on sexually mature young females.
Bargione, G., Donato, F., La Mesa, M., Mazzoldi, C., Riginella, E., Vasopollo, C., Virgili, M. & Lucchetti, A. 2019. Life-history traits of the spiny dogfish <i>Squalus acanthias</i> in the Adriatic Sea. <i>Scientific Reports</i> , 9:14317	Demography, reproductive biology	Fisheries survey	Adriatic Sea	Growth parameters were estimated for both males and females in the sampled area, as well as size at sexual maturity and fecundity. Parturition season was correspondent with the summer, which also coincides with peak catches, highlighting the importance of enforcing management policies to allow the stock to recover in the area.
Hobbs, C.A.D., Potts, R.W.A., Bjerregaard-Walsh, M., Usher, J. & Griffiths, A.M. 2019. Using DNA Barcoding to Investigate Patterns of Species Utilisation in UK Shark Products Reveals Threatened Species on Sale. <i>Scientific Reports</i> , 9:1028	Taxonomy	Fisheries-dependent	United Kingdom	DNA barcoding was used to investigate presence of shark products in fishmonger and fish and chip takeways in England. The majority of the samples taken identified the products to be spurdog. The results underline issues surrounding the use of confusing or cryptic terms to label many species, denying the customer their consumer choice.

<p>Silva, J.F. & Ellis, J.R. 2019. Bycatch and discarding patterns of dogfish and sharks taken in English and Welsh commercial fisheries. <i>Journal of Fish Biology</i>, 94(6):966-980</p>	<p>Fisheries</p>	<p>Fisheries-dependent</p>	<p>United Kingdom</p>	<p>A survey in the North Sea and Celtic Sea ecoregion showed size-related discarding for spurdog, where smaller individuals (<60 cm LT) were usually discarded. Additionally, temporal changes in retention patterns were observed, with increased regulatory discarding as management measures became restrictive.</p>
<p>O’Hea, B., Davie, S., Johnston, G. & O’Dowd, L. 2020. Assemblages of deepwater shark species along the north east Atlantic continental slope. <i>Deep Sea Research Part I: Oceanographic Research Papers</i>, 157:103207</p>	<p>Distribution</p>	<p>Fisheries survey</p>	<p>Ireland</p>	<p>Results show spurdog is distributed until 500 m of depth in the area surveyed, making it vulnerable to bottom and demersal trawling as fisheries at that depth with said technology are allowed. Additionally, spurdog would most likely not enter inside the category of deep-sea sharks.</p>
<p>Parton, K.J., Godley, B.J., Santillo, D., Tausif, M., Omeyer, L.C.M. & Galloway, T.S. 2020. Investigating the presence of microplastics in demersal sharks of the North-East</p>	<p>Contaminants</p>	<p>Fisheries survey</p>	<p>Northeast Atlantic</p>	<p>Ingestion of microplastics and anthropogenic fibers was evidenced for four demersal shark species, amongst them the spurdog. At least 67% of samples contained at least one contaminant, with number of particle burden increasing with body size but not with sex or</p>

Atlantic. <i>Scientific Reports</i> , 10:12204				species. Most of the contaminants were identified as synthetic cellulose, polypropylene, polyacrylamides and polyester. Whether these contaminants have an effect on the species is unknown.
Rindorf, A., Gislason, H., Burns, F., Ellis, J.R. & Reid, D. 2020. Are fish sensitive to trawling recovering in the Northeast Atlantic? <i>Journal of Applied Ecology</i> , 57(10):1936-1947	Conservation	Available literature	Northeast Atlantic	Using life-history parameters and knowledge of fish shape and habitat, the sensitivity of spurdog (amongst other 269 species) to demersal trawling was estimated and it was compared to the recent IUCN categorization. Spurdog was found to be sensitive to trawling, although stock levels appear to be an increasing path. Sensitivity analysis agrees with current IUCN listing.
Gül, G. & Demirel, N. 2021. Evaluation of the comprehensive feeding strategy and trophic role of overexploited mesopredator species in the Sea of Marmara (northeastern	Trophic ecology	Stable isotopes	Sea of Marmara	Spurdog occupies a high trophic level in the Sea of Marmara, mainly feeding on teleosts. Results demonstrated an isotopic niche overlap between spurdog and <i>Scyliorhinus canicula</i> , indicating both species exploit similar food resources.

Mediterranean). <i>Estuarine, Coastal and Shelf Science</i> , 259:107448				
ICES WGEF. 2021. Spurdog in the Northeast Atlantic. <i>ICES Scientific Reports</i> 3:59:31-105.	Biology, ecology, reproductive biology, stock assessment, fisheries management	Multiple, including fisheries-dependent and independent, literature available, economic and political traits	Northeast Atlantic	Report integrates all information available for the spurdog stock in the Northeast Atlantic, including stock distribution, data about the fishery, catch data, life-history, stock assessment, conservation efforts, management policies and advice, amongst others.
Jac, R., Höffle, H., Albretsen, J., Jakobsdóttir, K., Staby, A., Søvik, G. & Junge, C. 2021. Of three sharks and one chimaera: varied habitat preferences across a latitudinal range revealed by coastal and offshore surveys. <i>Journal of Fish Biology</i> , 100(3):660-674	Habitat preference	Fisheries survey	North Sea, Norwegian Sea	Results show the spurdog prefers warmer (7-9°C), shallower waters with a salinity of 34.54, which is why it is only present in lower latitudes in the Norwegian Sea and is more widespread in the North Sea. In the region of study, the eastern part of the Skagerrak, the north of Scotland, and the area between Scotland and Norway presented the highest densities.
Mérillet, L., Pavoine, S., Kopp, D., Robert, M. & Mouchet, M. 2021. Biomass of slow life history species increases as local bottom trawl	Fisheries	Available literature	Northeast Atlantic	While not solely focused on spurdog, this study found a negative relationship between the biomass of spurdog and bottom trawling

effort decreases in the Celtic Sea. <i>Journal of Environmental Management</i> , 290:112634				pressure, as well as an increase in their total biomass in the Celtic Sea with less trawling.
Börjesson, P., Norén, K. & Valentinsson, D. 2022. Occurrence of sharks, rays and rabbit fish in the Greater North Sea – and catches in Swedish fisheries. <i>Department of Aquatic Resources</i> , Sveriges lantbruksuniversitet, Aqua reports:14	Fisheries	Fisheries-dependent	Norway and Sweden	Spurdog is one of the most common elasmobranch species in the Greater North Sea area. Additionally, it showed a seasonal trend, being more common along the Norwegian coast and in offshore parts of the Skagerrak during the first quarter of the year, and then closer to the Swedish coast in the third and fourth quarter. Historical information suggests bycatch of spurdog in gillnet fisheries was extensive; however, as landings were prohibited in 2010, there is no information about bycatch nowadays. Most of spurdog is discarded by Swedish fisheries (>90%).
Ovegård, M., Högvall, J., Ovegård, M., Wikström, A. & Wennhage, H. 2022. Previously undocumented relationship between spiny dogfish	Ethology	Stereo-BRUVS (baited remote underwater stereo-	Kattegat, Sweden	First record of a previously undocumented association between the spurdog and the Atlantic horse mackerel. The relationship between these two species is not specified, but

<p><i>Squalus acanthias</i> and juvenile Atlantic horse mackerel <i>Trachurus trachurus</i> revealed by stereo-BRUV. <i>Environmental Biology of Fishes</i>, 105:453-458</p>		<p>video systems) footage</p>		<p>the study shows the potential of using BRUVS and non-invasive methods to increase the ecological knowledge of marine species.</p>
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4.1.2 Genetic population structure and diversity of the spurdog and related species in the Northeast Atlantic Ocean and the Mediterranean Sea

The systematic review concerning the genetic population structure and diversity of the spurdog and other squaloids in the Northeast Atlantic Ocean and Mediterranean Sea showed the following number of peer-reviewed journal articles, governmental and non-governmental reports, and doctoral theses available for each search string (Table III).

Table III. Search strings employed for the systematic review concerning the spurdog's and other squaloids' genetic structure and diversity in the areas of study and number of hits obtained

Search strings	Number of hits
1b. (“squalus acanthias”) AND (“genetic structure	n=432
2b. (“spurdog”) AND (“genetic structure”)	n=148
3b. (“piked dogfish”) AND (“genetic structure”)	n=20
4b. (“squalus acanthias”) AND (“genetic diversity”)	n=634
5b. (“spurdog”) AND (“genetic diversity”)	n=209
6b. (“piked dogfish”) AND (“genetic diversity”)	n=35
7b. (“squalidae”) AND (“genetic structure”)	n=134
8b. (“squalidae”) AND (“genetic diversity”)	n=202
9b. (“squaloid”) AND (“genetic structure”)	n=81
10b. (“squaloid”) AND (“genetic diversity”)	n=68
TOTAL: n=1570	

Out of the 432 documents available for string 1b, 428 were excluded after the initial screening. The most common reasons for exclusion were the document not concerning the species of interest or the study not dwelling on genetic population structure and diversity. For search string

7b, 133 documents were excluded for the same reasons or due to repetition. Search strings 2b, 3b, 4b, 5b, 6b, 8b, 9b, and 10b, had all the documents excluded at the screening process. In this case, out of all the hits obtained, only 5 peer-reviewed journal articles went onto the eligibility process (3 of them focused on the spurdog and 2 of them on other squaloids), with all of them being included in the synthesis (Figure 3).

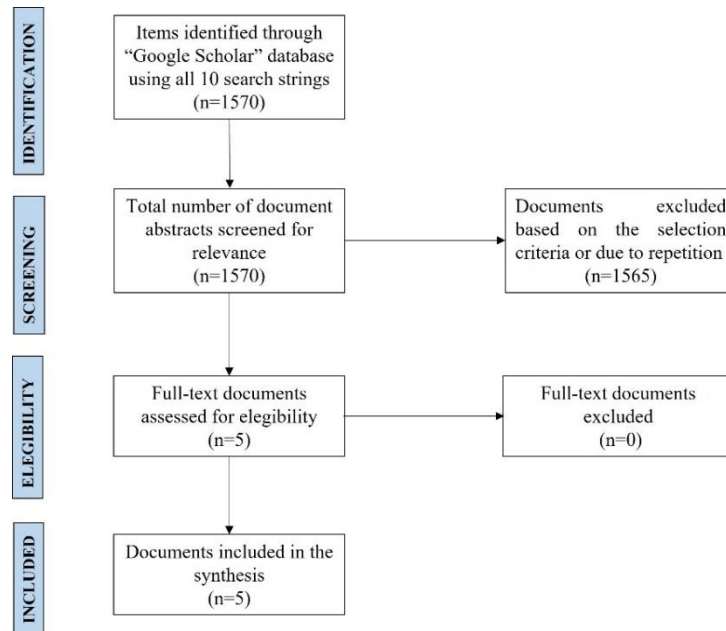


Figure 3. Conceptual map showing the process of the systematic review concerning the genetic population structure and diversity of the spurdog and other squaloids in the Northeast Atlantic Ocean and the Mediterranean Sea.

As mentioned before, only three peer-reviewed journal articles were found when doing the systematic review for the genetic population structure and diversity of the spurdog (Table IV), with two corresponding to the Northeast Atlantic Ocean (Veríssimo *et al.*, 2010; Thorburn *et al.*, 2018) and one to the Adriatic Sea (Gračan *et al.*, 2020). Both Veríssimo *et al.* (2010) and Thorburn *et al.* (2018) sequenced the same nuclear microsatellite loci, with the exception of one (Saca4234), which was only included by the first. In the case of Gračan *et al.* (2020), they sequenced the same microsatellite loci as Veríssimo *et al.* (2010), plus 5 more (DFV296, DFU273, DFH429, DFH434, Saca7551). All three of these studies used mitochondrial (mt)DNA sequences as well, although Veríssimo *et al.* (2010) and Gračan *et al.* (2020) used the NADH2 gene as marker, while Thorburn used the control region. Neither Veríssimo *et al.* (2010) nor Thorburn *et al.* (2018) found a genetic population structure amongst the sampled collections in the Northeast Atlantic Ocean, supporting the idea of one single stock in the area.

However, Gračan *et al.* (2020) found fine population structuring for the samples collected in the Adriatic Sea, and when compared to sequences from the Northeast Atlantic, it resulted in no genetic connection between them (therefore, different subpopulations). In terms of genetic diversity, the three studies found high levels of genetic diversity within the sampled populations. Veríssimo *et al.* (2010) concluded this diversity was homogeneously distributed between the samples from the South and North Atlantic, with very few distinct haplotypes not shared by these two locations. This indicates there was once gene flow between the North and South Atlantic populations, with the recent appearance of a restriction to trans-equatorial migrations given the distinct haplotypes not shared by these two. Thorburn *et al.* (2018) concluded the high genetic diversity present in the sampled specimens in the United Kingdom was homogeneously distributed between locations, with low genetic differentiation, possibly due to the formation of aggregations leading to gene flow. Gračan *et al.* (2020) concluded there was high genetic diversity within the samples collected in the Adriatic Sea. Haplotypes were distinct from the ones shared by Northeast Atlantic subpopulations, supporting the claim that the Adriatic Sea subpopulation should be treated as a different stock (Table IV).

When it came to finding literature concerning genetic population structure and diversity of similar species in the area, only one study was found for a species of the same genus (*Squalus blainville*; Kousteni *et al.*, 2016), and one for a species of the same order (Squaliformes, *Centroscymnus coelolepis*; Veríssimo *et al.*, 2011). Both studies sequenced nuclear microsatellite loci and mtDNA as well. Veríssimo *et al.* (2011) included 4 microsatellite loci that were not used by any of the other 4 studies (Ccoe25, Ccoe55, Ccoe61, Ccoe75), while all the microsatellite loci included by Kousteni *et al.* (2016) were used in either Veríssimo *et al.* (2010, 2011), Thorburn *et al.* (2018) or Gračan *et al.* (2020). Both studies employed sequences from mtDNA as well, with Veríssimo *et al.* (2011) using the control region as marker, while Kousteni *et al.* (2016) used the cytochrome oxidase 1 marker. Results for both studies did not find a significant genetic structure in either of the species, concluding both *C. coelolepis* and *S. blainville* should be treated as one single stock throughout their distribution in the Eastern Atlantic Ocean (Veríssimo *et al.*, 2011) and the Mediterranean Sea (Kousteni *et al.*, 2016), respectively. Finally, both studies found high genetic diversity for each one of the species, although it was homogeneously distributed within the samples, and therefore, no genetic divergence was detected (Veríssimo *et al.*, 2011; Kousteni *et al.*, 2016) (Table IV).

Table IV. Synthesis of documents included after the systematic review of the genetic population structure and diversity of the spurdog (*S. acanthias*) and other related species in the area of interest.

The literature was ordered according to the year in which it was published, with articles referring to the spurdog shown first, and lastly the articles referring to other species.

Citation Information	Sample Location	Sample Size	Sequenced Marker(s)	Structure Found	Diversity Estimators	Main Conclusions
Veríssimo, A., McDowell, J.R. & Graves, J.E. 2010. Global population structure of the spiny dogfish <i>Squalus acanthias</i> , a temperate shark with an antitropical distribution. <i>Molecular Ecology</i> , 19(8):1651-1662	-North Atlantic: Irish Sea (UK), Ireland (IRE), Massachusetts (MA), Virginia (VA). -South Atlantic: Argentina (ARG). -North Pacific: California (CA), Washington-Oregon Border (WAOR), Japan (JA).	-UK (48) -IRE (56) -MA (48) -VA (55) -ARG (48) -CA (49) -WAOR (50) -JA (49) -CH (18)	-8 nuclear microsatellite loci: DFU285, DFT289, DFJ451, DFJ445, SacaGa11, Saca3853, Saca4234, Saca6396. -MtDNA sequences of the NADH dehydrogenase 2 gene (566bp).	A strong genetic divergence was found between the North Pacific samples and the South/North Atlantic, delineating different stocks. Low differentiation between the southern and northern collection of Atlantic samples, with few haplotypes	-Haplotype diversity -F _{ST} (Fixation index)	Cluster formed by North Pacific collection divergent from Southern and North Atlantic collections. In the case of the Atlantic collections, a small genetic variation was found, with only a few distinct haplotypes differing between regions. This supports the claim of gene flow happening

	-South Pacific: Chile (CH), New Zealand (NZ).	-NZ (46) Total: 454		not shared between them.		between the North and South Atlantic populations until recently. Now, there seems to be a restriction on trans-equatorial migrations, with the appearance of haplotypes not shared between them. The results also supported the resurrection of <i>Squalus suckleyi</i> , done by Ebert <i>et al.</i> in a posterior study (2010).
Thorburn, J., Jones, R., Neat, F., Pinto, C., Bendall, V., Hetherington, S.,	United Kingdom	295	-7 nuclear microsatellite markers: DFT289, DFJ451, DFU285,	No genetic structure was found in the UK, with weak and non-significant	-Haplotype diversity -F _{ST}	Results of this study show genetic mixing of spurdogs in British waters, supporting the

<p>Bailey, D.M., Leslie, N. & Jones, C. 2018. Spatial versus temporal structure: Implications of inter-haul variation and relatedness in the Northeast Atlantic spurdog <i>Squalus acanthias</i>. <i>Aquatic Conservation: Marine and Freshwater Ecosystems</i>, 28(5):1167-1180</p>			<p>DFJ445, SacaGA11, Saca3853, Saca6396 (295 individuals). -MtDNA control region (829bp; 228 individuals).</p>	<p>differentiation between the sampled areas. However, a high level of distinct haplotypes was found, indicating high genetic diversity within the specimens sampled.</p>	<p>-F_{IS} (inbreeding index)</p>	<p>treatment of spurdog as a single genetic stock, and therefore a single management unit. High genetic diversity was found within the sampled individuals, possibly due to different sub-populations forming aggregations; despite high genetic diversity, no differentiation was found.</p>
<p>Gračan, R., Lazar, B., Zupan, S. & Bužan, E. 2020. Genetic characterisation of the spiny dogfish <i>Squalus acanthias</i> in the Adriatic Sea: evidence</p>	<p>North-central Adriatic Sea</p>	<p>124</p>	<p>-13 nuclear microsatellite loci: DFU285, DFV296, DFT289, DFU273, DFJ451, DFH429, DFJ445, DFH434, Saca3853, Saca4234,</p>	<p>12 unique haplotypes were found, as well as high genetic variation in the Adriatic-Mediterranean</p>	<p>-Haplotype diversity -F_{ST}</p>	<p>Atlantic-South Pacific origin for spurdog in the Adriatic Sea, with high genetic diversity, fine stock structuring, and no present-day connectivity to the</p>

<p>for high genetic diversity and an Atlantic-South Pacific origin. <i>Marine and Freshwater Research</i>, 72(1):131-139.</p>			<p>Saca6396, SacaGA11, Saca7551 (124 individuals). -MtDNA NADH dehydrogenase subunit 2 gene (486bp; 31 individuals).</p>	<p>region; significant genetic heterogeneity and fine scale stock structuring, possibly linked to the sharks' residential behavior and low vagility. No connection with Atlantic populations.</p>		<p>Atlantic populations; therefore, it should be considered as another stock, with individual regional management plans.</p>
<p>Veríssimo, A., McDowell, J.R. & Graves, J.E. 2011. Population structure of a deep-water squaloid shark, the Portuguese dogfish (<i>Centroscymnus coelolepis</i>). <i>ICES</i></p>	<p>Eastern Atlantic: Ireland (IRE), Portugal (POR), Madeira (MAD), Mauritania (MAU), Azores (MAR), South Africa (SA).</p>	<p>-IRE (45) -POR (41) -MAD (17) -MAU (46) -MAR (40) -SA (22)</p>	<p>-8 nuclear microsatellite loci: Ccoe25, Ccoe55, Ccoe61, Ccoe75, Saca7551, DFJ451, SacaGA11, Saca3853. -MtDNA control region (496bp).</p>	<p>High levels of genetic diversity were found at the microsatellite loci, but low at the mtDNA control region loci. This genetic diversity was homogenously distributed between</p>	<p>-Haplotype diversity -F_{ST}</p>	<p>Despite high genetic diversity at the nuclear microsatellite loci, this diversity was homogenously distributed throughout the sampled locations. Therefore, no genetic differentiations was found, as well as no</p>

<p><i>Journal of Marine Science</i>, 68(3):555-563</p>		<p>Total: 211</p>		<p>the sampled locations, resulting in low genetic differentiation and no genetic structure found for <i>C. coelolepis</i> in the Eastern Atlantic. Results suggest high dispersal potential for this species and no major barriers to it in the Eastern Atlantic.</p>		<p>genetic structure found for the species. Stock appears to have been stable throughout time and given the results, it should be considered as one management unit throughout the entirety of the Eastern Atlantic, due to the connectivity found between sampled individuals from the Northeast Atlantic and South Africa.</p>
<p>Kousteni, V., Kasapidis, P., Kotoulas, G. & Megalofonou, P. 2016. Evidence of high genetic connectivity for</p>	<p>Mediterranean Sea: Ionean, Aegean, and Lybian Seas, and</p>	<p>577</p>	<p>-7 nuclear microsatellite loci: DFH429, DFH434, DFT289, DFU285, Saca3853, Saca6396,</p>	<p>High genetic diversity distributed homogenously in the collected samples. No genetic</p>	<p>-Haplotype diversity -F_{ST}</p>	<p>No genetic differentiation and population structure found since both haplotype and</p>

<p>the longnose spurdog <i>Squalus blainville</i> in the Mediterranean Sea. <i>Mediterranean Marine Science</i>, 17(2):371-383</p>	<p>off the Balearic Islands</p>		<p>SacaGA11 (577 individuals). -MtDNA cytochrome c oxidase subunit I gene (585bp; 107 individuals).</p>	<p>differentiation and population structure found; both diversity estimators indicate a single panmictic population.</p>	<p>genotype variation were homogeneously distributed among the sample collections, despite the high haplotype diversity. The species has possibly a high dispersal potential and should be considered a single genetic stock. It is important to point out that a subtle genetic structure might exist if more microsatellite loci would have been analyzed.</p>
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4.2 Phylogenetic analyses

4.2.1 Phylogenetic tree of the *Squalus* genus

Based on the second systematic review and the number of sequences available in Genbank, NADH2 was chosen as the most promising marker for the analyses (626 sequences for all the species in the *Squalus* genus, 82 for *S. acanthias*). In comparison, cytochrome oxidase I, control region, and/or microsatellites had very few sequences available. Before constructing the phylogenetic trees, a test was run to find the best DNA/protein models, being a maximum likelihood phylogenetic tree with a Tamura-Nei substitution model the preferred choice. Every phylogenetic tree was run with the previous settings, together with a bootstrap of a 1000.

626 sequences were used to construct the phylogenetic tree. Results representing the taxonomical relationships between all the sequences available for the genus *Squalus* (Figure 4) showed three important findings. Firstly, sequences from *Squalus mitsukurii* formed a monophyletic clade with sequences from multiple other species, including *Squalus japonicus* (Figure 4a), *Squalus formosus* (Figure 4b), and *Squalus clarkae* (Figure 4c). Support for the clade formed between *S. mitsukurii* and *S. japonicus* was extremely low (2%; Figure 4a), while support for the clades formed between *S. mitsukurii* with *S. formosus* (Figure 4b) and *S. mitsukurii* with *S. clarkae* (Figure 4c) were above 60%. Secondly, sequences from *Squalus megalops* formed monophyletic clades with sequences from *Squalus cubensis* (Figure 4d), *S. blainville* (Figure 4e), and *Squalus chlorolocus* (Figure 4f). Support for the previous clades was low in every case. Finally, in some cases, sequences from *Squalus suckleyi* formed monophyletic clades with sequences of *S. acanthias* (Figure 4g, Figure 4h). Support for these clades varied between 40% and 64%.

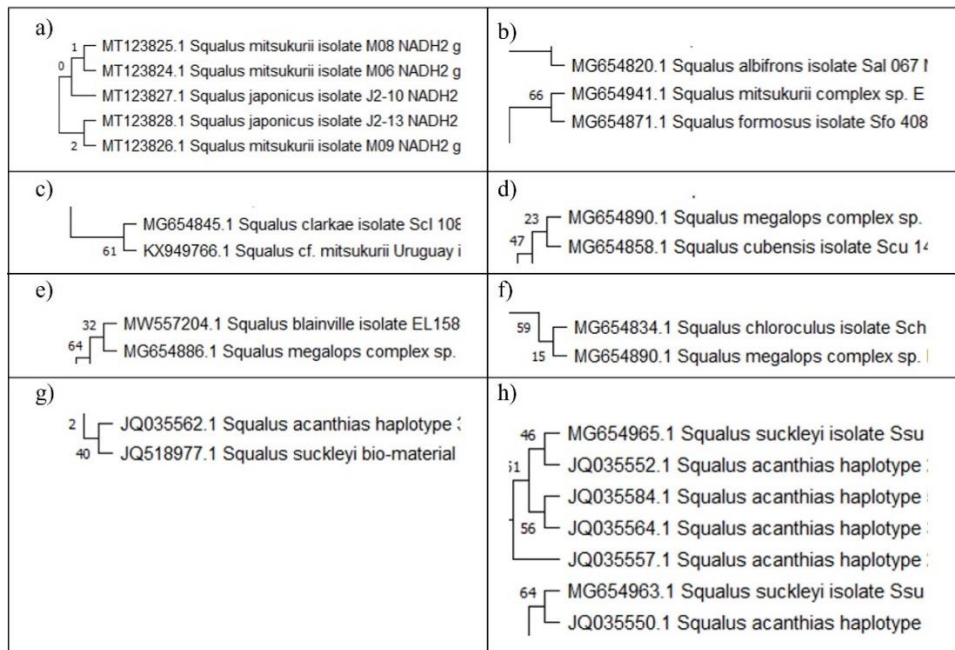


Figure 4. Extracts of the maximum likelihood phylogenetic tree showing the main results obtained about the taxonomical relationships of available sequences within the *Squalus* genus.

a) Monophyletic clade formed between *S. mitsukurii* and *S. japonicus*; b) Monophyletic clade formed by *S. mitsukurii* and *S. formosus*; c) Monophyletic clade formed by *S. mitsukurii* and *S. clarkae*; d) Monophyletic clade formed by *S. megalops* and *S. cubensis*; e) Monophyletic clade formed by *S. megalops* and *S. blainville*; f) Monophyletic clade formed by *S. megalops* and *S. chloroculus*; g), h) Monophyletic clade formed by *S. acanthias* and *S. suckleyi*

4.2.2 Phylogenetic tree of *Squalus acanthias*

Results from the rooted tree, using sequences from *S. cubensis*, *S. mitsukurii*, and *S. clarkae*, showed these sequences are well differentiated from the sequences belonging to *S. acanthias*, fulfilling their function as appropriate outgroups in the phylogenetic tree. Sequences for both *S. suckleyi* and *S. blainville* were not used as outgroups, given that in some cases they formed monophyletic clades with *S. acanthias*.

After constructing the rooted tree and confirming the accuracy of the sequences chose as outgroups, a final phylogenetic tree was constructed exclusively using *S. acanthias* sequences (n=82) from the North and South Atlantic Ocean, Mediterranean Sea, and South Pacific Ocean. Results from this tree (Figure 5) showed all the samples and sequences collected throughout the Atlantic Ocean, Mediterranean, and South Pacific Ocean basins correspond to the same species, as they were all grouped in one big monophyletic cluster. In some situations, monophyletic clades were identified according to location, namely Mediterranean sequences (enclosed by a

red box), Argentinian sequences (enclosed by a dark green box), Irish sequences (enclosed by a dark blue box), Chilean sequences (enclosed by a light blue box), and eastern American (Virginia/Massachusetts; enclosed by a black box). Additionally, there were monophyletic clades grouping sequences from different locations; such examples are: United Kingdom/Ireland with New Zealand (enclosed by a yellow box), Eastern coast of the United States with New Zealand (enclosed by a pink box), Eastern coast of the United States with Ireland (enclosed by a brown box), and Chile with Tasmania (enclosed by a light green box).



Figure 5. Complete maximum likelihood phylogenetic tree of *S. acanthias* using NADH2 sequences from the Atlantic Ocean, Mediterranean Sea, and the South Pacific Ocean.

The tree was divided into two images for easier reading; left-hand image corresponds to the upper half of the tree, right-hand image to the lower half. Red box: Mediterranean clade; dark green box: Argentinian clade; dark blue box: Irish clade; light blue box: Chilean clade; black box: Eastern US clade; yellow box: British/Irish-New Zealander clade; pink box: Eastern US-New Zealander clade; brown box: Easter US-Irish clade; light green box: Chilean-Tasmanian clade

5 Discussion

The discussion of the present work will be divided into four sections: (1) a discussion focused on the results obtained from the systematic reviews, (2) one focused on the results obtained from the phylogenetic analyses, (3) limitations found throughout the study and identification of knowledge gaps on population structure and diversity of the species in the area, and (4) recommendations for the establishment of appropriate fisheries management schemes that can aid to the regulation of the extraction of this species.

5.1 Systematic Review

5.1.1 The spurdog and its stock in the Northeast Atlantic

Results from the systematic review on the spurdog and its stock in the Northeast Atlantic Ocean and Mediterranean Sea revealed only 38 documents after an exhaustive search (Table II). The topics in which the literary content of the species revolves around align with the traditional information used to advise management schemes in most nations and areas (Mäntyniemi *et al.*, 2009), with them including reproductive biology, life history traits and demography, and catch/landing data. However, and judging from the amount of literature that was encountered despite it being once one of the most fished sharks in the area, *S. acanthias* could be classified as a species with “low information”. This could be a consequence of both little interest in the species until around the 1990s (Vince, 1991; Hammond & Ellis *et al.*, 2005) and the introduction of restrictive management policies for the species in the mid-2000s (Albert *et al.*, 2019; ICES WGEF, 2021), in which a zero TAC for the study areas was introduced. By doing so, data collection and sampling has been reduced to fisheries surveys for the most part (Serena *et al.*, 2009; Capapé *et al.*, 2011; Gračan *et al.*, 2013; Gračan *et al.*, 2015; Albert *et al.*, 2019; Bargione *et al.*, 2019; Hobbs *et al.*, 2019; O’Hea *et al.*, 2020; Parton *et al.*, 2020; Gül & Demirel, 2021; Jac *et al.*, 2021), which are appropriate given the management policies in effect but do restrict the amount of information that can be collected about the species (if compared to data sampling through commercial fisheries). This highlights the need to generate information

through less invasive, fisheries independent methods, such as tagging, telemetry (Williamson *et al.*, 2019), and genetic and trophic analyses using biopsies (Meyer *et al.*, 2018). Despite the availability of these data collection methods, the results from the present work show they have not been widely used for this species, with just a few studies employing them (Templeman, 1976; Gauld *et al.*, 1982; Vince, 1991; Thorburn *et al.*, 2015).

Furthermore, it is important to mention most of the documents selected through the systematic review were done either in Norway or in the United Kingdom (including Ireland, North Sea, and Celtic Sea) for the Northeast Atlantic Ocean and in the Adriatic Sea area of the Mediterranean Sea (Table II). Given that the species has a distribution from Norway and all the way to Morocco, including all the Mediterranean Sea (Compagno, 1984) in the area of interest, it raises the question as to why there is none or very few studies concerning other ICES areas in the Northeast Atlantic or other regions within the Mediterranean. The answer to the previous question may be related to (1) the fact that, historically, some nations have reported landings of squaloids under generic dogfish categories, rendering species-specific information useless or (2) because there always existed (and exists) some uncertainty over the accuracy of landing data given the difficulty to identify the different species of the *Squalus* genus through a morphological approach (e.g., the ID issue between *S. acanthias* and *S. blainville* in southern European waters; ICES WGEF, 2021, Ariza *et al.*, 2022).

In general, the quality of the data used for stock assessments (particularly without an accurate estimate of bycatch and discarded spurdogs), the general lack of information for the species, and the lack of information coming from other areas besides Norway, the United Kingdom, and the Adriatic Sea have already been mentioned as some of the most important issues to resolve in an effort to improve management schemes for the species (ICES WGEF, 2021).

5.1.2 Genetic population structure and diversity of the spurdog in the Northeast Atlantic Ocean

Out of the three documents on genetics selected through the systematic review and concerning the spurdog, both studies in the Northeast Atlantic Ocean did not find genetically stratified populations for the spurdog, supporting the claim of treating its stock as a unique one throughout its whole distribution in the Northeast Atlantic (Veríssimo *et al.*, 2010; Thorburn *et al.*, 2018; ICES WGEF, 2021). However, Gračan *et al.* (2020) did find a strong genetic structure for the sampled subpopulations in the Adriatic Sea, implying the Mediterranean serves as a barrier to

gene flow, and consequently, this stock should be treated as a distinct one in relation to the Northeast Atlantic one. This has important consequences for the implementation of fisheries management schemes, as the stocks should have individual management plans if the demographical characteristics of these differ greatly from one another and align towards certain, unique management goals according to the areas (Palsbøll *et al.*, 2007; Lowe & Allendorf 2010; Ovenden *et al.*, 2013). Given the availability of some information on genetic structure and diversity of the species, together with updated information concerning the demography and reproductive biology of the species in the Northeast Atlantic (Albert *et al.*, 2019; ICES WGEF, 2021) and the Mediterranean (Gračan *et al.*, 2013; Gračan *et al.*, 2015; Bargione *et al.*, 2019), this could be used to aid towards future management plans in the areas of interest.

Previously, it was thought large sharks with high vagility tended towards panmictic populations (no genetic structure), such as tiger sharks (*Galeocerdo cuvier*, Pirog *et al.*, 2019). The contrary was assumed for smaller species with limited movement. Nowadays, it has been determined that these are not the usual cases. Examples of this include the lack of genetic structure for the spurdog (*S. acanthias*) (Veríssimo *et al.*, 2010; Thorburn *et al.*, 2018), the longnose spurdog (*S. blainville*) (Kousteni *et al.*, 2016) and the Portuguese dogfish (*C. coelolepis*) in the Northeast Atlantic, Mediterranean Sea, and Eastern Atlantic, respectively (Veríssimo *et al.*, 2016), evidencing the high dispersal potential and gene flow present in smaller, demersal species of sharks. Examples of the opposite case (fine genetic structuring) have been documented for small, mid-sized, and large species. For small species of sharks, the small-spotted catshark (*Scyliorhinus canicula*) in the Mediterranean Sea presented a strong population structure and even highly different demographical traits between distinct sub-populations in the region (Kousteni *et al.*, 2015). For mid-sized species, the presence of a distinct population structure for scalloped hammerheads (*Sphyrna lewini*, mid-sized, highly vagile species) in the Arabian Peninsula was found, differing from the rest of the stock in the Indian Ocean (Spaet *et al.*, 2015). Finally, for large-sized species, the presence of distinct subpopulations of great white sharks (*Carcharodon carcharias*, large-sized, highly vagile species) between the eastern and southwestern coasts of Australia (Blower *et al.*, 2012) serves as another example. The results from all these studies highlight the importance of carrying out genetic population structure analyses to distinguish subpopulations and stocks, without arbitrarily establishing them based on the characteristics of a species.

All the studies included in the systematic review found high levels of genetic diversity, although in most cases, it was distributed homogeneously throughout all the samples, indicating no genetic differentiation between locations or subpopulations (Table IV). Only Gračan *et al.* (2020) found genetic differentiation between the samples collected in the Adriatic Sea in relation to the ones from the Northeast Atlantic. Overfishing can lead to the loss of genetic diversity and evolutionary potential in populations, mostly because of increased inbreeding and genetic diversity erosion brought by genetic drift (Rodrigues-Domingues *et al.*, 2018). This lack of diversity can lead to an increased probability of fixating deleterious alleles and the overall reduction of the resilience of a species (Rodrigues-Domingues *et al.*, 2018). Even if the documented information on genetic diversity of *S. acanthias* is limited, the fact that its haplotypic diversity (and in some cases nucleotide diversity; Thorburn *et al.*, 2018; Gračan *et al.*, 2020) in both the Northeast Atlantic and the Mediterranean Sea is high is a good sign, despite its long history of exploitation. The importance of constantly monitoring genetic diversity and its inclusion in fisheries management schemes is highlighted here as a way to monitor populations and their ability to withstand both anthropogenic and natural pressures (Rodrigues-Domingues *et al.*, 2018).

To end this section, it is important to mention that while not included in the systematic review, most of the genetic studies concerning the spurdog and other squaloids focused on DNA barcoding and resolving taxonomical issues, which will be discussed in further sections.

5.2 Phylogenetic analyses

5.2.1 Taxonomical relationships between the species within the *Squalus* genus

Results from the phylogenetic analysis showing the taxonomical relationships between the different species from the *Squalus* genus evidenced multiple issues. Firstly, *S. mitsukurii* was clustered together with *S. japonicus* (Figure 4a), *S. formosus* (Figure 4b), and *S. clarkae* (Figure 4c). There is literature documenting the taxonomical complexity of *S. mitsukurii* (Ziadi-Künzli *et al.*, 2020; Ariza *et al.*, 2022). It is now agreed upon the fact that the once considered globally distributed *S. mitsukurii* is in fact endemic to the Northwestern Pacific, particularly to the temperate waters of Japan and Korea, with *S. japonicus* been its closest relative (Ziadi-Künzli *et al.*, 2020). Given that *S. japonicus*' distribution coincides with the prior, the most plausible reason for this clustering relies on the morphological misidentification of both species, and the

sequences available online being wrongly listed (Ziadi-Künzli *et al.*, 2020). The situation described between *S. mitsukurii*+*S. japonicus* applies as well to *S. formosus*, since it is morphologically very similar to the first one, and it is also distributed in the same area as *S. mitsukurii* and *S. japonicus* (Nakabo, 2013; Ziadi-Künzli *et al.*, 2020). The issue between *S. mitsukurii* and *S. clarkae* relies on the fact that until recently, *S. clarkae* was considered as *S. mitsukurii* specimens from the Gulf of Mexico, based on morphological features (Ziadi-Künzli *et al.*, 2020). It was not until 2018 that Pflieger *et al.* (2018), through genetic analyses, found evidence for the establishment of a new species, *S. clarkae*, distributing in the Gulf of Mexico. It is possible that the sequences of *S. mitsukurii*, which clustered with *S. clarkae* are actually sequences from the latter species, wrongly listed as the first one. Despite these being the major issues encountered with *S. mitsukurii*, it is important to mention that taxonomical problems between this species and *S. montalbani* (Ziadi-Künzli *et al.*, 2020) and *S. hawaiiensis* (Daly-Engel *et al.*, 2018) have also been registered.

The same phylogenetic analysis found discrepancies for *S. megalops*, forming monophyletic clades with *S. cubensis* (Figure 4d), *S. blainville* (Figure 4e), and *S. chlorolocus* (Figure 4f). As with *S. mitsukurii*, *S. megalops* has a complex taxonomical status within the *Squalus* genus, with *S. megalops*/*S. cubensis* usually grouped together given their genetic closeness, their difficulty of distinguishing them morphologically, and their shared distribution (Pajuelo *et al.*, 2011). Therefore, it is most likely the case that sequences from either of these species belong to the other one, as with the first three cases described above, and this is why they were clustered together. Taxonomical difficulties have been reported between *S. megalops* and *S. blainville* as well (Marouani *et al.*, 2012), although judging from where the sequences were obtained, it is possible the sequence belonging to *S. megalops* and clustered with *S. blainville* is actually from the latter species, given that the presence of *S. megalops* in the Mediterranean Sea is still contested, and, if present, it is only an occasional visitor and does not figure heavily in both landings and sampling (Ferrari *et al.*, 2021). There is no information available regarding the taxonomical relationship between *S. megalops* and *S. chlorolocus*; however, confusion between *S. megalops* with both *S. mitsukurii* and *S. montalbani* have been reported before (Last *et al.*, 2007). As with the other cases, it is probably a misidentification at the moment of sampling.

Lastly, further taxonomical issues were found between *S. acanthias* and *S. suckleyi* (Figure 4g, 4h). This is due to the fact that some of the sequences used for *S. acanthias* were retrieved from

studies (Veríssimo *et al.*, 2010) prior to the resurrection of *S. suckleyi* as a species within the genus (Ebert *et al.*, 2010). In their study, Veríssimo *et al.* (2010) listed some of the sequences obtained from the North Pacific as *S. acanthias*, although they already mentioned there was strong evidence for these ones belonging to another species given the phylogenetic analyses; afterwards, Ebert *et al.* (2010) described them as *S. suckleyi*. Additionally, the rooted phylogenetic tree for *S. acanthias*, constructed as an intermediate step, showed the formation of monophyletic clades between *S. acanthias* and *S. blainville*. This has already been reported by several authors as a misidentification between both species (Kousteni *et al.*, 2016; ICES WGEF, 2021), given that the information concerning *S. blainville* is quite limited (Kousteni *et al.*, 2016; Gračan *et al.*, 2020).

Conclusions drawn from this analysis support the claim of a complex taxonomical distinction within this genus (Ziadi-Künzli *et al.*, 2020; Ariza *et al.*, 2022). This is explained by the difficulty of using morphological traits to identify between species, which are usually based on morphometrics, dentition, color pattern, and skeletal morphology, with some of them being characteristics that can be hard to identify in the field or during commercial fisheries trips (Viana *et al.*, 2016). Given the poor knowledge on most of these species, stock assessments are virtually impossible to obtain for those, which render species-specific management plans a very hard goal to attain. However, studies focused on reproductive biology and demography of different species distributed in the same area may be useful. If these species possess similar reproductive and demographical traits, then there is the possibility of managing all the species as a unique stock in said area. However, if it is not the case, efforts should be concentrated into training fishers and field researchers into identifying the species to have accurate data.

5.2.2 *Squalus acanthias* phylogenetic tree

The *S. acanthias* phylogenetic tree (Figure 5) established a few monophyletic clades based on the location in which the samples were taken. However, sequences pertaining to the locations forming monophyletic clades were also found in individual clades throughout the phylogenetic tree. This may be due to the fact that almost all of the sequences downloaded from Genbank corresponded to single discrete haplotypes from the different locations, meaning none of the studies published all of the sequenced individuals per region (Veríssimo *et al.*, 2010; Naylor *et al.*, 2012; Veríssimo *et al.*, 2016; Daly-Engel *et al.*, 2018; Ramírez-Amaro *et al.*, 2018; Gračan *et al.*, 2020). Therefore, high genetic variations are expected to be present within the populations

of each region when discrete haplotypes are used, explaining the inability of the phylogenetic tree to group the sequences by region.

Two main issues were detected when constructing the phylogenetic tree. The first one, which has already been mentioned, was the unavailability of several sequenced individuals per region. The importance of sample size has already been mentioned in the introduction of the present work. For stock delineation and detection of genetic structure, a sample size of at least 25-50 individuals should be used (Foster *et al.*, 2021). All the studies from which the sequences were retrieved had bigger sample sizes (Veríssimo *et al.*, 2010; Naylor *et al.*, 2012; Veríssimo *et al.*, 2016; Daly-Engel *et al.*, 2018; Ramírez-Amaro *et al.*, 2018; Gračan *et al.*, 2020; Appendix Table D). However, only discrete haplotypic sequences were uploaded to Genbank, rendering analyses of fine genetic structuring almost impossible. The second one was the use of mitochondrial markers (particularly NADH2) for the analysis. The latter was used since it had the highest number of sequences available in Genbank. However, mitochondrial markers may not be robust enough to distinguish subpopulations at a fine scale and aid towards stock delineation, since they are transmitted via maternal lineage, they are single locus markers, and only a part of the population is observed (Freeland *et al.*, 2011). Therefore, now it is recommended to use markers such as microsatellites (although all studies employed them, there was a low number of them at Genbank) or SNPs (Tsykun *et al.*, 2017) to detect fine population structure.

5.3 Limitations found throughout the study and identification of knowledge gaps on population structure and diversity of the species in the area

Several limitations have been found throughout this study. The following paragraph highlights the most important ones. First, and aligning with what the ICES “Working Group on Elasmobranch Fishes” have already pointed out as pressing issues, there is very limited information about the species in the areas (ICES WGEF, 2021). This includes limited geographical sampling, as most studies pertain to Norway or the United Kingdom in the Northeast Atlantic and the Adriatic Sea region in the Mediterranean. Additionally, since the introduction of the 0 TAC allowance in the area, data collection has only been attained by fisheries surveys, which are somewhat limited. Therefore, other methods should be used, particularly less invasive ones, such as tagging, telemetry, stable isotopes, and genetic analyses.

Despite the availability of these methods, the number of studies utilizing these techniques are still quite limited (Templeman, 1976; Gauld *et al.*, 1982; Vince, 1991; Thorburn *et al.*, 2015). Next, there seems to be a great deal of problems when it comes to field identification of the different species belonging to the genus, given the morphological similarities between most of them (Ziadi-Künzli *et al.*, 2020; Ferrari *et al.* 2021; Ariza *et al.*, 2022). For the areas of interest, this seems to be the case between *S. acanthias*, *S. blainville*, and *S. megalops* (Kousteni *et al.*, 2016; Gračan *et al.*, 2020; Ferrari *et al.*, 2021) whose mix-ups seem to be common. Without solving these issues, catch and landing data loses credibility given the possible misidentification of the species, leading to under or overestimating the biomass for stock assessments and hence the capacity of the stock to withstand fishing activities. Therefore, efforts should first concentrate on establishing clear taxonomical relationships between the species within the genus, paired with accurate field ID, particularly for southern European waters and related to *S. blainville* and *S. megalops*. Additionally, bycatch and discards need to be reported and considered in catch/landing data to make more accurate stock assessments. As of now, it is difficult to conclude the spurdog represents a unique stock in the Northeast Atlantic, given the extremely low amount of information backing up this claim. This claim is based on limited biological information and three genetic studies, which is why this delineation should be supported by a multidiscipline approach, including more demographical information, telemetry studies, genetic structure, and genetic diversity from samples collected in other regions besides Norway, the United Kingdom, and the Adriatic Sea.

Referring to methodological issues, a problem that came up during the present study was the lack of availability of genetic sequences in Genbank, given that most markers had a very low number of sequences published, and NADH2 had mostly discrete haplotypic sequences in the database, which are not enough to detect fine population structuring. This has represented a problem before, as stated by some authors, which is why now it is recommended to explore which genetic marker would be the best suited for the goals of the study, or, in some cases, which combination of genetic markers would be appropriate to answer the question at hand (Veríssimo *et al.*, 2010; Veríssimo *et al.*, 2016; Ziadi-Künzli *et al.*, 2020).

5.4 Recommendations for the establishment of appropriate fisheries management schemes regulating the extraction of this species

As a conclusion, the following states a concise and orderly plan tackling the main issues found in the present study, in order to develop appropriate fisheries management schemes for the spurdog in the Northeast Atlantic Ocean and Mediterranean Sea.

The first issue at hand would be to clear taxonomical issues present within the genus, and particularly for those three species which are distributed in the area of interest (*S. acanthias*, *S. blainville*, and *S. megalops*). Additionally, this implies an improvement on field identification, which could be attained by establishing training programs, workshops, and clear field guides for the people tasked with this process (particularly in southern European waters where all three species coincide in the area). In the meantime, information regarding the species, and mainly focusing on demography, site fidelity, and an estimation of bycatch and discards on different regions of the Northeast Atlantic and Mediterranean Sea, could be collected, in order to update it and have accurate information which will then be used in the stock assessments. With this, the next step would be to increase the amount of genetic information regarding the species, starting with genetic structure and diversity, with the design of a large-scale study including major fishing areas in the Northeast Atlantic Ocean (and not only Norway or the United Kingdom) and the Mediterranean Sea (not only the Adriatic Sea), and using genome-wide nucleotide markers. Once the results from the genetic analyses are available, an informed decision on whether the stocks are in fact only one for the Northeast Atlantic Ocean and one for the Mediterranean Sea, or more than one for these regions can be taken. If more than one stock per region is identified, demographic, reproductive, and site fidelity information, together with economic and social traits of the fisheries harvesting them, should inform towards one or more fisheries management schemes. Finally, all this information could be used to carry on with an accurate stock assessment, establishing a total allowable catch at MSY (if possible) and aiding towards fisheries management schemes in the future.

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7 Appendix

Appendix Table I. References from the literature from which the sequences for *S. acanthias* were extracted and downloaded. These references only include sequences for the NADH2 marker.

Isolate/Voucher	Sequence Length	Genbank accession no.	Literature Reference	Area	Aim of the study
Haplotype 1 to 12	486bp.	MT263520- MT263531	Gračan, R., Lazar, B., Zupan, S. & Bužan, E. 2020. Genetic characterisation of the spiny dogfish <i>Squalus acanthias</i> in the Adriatic Sea: evidence for high genetic diversity and an Atlantic-South Pacific origin. <i>Marine and Freshwater Research</i> , 72(1):131-139.	Adriatic Sea	Genetic diversity and structure
Haplotype 1 to 103	566 bp.	JQ035532- JQ035634	Veríssimo, A., McDowell, J.R. & Graves, J.E. 2010. Global population structure of the spiny dogfish <i>Squalus acanthias</i> , a temperate shark with an antitropical distribution. <i>Molecular Ecology</i> , 19(8):1651-1662.	North and South Pacific and Atlantic Oceans	Global genetic population structure
G12016	954 bp.	MG913596	Ramírez-Amaro, S., Ordines, F., Picornell, A., Castro, J.A., Ramon, C., Massutí, E. & Terrasa, B. 2018. The evolutionary history of Mediterranean Batoidea (Chondrychthyes:	Mediterranean Sea	Bathoid phylogeny

			Neoselachii). <i>Zoologica Scripta</i> , 47(6):686-698.		
-South Africa #323 -Gulf of Lion #PS280212 -Gulf of Lion #LL101111 -Gulf of Lion #LL010312	526 bp.	-KX949765 -KX949764 -KX949751 -KX949750	Veríssimo, A., Zaera-Perez, D., Leslie, R., Iglésias, S.P., Séret, B., Grigoriou, P., Sterioti, A., Gubili, C., Barría, C., Duffy, C., Hernández, S., Batjakas, I.E. & Griffiths, A.M. 2016. Molecular diversity and distribution of eastern Atlantic and Mediterranean dogfishes <i>Squalus</i> highlight taxonomic issues in the genus. <i>Zoologica Scripta</i> , 46(4):414-428.	Eastern Atlantic, Mediterranean Sea	Taxonomy of the genus <i>Squalus</i>
Bio-material GN6336	1044 bp.	JQ518978	Naylor, G.J.P., Caira, J.N., Jensen, K., Rosana, K.A.M., Straube, N. & Lakner, C. 2012. Elasmobranch Phylogeny: A Mitochondrial Estimate Based on 595 Species. <i>In: Carr, J.C. Biology of Sharks and Their Relatives</i> . 2 nd edition, CRC Press. 26pp.	Atlantic Ocean, USA	Taxonomy
Sac_037, 036, 035, 034	529 bp., 476 bp.	MG654814. 1, MG654813. 1, MG654812. 1, MG654811. 1	Daly-Engel, T.S., Koch, A., Anderson, J.M., Cotton, C.F. & Dean-Rubbs, R. 2018. Description of a new deep-water dogfish shark from Hawaii, with comments on the <i>Squalus mitsukurii</i> species complex	West Pacific Ocean	Taxonomy

			in the West Pacific. <i>Zootaxa</i> , 798:135-157.		
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