Status and conservation of sharks

in the Northeast Atlantic

by

Manuel Dureuil

mdureuil@geomar.de

Thesis submitted in fulfilment of the

requirements for the degree of

Master of Science in Biological Oceanography

University of Kiel

1st referee: Prof. Dr. Thorsten Reusch (GEOMAR, Germany)

2nd referee: Dr. Rainer Froese (GEOMAR, Germany)

Additional supervision: Prof. Dr. Boris Worm (Dalhousie University, Canada)

November 2013

Dedication

This thesis is dedicated to my parents who have always supported and believed in me.

Abstract

Declining populations, increasing extinction risk, and growing awareness of their important ecological role have brought sharks increasingly into the public's interest. New legislation has been introduced in various areas to ensure shark conservation and sustainable use. One of these areas is the Northeast Atlantic. Here, rapid losses in large predatory fish biomass have been observed. Nevertheless, only a small number of shark species have been formally assessed in this region to date. In light of current legislation, however, improved information on stock condition, critical habitat and fishing mortality rate is urgently needed to develop appropriate management. In this thesis, critical habitat areas, exploitation levels and abundance trends for three species of Northeast Atlantic sharks are presented: the tope shark (*Galeorhinus galeus*), starry smoothhound (*Mustelus asterias*) and spurdog (*Squalus acanthias*). An overview on their life history and biology is given, which includes von Bertalanffy growth parameters of tope, estimated via a novel approach from tagging data. When analysing critical habitats, evidence was found that important nursery grounds exist in the north-west of Scotland, the Outer Thames Estuary and along the Frisian Islands. Areas with high conservation value for mature sharks include the north coast of Ireland, the Vidal Bank region, the Anglesey Reef (central Irish Sea), the east coast of England and the southern Celtic Sea. Mating is suggested in some of these areas. The current population trends of the three species varied substantially: starry smoothhound and spurdog showed some evidence of recent increase, whereas tope sharks declined by more than 70% over the last two decades. The study revealed that all investigated species are currently exploited above levels that produces maximum sustainable yield (MSY), raising concern about the long-term future of these populations. Furthermore, it is demonstrated that for long living, late maturing and slow growing sharks, the size at first capture is essential for management and that sustainable exploitation may not be achieved if the size at first capture is too low. In conclusion, this study provides an overview on life history traits of tope, starry smoothhound and spurdog in the Northeast Atlantic, the current status is evaluated, and different conservation opportunities are presented.

Acknowledgements

Table of contents

Table of contents

Table of contents

Table of contents

1. General Introduction

1.1 Introduction

Fish with low intrinsic rates of population increase, large maximum size and late maturity are less capable to withstand fishing pressure (Jennings et al. 1998). As a result, the abundance of fishes occupying higher trophic levels has declined dramatically (Pauly et al. 1998, Baum et al. 2003, Myers and Worm 2003) making rebuilding of fish stocks one of the great challenges of this century (Worm et al. 2009). Christensen et al. (2003) showed that the North Atlantic has already lost about 90% of its high trophic level fish biomass since 1900. Furthermore, most fishery resources in the Northeast Atlantic are fully exploited, overexploited or depleted (Froese and Kesner-Reyes 2002, Froese et al. 2012). Sharks are particularly vulnerable to even mild exploitation rates (Myers and Worm 2005, Ward-Paige et al. 2012) and substantial amounts of shark mortality have stemmed from discards (Worm et al. 2013) making evaluation of exploitation difficult. At present, almost half of the exploited shark populations are exploited above their rebound potential, raising concerns about growing extinction risks (Worm et al. 2013). Sharks fulfil an important role in marine ecosystems and their depletion might have serious consequences for the structure, function and stability of marine food webs and ecosystems (Stevens et al. 2000, Myers et al. 2007, Baum and Worm 2009, Ferretti et al. 2010). These findings have recently brought sharks more into public focus. Several legally binding and non-binding legislations have been established to protect, rebuild or ensure sustainable use of sharks. This includes legislation directed towards fish in general as well as those specifically designed for sharks. Within the Law of the Sea (UNCLOS 1982), the signatory countries agreed that exploitation has to be at levels that can produce maximum sustainable yield (MSY). In 2009, the European Community Action Plan for the Conservation and Management of Sharks was released. According to the plan, aims were that shark fisheries have to be sustainable with set catch limits, by-catch has to be regulated and finning was banned (EC 2009). This plan is based on the International Action plan for the Conservation and Management of Sharks adopted and endorsed by the FAO (Food and Agriculture Organization of the United Nations) in 1999. Furthermore, the Marine Strategy Framework Directive holds that European Union members have to achieve or maintain good environmental status in the marine environment by the year 2020 at the latest (EU 2008). This of course includes a good status of shark populations. To achieve these goals, however, the population status has to be known and reference points for management have to be set.

Introduction

Unfortunately, such data is lacking for the majority of shark species in the Northeast Atlantic region. This is a more general problem, evidenced by the number of sharks listed as *Data Deficient* in the IUCN Red List of Threatened Species and the small number of sharks for which advice is given by ICES (International Council for the Exploration of the Sea). In total, the Northeast Atlantic region is home to approximately 65 species of sharks (Compagno 2005) of which 60 are assessed by the Red List. About 37% of the assessed sharks are considered to be threatened, while about 22% are assessed to be *Data Deficient* (IUCN 2013). Two economically important species are declared as *Critically Endangered*, the spurdog (*Squalus acanthias*) and the porbeagle (*Lamna nasus*), both have experienced dramatic declines in the past (Fordham et al. 2006, Stevens et al. 2006, Gibson et al. 2008). Recently, there is zero allowable catch on spurdog (ICES 2012), but specific bycatch regulations still allow for some exploitation of this species (ICES 2009, ICES 2012, STECF 2012), which may counteract a recovery. In contrast, increasing landings have been reported for the starry smoothhound (*Mustelus asterias*) and may reflect its use as replacement species of the spurdog (ICES 2012). However, increasing landings do not provide information about the status of the stock, in terms of sustainable fishing mortality rates or abundance trends, which are important criteria for management purposes. Currently, no management is in place to guarantee appropriate fishing mortality rates of starry smoothhound, although management plans should be implemented before a fishery starts, due to the low productivity of sharks (Musick et al. 2000). Moreover, the increasing demand of shark products (Clarke 2004, Hareide et al. 2007) raises concern about the future development of the starry smoothhound fishery, even though this species is listed as *Least Concern* on the IUCN Red List (Serena et al. 2009). Another species, the tope (*Galeorhinus galeus*) was declared as *Data Deficient* for the Northeast Atlantic, although its status is *Vulnerable* worldwide (Gibson et al. 2008). There have been serious declines in the Californian tope fisheries (Ripley 1946) and in Australia (Olsen 1959, Punt and Walker 1998). Furthermore, reports from South Africa suggested that an increase in fishing could lead to a stock collapse (McCord 2005). Although tope is not a main target species in the Northeast Atlantic shark fishery, it is subject to bycatch (Walker et al. 2006). Mixed species fisheries targeting teleosts also take less productive shark species as bycatch, which is a significant factor in shark mortality and depletion (Musick et al. 2000). Given its status on the IUCN Red List, the limited information about its biology in the Northeast Atlantic and the fact, that this species is mainly targeted indirectly by unregulated and unreported bycatch, means that information for management is urgently needed to prevent situations similar to the spurdog or porbeagle.

Introduction

The management of fisheries in the Northeast Atlantic is the responsibility of the European Community, which provides the annual quotas for allowed catches. The European Community utilises advice from ICES under the MSY approach. However, ICES provides advice for only nine species of sharks (ICES 2012). In addition to setting sustainable exploitation rates, protected areas can be an important conservation tool for sharks (Camhi et al 1998). It has been shown that effective management in fishes can be achieved by a combination of different strategies, such as catch restrictions and habitat protection (Worm et al. 2009). According to this, reliable reference points, critical areas, current and historical exploitation levels and information about the abundance trends are urgently needed to rebuild the shark stocks, ensure sustainable use, derive management strategies and fulfil legislations. Therefore, the aims of this study are: 1) to summarise the available information on the biology and life history traits of tope, starry smoothhound and spurdog 2) to identify habitat areas within the Northeast Atlantic that are critical in sharks life cycle 3) to evaluate the current status and temporal trend of tope, starry smoothhound and spurdog by examining historical and recent exploitation rates and abundance trends 4) and to analyse the importance of the length at first capture for sustainable management.

1.2 Thesis outline

Section 2 describes the basis of data and specific methods applied in this study to investigate the main research objectives, as formulated in the introduction. Sections 3, 4 and 5 summarise the biology and life history of tope, starry smoothhound and spurdog, respectively. To avoid repetition, a general introduction to biology and life history traits is given for tope and referred to in the sections of the other two species. The results of the specific methods are also presented and discussed in the corresponding species section. A general discussion is provided in section 6.

2. The analysis of survey data with specific methods

2.1 Survey data

The investigation of critical habitats, exploitation levels and abundance trends were based on scientific surveys conducted in the Northeast Atlantic. Raw data were obtained from trawl surveys compiled by ICES and freely available from DATRAS, http://datras.ices.dk, consulted on 2012−08−26. Only surveys that used the Grande Ouverture Verticale (GOV) gear were considered to allow comparison between catches. This gear type caught the highest numbers for all of the three species. Likewise, all catches were standardised to one hour of hauling, denoted as number per hour. The area covered by the surveys is shown in Figure 1.

Figure 1: Survey area covered by ICES of surveys undertaken with the Grande Ouverture Verticale (GOV) gear. This gear type was most efficient in catching tope, starry smoothhound and spurdog specimens. The roman numerals refer to the ICES Divisions.

The surveys used in this study were conducted from 1967 − 2012 and ranged in depth from 10 m to 750 m. Hauls at depths greater than the maximum reported depth for the corresponding species were discarded. In addition, the ROCKALL survey was only considered for spurdog, because the other two species were absent in that survey.

Species data were extracted from raw data by their *WoRMS AphiaID* and the *TSN Code*, except for starry smoothhound. This is because two species of the genus *Mustelus* occur in the Northeast Atlantic, the starry smoothhound (*Mustelus asterias*) and the common smoothhound (*Mustelus mustelus*). These two have often been confused with each other (Wheeler 1969). They are usually distinguishable by the presence of white spots exhibited by *M. asterias*. However, there is a high degree of intraspecific variability and these spots can be faint or absent (Farrell 2010) and thus do not represent a reliable taxonomic tool (Farrell et al. 2009). Farrell et al. (2009) developed a genetic identification tool and applied it to 431 specimens of the genus *Mustelus* sampled in all seasons and all large geographic areas within the Northeast Atlantic. Of these 431, 43 were morphologically identified as *M. mustelus* and the remaining individuals as *M. asterias*, but his result revealed that all specimens actually belonged to *M. asterias*. Farrell (2010) concluded that *M. asterias* is the only species inhabiting Northeast Atlantic waters and that single *M. mustelus* specimens would be vagrants. Given that there is no evidence of reliable identified *M. mustelus* within the investigated area, all species assigned as *Mustelus spp*. and *M. mustelus* during the ICES surveys have been classified as *M. asterias*. The number of individuals identified as *M. mustelus* made up approximately 15%, and the percentage of *Mustelus spp*. made up about 4% of the dataset. After species data extraction from raw data, all individuals above the maximum reported size for males were assigned as females, if sex was not determined. The maximum size utilised of male *M. asterias* was 104 cm (Farrell et al. 2010a). The maximum size of male spurdogs was set to 110 cm, the largest male recorded in the DATRAS. In the case of the tope shark, the largest male specimens caught were smaller than the reported maximum length. Finally, all individuals with a length smaller than the reported length at birth were discarded, because of the likelihood of premature birth in the net.

2.2 Identification of critical habitats

Habitat protection is an important component of shark conservation (Camhi et al. 1998, Kinney and Simpfendorfer 2009, Knip et al. 2012) and an important conservation tool in fisheries as such (Worm et al. 2009). Pupping grounds, nursery areas and spawning grounds are critical for recruitment success. Therefore, area protection should focus on different life stages (Kinney and Simpfendorfer 2009). In addition, fishing intensity in the North Atlantic increased by more than twice since 1950 (Christensen et al. 2003), making refuges essential for conservation purposes. Here, pupping and nursery grounds were investigated, as well as aggregation sites of mature individuals.

The analysis of survey data with specific methods

The identification process was based on mean catch per unit effort (*CPUE*) per ICES statistical rectangle, obtained from survey data. The calculation followed the ICES index calculation procedure (ICES 2006). Note that here the simplifying assumption that all statistical rectangles have the same size was made, although costal rectangles can be smaller. Furthermore, DATRAS raw data gives the number caught per length per haul. These numbers were summarised before calculating the mean *CPUE* for the length classes corresponding to the different life stages. A hypothetical example of the calculation procedure is given in Table 1. In total, the following steps were applied:

1. Four datasets were generated to investigate the aggregation sites of different life stages or sexes:

1) Dataset *pups*, containing all individuals with published length range at birth (see *Reproductive biology* sections), to identify pupping areas.

2) Dataset *early juveniles*, containing all individuals from lengths larger than maximum published length at birth up to 50 cm, to identify nursery areas.

3) Dataset *mature specimens*, containing all individuals with length equal or larger than length at maturity, to identify critical areas of adults. If sex was not given, the length at 50% maturity of females was used.

4) Dataset *mature females*, containing all mature specimens except males, i.e. also those with unreported sex, to identify the most likely distribution for females.

2. The numbers caught per length *L* and haul *H* were summarised for each dataset by statistical rectangle (*StatRec*), year *y* and quarter *q*, to generate the total number caught for the given life stage in the statistical rectangle, quarter and year:

$$Number_{StatRec,y,q} = \sum_{StatRec,y,q} Number\ per\ hour_{H,L} \tag{1}$$

3. The mean *CPUE* per year and quarter in the statistical rectangle was obtained by dividing the number caught in the statistical rectangle, year and quarter with the total numbers of hauls made in the statistical rectangle, year and quarter:

$$mCPUE_{StatRec,y,q} = \frac{Number_{StatRec,y,q}}{\sum_{StatRec,y,q} H} \tag{2}$$

4. In addition to the ICES index calculation procedure, the mean *CPUE* per statistical rectangle was calculated over all years. Therefore, the mean *CPUE* per statistical rectangle, year and quarter was added for each statistical rectangle and divided with the total number of years fished in this statistical rectangle:

$$mCPUE_{StatRec} = \frac{\sum_{StatRec} mCPUE_{StatRec,y,q}}{\sum_{StatRec} y_{fished}} \tag{3}$$

5. Distribution maps were generated on the basis of mean *CPUE* per statistical rectangle to investigate aggregation sites of the different life stages.

6. For the purpose of this study, areas were developed and assigned on the basis of abundance patterns, obtained from the distribution maps. The mean *CPUE* per area ($mCPUE_{area}$) was calculated by taking the mean of equation 2, i.e. the average *CPUE* per year and quarter of all statistical rectangles in that area. Under this definition the size of the area is not considered.

7. The month with the highest number of catches in the assigned area ($mCPUE_{month}$) was examined by taking the average for each month of the total number caught in a month per statistical rectangle divided by the total number of hauls in this month and rectangle.

The final identification of critical areas was based on a combination of side fidelity, i.e. over how many years catches have been reported, and abundance. This is consistent with criteria given by Heupel et al. (2007) for shark nursery grounds, suggesting that these sites have a greater abundance of pups than other areas and that the same areas are repeatedly used across years. Likewise, it was assumed in this study that adult aggregation sites show a higher abundance of mature individuals across years than elsewhere. In addition, the monthly distribution was used trying to cover different season by the critical areas and to detect seasonal patterns. Note that this accounts rather for species presence in that area during the month, because surveys were not made in every month in all areas.

Table 1: Hypothetical example of the *CPUE* calculation procedure applied in this study. Here, the area used to determine the mean *CPUE* per area and the mean *CPUE* per month is assumed to consist of two rectangles (40F0, 39F1).

StatRec	40F0	40F0	40F0	40F0	40F0	39F1	39F1	39F1	39F1	39F1
year	2000	2000	2000	2001	2001	2002	2002	2002	2003	2004
quarter	1	1	4	4	4	2	4	4	1	1
haul no	H1	H1	H2	H1	H2	H1	H1	H2	H1	H1
length (cm)	30	70	40	0	90	70	100	0	0	0
month	1	1	11	11	11	5	11	11	1	1
$Number\ per\ hour_{H,L}$	3	5	2	0	6	7	3	0	0	0
$Number_{StatRec,y,q}$	8		2	6		7	3		0	0
$\sum\limits_{StatRec,y,q} H$	1		1	2		1	2		1	1
$mCPUE_{StatRec,y,q}$	8		2	3		7	1.5		0	0
$\sum\limits_{StatRec} mCPUE_{StatRec,y,q}$	13					8.5				
$\sum\limits_{StatRec} y_{fished}$	2					3				
$mCPUE_{StatRec}$	6.5					2.83				
$mCPUE_{area}$	3.07									
$mCPUE_{month}$	4		2.08			7				

2.3 Biological reference points for fishing mortality

Sustainable exploitation is the prescribed target for fisheries management. Here, two methods were applied to estimate proxies of the fishing mortality which produces maximum sustainable yield F_{msy}.

Method 1:

The first method derives F_{msy} from the potential of a population to grow, i.e. the intrinsic rate of population increase r (Simpfendorfer 2005). It is used to estimate F_{msy} according to (Ricker 1975) as:

$$F_{msy} = 0.5r \tag{4}$$

The intrinsic rate of population increase under stable age conditions was obtained from the Euler-Lotka equation by following a life table approach (e.g. Calliet 1992, Simpfendorfer 2005):

$$\sum_{x=t_m}^{t_{max}} e^{-rx} l_x m_x = 1 \tag{5}$$

where m_x is the age x specific fecundity (i.e. number of female offspring per female), l_x is the proportion of individuals surviving to age class x, t_m is the age at maturity and t_{max} is the maximum age. The number of female embryos produced by each female per year was obtained by multiplying the fecundity at length times the proportion of females mature at this length. To account for sex ratio, resting stages and the complete reproductive cycle, the product was multiplied with 0.25 for all species. Age was obtained from length by applying the von Bertalanffy growth function. The survival to age l_x was calculated from age zero to maximum age after the following relationship:

$$l_x = l_{x-1} * e^{-M} \tag{6}$$

where M is the natural mortality. The initial value l_0 was set to 1, to investigate if that recruit will be replaced by the population (Simpfendorfer 2005) and natural mortality was assumed constant. Finally, r was estimated iteratively using Excel Solver. The intrinsic rate of population increase is obtained if the sum from age at maturity to maximum age of equation 5 equals 1. A hypothetical example is presented in Table 2.

Method 2:

The rate of natural mortality M has been widely used in fisheries management as a proxy for F_{msy} (e.g. Gulland 1971, Shepherd 1981, Clark et al. 1985, Beverton 1990, Patterson 1992, MacCall 2009, Pikitch et al. 2012). However, $F_{msy} \gg 0.5M$ should be carefully justified (Walters and Martell 2002) and recent estimates for chondrichthyans derived from empirical data suggested $F_{msy} = 0.41M$ (Zhou et al. 2012). Therefore, this study uses $F_{msy} = 0.5M$ as a second proxy for the fishing morality rate which achieves maximum sustainable yield.

Table 2: Hypothetical example of a life table used to determine the intrinsic rate of population increase r. Age at maturity was assumed at age 3 and natural mortality at 0.2 yr^{-1}. Hypothetical numbers were used for the age specific fecundity, i.e. the number of pups produced by a female per year m_x. The initial value for the survival to age l_x was set to 1. The survival to age x was calculated as described in equation 6, e.g. $l_1 = 1.00 \ast e^{-0.2}$, $l_2 = 0.82 \ast e^{-0.2}$. The product of m_x and l_x is the annual reproductive rate per generation. Excel Solver was used to iteratively solve the equation $l_x m_x \ast e^{(-rx)}$. The intrinsic rate of population increase is obtained if the sum of $l_x m_x \ast e^{(-rx)}$ from age at maturity to maximum age (ages shown in bold) equals 1. Thus, r would be at 0.055 yr^{-1} in this example.

Age	m_x	l_x	$l_x m_x$	$l_x m_x \ast e^{(-rx)}$
0		1.00		
1		0.82		
2		0.67		
3	0.5	0.55	0.27	0.233
4	0.75	0.45	0.34	0.271
5	1	0.37	0.37	0.280
6	1	0.30	0.30	0.217

2.4 Estimation of total and fishing mortality

The low productivity of sharks makes them extremely vulnerable to already modest levels of fishing mortality (Camhi et al. 1998), although sustainable exploitation is thought to be possible at least in some species (Walker 1998). The evaluation of the stock exploitation can be made by comparing its fishing mortality rates with sustainable rates such as F_{msy}. Here, the exploitation levels were examined for tope, starry smoothhound and spurdog. Two procedures were applied to obtain total instantaneous mortality Z, from which fishing mortality can be derived. Age was obtained from length trough the von Bertalanffy growth function.

1) If data was limited, a catch curve was generated. Catch curves track a yearclass over time and assume that a decrease in numbers is solely based on morality Z (no emigration or immigration or a balance between these):

$$N_{t+1} = N_t e^{-Z} \tag{7}$$

The numbers are log-transformed and plotted over age. In a fished population, the slope of a regression line of the right descending arm of the plot is the total instantaneous mortality rate Z. Here, a linear regression weighted by the numbers caught per hour was applied, because of a greater degree of belief in catches where more individuals were reported. In addition, the numbers were pooled across years as described by Beerkircher et al. (2003), due to small sample size.

2) If the sample size was large, the trend of exploitation in subsequent years was investigated. Here, total mortality rates were calculated via catch ratios of pooled ages to obtain the total instantaneous mortality rates in a given year Z_y:

$$Z_y = LN \left[\frac{\sum_{t_r}^{t_{max}-1} N_t}{\sum_{t_r+1}^{t_{max}} N_{t+1}} \right] \tag{8}$$

where t_r is the age of recruitment, t_{max} is the maximum age and N_t is the number caught at this age. A hypothetical example of the catch ratio calculation procedure is given in Table 3. These ratios assume no error in catch, therefore a three years moving average was applied to the numbers caught by age and year. Under this definition, the first and last values were based on only two data points, due to border effects. The calculation was based on pseudocohorts, representing a snapshot across cohorts in one year.

The fishing mortality rates for both procedures can be obtained from total mortality rates by subtracting natural mortality:

$$F = Z - M \tag{9}$$

Note that ages calculated from length larger than 95% of the asymptotic length were not included into the mortality model.

Table 3: Hypothetical example of the calculation procedure applied in this study, to obtain instantaneous fishing mortality rates F per year from pooled catch at age ratios. Here, a natural mortality rate of $M = 0.2$ yr^{-1} was assumed for demonstration purposes. Z was estimated for ages 2 to 6 (bold), assuming that recruitment is at age 2 and the sample is representative till age 6. The total mortality Z in year 2000 is obtained as: $LN((950+700+450+250)/(700+450+250+50)) = 0.48$. F is obtained by subtracting M from Z.

year	number per age class										Z	F
	age 0	age 1	**age 2**	**age 3**	**age 4**	**age 5**	**age 6**	age 7	age 8	age 9		
2000	1000	900	950	700	450	250	50	30	20	1	0.48	0.28
2001	800	700	750	500	250	50	20	60	30	0	0.64	0.44
2002	900	800	850	600	350	150	30	70	40	0	0.55	0.35
2003	1100	1000	1050	800	550	350	150	100	30	2	0.40	0.20
2004	950	850	900	650	400	200	70	30	0	0	0.49	0.29
2005	1000	900	950	700	450	250	50	20	10	5	0.48	0.28

2.5 Estimation of relative exploitation levels

In data-poor situations, where it was not possible to estimate fishing mortality rates across years, relative exploitation levels can be used instead, to investigate the temporal trend of exploitation. Here, an index based assessment was applied (e.g. NEFSC 2002, Cadrin et al. 2004). Relative exploitation ratios U_{rel} can be obtained from the relationship of total landings to the corresponding survey biomass index *SBI*:

$$U_{rel} = total\ landings/SBI \qquad\qquad (10)$$

SBI was calculated as the weight of all individuals per one hour of hauling, with weight estimated from length by applying a length-weight relationship. Total landings were obtained from the Eurostat/ICES database on catch statistics (ICES 2013), version 07-03-2013 available at http://ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx. A 1:1 replacement ratio was used to investigate, if the exploitation ratios allow the stock to replace itself. Therefore, the rate of change was calculated by dividing the *SBI* of a given year with the average of the five previous years. The reference value that allows the stock to replace itself can be obtained by applying a power function of the rate of change versus the relative exploitation rate. Replacement is achieved at the relative exploitation ratio where the regression line equals a rate of change of one. In other words, if the exploitation rate is below this proxy, the population can presumably withstand the rate of exploitation.

2.6 Investigation of abundance trends

The abundance trends over the last decades of tope, starry smoothhound and spurdog in the Northeast Atlantic were investigated. A standardised Catch per unit effort (*CPUE*) series was used as a measure of abundance to detect trends over time. *CPUE* was calculated as described in ICES (2006). First, the sum of the numbers caught per statistical rectangle, year and quarter was divided with the total number of hauls per statistical rectangle year and quarter (section 2.2, equation 2). Then, the result was summarised per year and divided with the total number of rectangles fished this year. Note that under this definition, the area consists of the total survey area corrected for depth strata (Figure 1), assuming that a given species can occur in every statistical rectangle. Furthermore, it derives that all statistical rectangles have the same size. The time period used for each species was defined from the first year where all age classes have been caught representatively till 2012. The trend was estimated via an exponential model. The mean *CPUE* over the whole time series served as reference point.

2.7 The importance of length at first capture

If fishes are caught several years before they reach maturity, then a stock may not be able to recover, even if fishing mortality is F_{msy}. It has been shown, that the exploited cohort biomass and the yield decrease, if the size at first capture is too small (Froese et al. 2008, Colloca et al. 2013). Furthermore, neither yield nor biomass can be maximised under sustainable exploitation without optimising size selectivity (Colloca et al. 2013). In bony fishes, an optimum length L_{opt} can be used as a reference point for growth overfishing (Froese 2004) and Froese et al. (2008) showed, that stocks where fishes are caught after they have reached L_{opt} show healthy age composition and higher biomass. Here, the importance of the length and age at first capture in the management of sharks as well as the effect of fishing at the optimum size and age was investigated. Therefore, the cohort biomass was calculated for different fishing scenarios (no fishing $F = 0$, sustainable fishing mortality rate F_{msy} and current fishing mortality rate $F_{current}$) and ages at first capture. The tope shark served as reference species, because it attains the highest maximum age of all species in this study, making it presumably more vulnerable if fishing starts at young ages. First, the number at each age in the cohort N_t under different scenarios of fishing mortality F_{sce} and age at first capture t_c was derived from:

$$N_t = N_{t-1} * e^{-M} \qquad \text{for } t < t_c \tag{11}$$

$$N_t = N_{t-1} * e^{-(M+F_{sce})} \qquad \text{for } t \geq t_c \tag{12}$$

where M is the natural mortality. The other parameters have been defined above. An arbitrary value of 100 was used as initial value for N_{t-1} (recruits). Then, cohort biomass was obtained by multiplying the number at age with weight at age W_t, obtained from the length weight relationship. The optimum length (L_{opt}) was calculated after Beverton (1992):

$$L_{opt} = L_\infty \frac{3}{3+\frac{M}{k}} \tag{13}$$

where M is the natural mortality, L_∞ the asymptotic length and k the von Bertalanffy growth coefficient. Ages were translated in length by applying the von Bertalanffy growth function. A hypothetical example is presented in Table 4.

Table 4: Hypothetical example of the length/age at first capture calculation procedure. Length was obtained from age by applying the von Bertalanffy growth function. Here an asymptotic length of 100 cm, length at birth of 10 cm and a von Bertalanffy growth parameter k of 0.5 were assumed, e.g. length at age 2 = $100-(100-10)*e^{(-0.5*2)}$. The fishing mortality rate was assumed at 0.3 yr^{-1}, the natural mortality rate at 0.2yr^{-1}. The optimum length was obtained from equation 13: $L_{opt} = 100*3/(3+0.2/0.5)$ and is 88 cm. Therefore, the optimum age at first capture is 4 (shown in bold). The number at each age in the cohort N_t was obtained from equation 11 and equation 12, the initial value was set to 100, e.g. $N_1 = 100*e^{-0.2}$, $N_5 = 27.25*e^{-(0.2+0.3)}$. The mean weight at age W_t was obtained from a length-weight relationship with $a = 0.01$ and $b = 3$, e.g. $W_5 = 0.01*92.61^3$. The cohort biomass is the product of mean weight at age and the number at age divided by 1000 to obtain tonnes.

length (cm)	age	N_t	W_t (gram)	cohort biomass (mt)
10.00	0	100.00	10.00	1
45.41	1	81.87	936.52	76.68
66.89	2	67.03	2992.95	200.62
79.92	3	54.88	5104.33	280.13
87.82	**4**	33.29	6772.95	225.45
92.61	5	20.19	7943.41	160.36

3. Biology and life history of *Galeorhinus galeus*

The tope (*Galeorhinus galeus*) (Figure 2) belongs to the family of *Triakidae*, one of the largest families within the order of the ground sharks (Carcharhiniformes) and it is the only species within the genus *Galoerhinus*. Its distribution is worldwide in temperate waters, but it is absent in the western North Atlantic. Other common names for tope are soupfin shark in the eastern Pacific and South Africa and school shark in Australia and New Zealand. Although this species has very low biological productivity, it is important in shark fisheries (Compagno 1984b, Compagno et al. 2005). In the following, the biology and life history traits needed to examine the status, trends and conservation opportunities for this species will be presented. The findings are summarised in the Supplementary Information (Table 2).
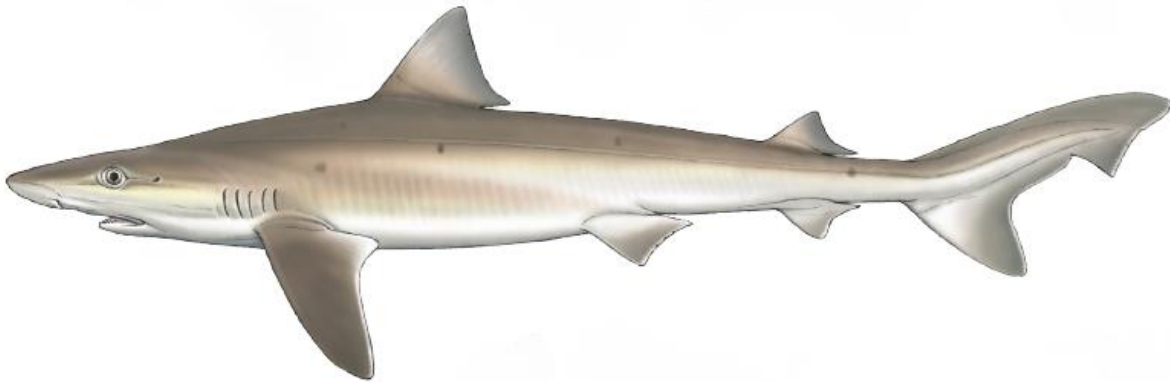
Figure 2: Illustration of *Galeorhinus galeus*, modified and taken from www.sharktrust.org.

3.1 Length-weight relationship

3.1.1 Introduction

Body weight can be obtained from length by a length-weight relationship of the form:

$$W = a * L^b \tag{14}$$

Where W is the weight and L the length. The parameter a describes the body shape and b indicates whether body shape is changed during growth. If b is ~ 3, growth is isometric (Froese 2006). Tope has a slender body (Figure 2), therefore the shape parameter a is expected to lie between 0.01 and 0.001 (Froese 2006).

3.1.2 Materials and methods

The length-weight relationship of the tope shark for the Northeast Atlantic was calculated using DATRAS raw data from ICES surveys available at http://datras.ices.dk, consulted on 2012−08−26. Records of weight and corresponding length were used only if one individual was reported, because of inconsistencies in hauls with several specimens. Additional length-weight values were derived from an electronic chart provided by Scottish Sea Angling Conservation Network (SSACN), available at http://www.ssacn.org/gfac/length-to-weight/tope, consulted on 2012−08−26. In this chart, data points were chosen every 10 cm from the regression line, and the weight in pounds was multiplied with 453.59 to obtain gram. Relationships were determined for males, females and both sexes combined.

3.1.3 Results

Length-weight relationships of tope are presented in Table 5. Total length is given in cm and weight is given in gram. The 123 length observations obtained from ICES surveys ranged from 33 cm to 163 cm in male sharks (n = 76) and from 34 cm to 148 cm for female sharks (n = 47). The 30 length values obtained from SSACN ranged from 50 cm to 200 cm for females and from 50 cm to 180 cm for males (Figure 3).
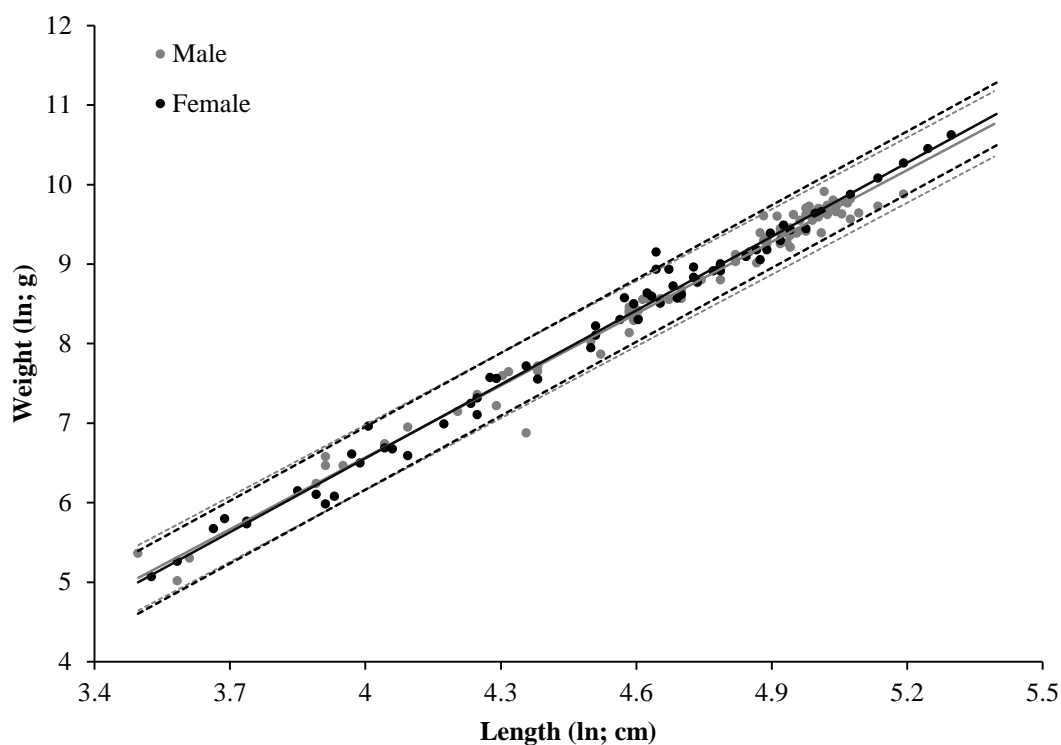
Figure 3: Relationship between the natural logarithm (ln) of body weight (grams) and the natural logarithm of total length (cm) of male and female tope for the Northeast Atlantic. The grey dashed line indicates the 95% confidence limits for males and the black dashed line the 95% confidence limits for females.

Table 5: Length-weight relationship of tope for the Northeast Atlantic. The total sample size (n) contained 153 individuals ranging from 33 cm to 200 cm in length. The 95% confidence limits (CL) are given for each sex and parameter.

sex	a	b	n	length range (cm)	95% CL a	95% CL b	r^2
male	0.0042	3.01	90	$33 - 180$	0.0028 - 0.0064	2.92 - 3.10	0.98
female	0.0029	3.10	63	$34 - 200$	0.0019 - 0.0044	3.01 - 3.19	0.99
combined	0.0037	3.04	153	$33 - 200$	0.0028 - 0.0049	2.98 - 3.10	0.99

3.1.4 Discussion

Larger specimens were not sampled effectively in the survey data (ICES 2009). Therefore, additional data was supplemented from SSACN to determine the length-weight relationship of tope for the Northeast Atlantic. Since b was close to 3, a can be interpreted as form factor. With 0.003 to 0.004 it falls between the 0.001 for eel-like fishes and 0.01 for fusiform fishes (Froese 2006), i.e. it is as expected for an elongated or slender fish (Figure 2). Although slightly lower, the results of the exponent b are similar to those from Australia (Olsen 1954). The mean of 3.04 indicates isometric growth, with a slight tendency to become more rotund with size (Froese 2006). These findings agree with those from the eastern Pacific, which have suggested, that females increase more in weight at the onset of maturity (Ripley 1946). However, the differences between males and females in length-weight relationship are not significant, as can be seen by the overlapping in confidence limits (Table 5).

3.2 Reproductive biology

3.2.1 Introduction

Information about reproductive biology is important for demographic life history models. Such information is lacking for tope in the investigated areas. However, tope in the Mediterranean Sea reach similar maximum size and weight as in the Northeast Atlantic (Capapé and Mellinger 1988, EFSA 2013). Moreover, migrations from Britain to the Mediterranean Sea, Madeira and the Azores have been reported (Fitzmaurice 1979, Sutcliffe 1994, Little 1995, Little 1998). Therefore, available information about the reproductive biology of tope from these three locations was analysed.

3.2.2 Materials and methods

Information was extracted from the literature. The size where 50% of individuals have reached maturity was obtained as mean values across all available studies.

If the size at 50% maturity was not given, but values of first and 100% maturity were, the average of these two values was used. A logistic regression model was applied to describe the proportion of females mature at a given length (e.g. Holden and Meadows 1964, Gauld 1979, Henderson et al. 2002, Farrell et al. 2010b, Couto 2013). Therefore, the minimum length of immature females, the mean length at 50% maturity and the maximum reported length at which all individuals are mature were fitted to the model. The coefficients *a* and *b* were estimated by using Excel Solver. For the purpose of this study, immature individuals were defined as the smallest mature individual minus one centimetre. Information about fecundity at length was obtained from literature and fitted with a power function (Froese and Luna 2004).

3.2.3 Results

The sizes at different maturity stages of males and females are given in Table 6. Males start to mature at a mean length of 114 cm and reach 50% maturity at a size of 121 cm. All males are mature at a size of 127 cm. Females start to mature at a size of 140 cm. All females are mature at a size of 182 cm and the length at 50% maturity is 155 cm. The length at birth ranges from 24 cm to 32 cm, with a mean size of 28 cm (Capapé et al. 2005). Fecundity ranges from 8 to 41 pups and increases with the length of the mother (Capapé and Mellinger 1988, Capapé et al. 2005). Observations on the number of embryos/eggs corresponding to the maternal length were obtained from Capapé et al. (2005). The relationship is described by:

$$litter\ size = 0.0001 * TL^{2.36} \ (r^2 = 0.19) \tag{15}$$

Given the data in Table 6, the proportion of females mature p can be described by:

$$p = 1/(1 + e^{-(-40.8 + 0.263 * TL)}) \tag{16}$$

where *TL* is the maternal total length in cm. The sex ratio at birth is in slight favour of males. From 120 embryos, 45.8% (Capapé et al. 2005) and from 115 embryos, 47.8% (Capapé and Mellinger 1988) were females. The average proportion of 46.8% female pups is close to the expected 1:1 ratio. The gestation time lasts approximately 12 months and reproduction occurs every other year, although a reproductive cycle of three years may be possible (Capapé et al. 2005). Information about the time of parturition differs across the literature. The Agri-Food & Biosciences Institute (2009) stated, that the main pupping season in southern British waters is from August to December, whereas other sources state, that tope gives birth during the warm summer months (Wheeler 1969, Little 1995, Nevell 1998).

Similarly, pupping was reported to occur from June to September at the northern French coast (Walker 1999). Capapé and Mellinger (1988) suggested that ovulation, mating and pupping occur from April to June in the Mediterranean Sea. Later, Capapé et al. (2005) suggested two breeding periods, one from December to February and the other one from April to June, with mating in June and August.

Table 6: Maturity stages of tope in the Northeast Atlantic. In bold are the mean values used in this study. The 95% confidence limits of length at 50% maturity estimates are given in parentheses.

| sex | length at maturity (cm) | | | region | source |
	first	50%	100%		
male	114	---	---	Mediterranean	Capapé and Mellinger (1988)
	122.5		127	Mediterranean	Capapé et al. (2005)
	---	120.5	---	Mediterranean	mean (Capapé and Mellinger 1988, Capapé et al. 2005)
	---	126	---	Azores	Couto (2013)
	---	115.9	---	Madeira	Couto (2013)
	114	**121** (±2.3)	**127**	NE Atlantic	this study [1]
female	150	---	182	Mediterranean	Capapé and Mellinger (1988)
	140	---	---	Mediterranean	Capapé et al. (2005)
	---	161	---	Mediterranean	mean (Capapé and Mellinger 1988, Capapé et al. 2005)
	---	153.1	---	Azores	Couto (2013)
	---	151.1	---	Madeira	Couto (2013)
	140	**155** (±2.3)	**182**	NE Atlantic	this study [1]

[1] mean length at 50% maturity and minimum or maximum length at first and 100% maturity, respectively.

3.2.4 Discussion

The sizes at maturity in Table 6 are in agreement with those reported from the eastern Pacific, a region where this species attains a similar maximum size (Ripley 1946). Moreover, the size at first maturity of females is consistent with results from the west of Ireland, where a 132 cm large female was recorded as immature (Henderson et al. 2003). Length at birth in the Northeast Atlantic is apparently slightly smaller than the 40 cm reported from other areas (Compagno 1984b). If one assumes an error of sex ratio of ±10%, then 46.8% would not be significantly different from 50%. Therefore a sex ratio of approximately 1:1 was confirmed, although sex ratios in favour of females have been reported from South Australia (Olsen 1954), whereas in the western South Atlantic males were the predominant sex (Peres and Vooren 1991, Lucifora et al. 2004). The reproductive cycle is consistent with observations from Australia (Olsen 1954), but less than the three years cycle reported from western South Atlantic (Peres and Vooren 1991, Lucifora et al. 2004).

The number of pups obtained from the relationship with maternal size found in this study was lower than in all other areas (Ripley 1946, Olsen 1954, Peres and Vooren 1991, Lucifora et al. 2004, Capapé et al. 2005), possibly due to the lower sample size of 13 individuals. Note that the relationship derived in this study uses the expected power function (Froese and Luna 2004) whereas the other studies used a linear relationship. The time of mating varies across literature and may be difficult to determine unless directly observed, because mating occurs up to five months before ovulation has been reported (Peres and Vooren 1991).

3.3 Age and growth

3.3.1 Introduction

Growth of chondrichthyans is commonly described by the von Bertalanffy growth function (Calliet et al. 2006). The original formula with length at birth L_0 instead of age at zero length t_0 as third parameter was applied in this study, as recommended for sharks (Calliet et al. 2006). The von Bertalanffy growth function is as follows (von Bertalanffy 1938):

$$L_{(t)} = L_\infty - (L_\infty - L_0)e^{-kt} \tag{17}$$

where $L_{(t)}$ is the length at age t, L_∞ is the length a fish would reach if it would grow forever and k is a curve parameter describing how fast L_∞ is approached. Age can be obtained by adjusting the formula:

$$t = \frac{1}{k} * LN((L_\infty - L_0)/(L_\infty - L_{(t)})) \tag{18}$$

Information about growth of the tope shark in the Northeast Atlantic is deficient. Henderson et al. (2003) examined the vertebrae of four males and estimated their ages. Stevens (1990) reported a mean annual growth of 7 cm in medium sized species and 2 cm in large species for both sexes combined. Here, von Bertalanffy growth parameters of tope for the Northeast Atlantic were derived from tagging data, with a new method (unpublished, Froese 2013, personal communication).

3.3.2 Materials and methods

An iterative approach was developed to estimate von Bertalanffy growth parameters of tope. The data was based on recaptures from different tagging programmes conducted in the Northeast Atlantic, the first initiated in early 1959 (Holden and Horrod 1979).

Information on sex, time at liberty and growth in weight or size was obtained from the literature (Holden and Horrod 1979, Stevens 1990, Little 1995) and the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) tagging database, the UK Shark Tagging Programme and the Scottish Sea Angling Conservation Networks (SSCAN) Shark Tagging Programme. Lengths obtained from weight by Stevens (1990) were back-calculated to weight by the formula he applied. Length was calculated from the inverted length-weight relationship obtained for the Northeast Atlantic (section 3.1), whenever weight was given instead of length or when length values were erroneous. Duplicate records in the different sources were deleted. Information on growth rates from tagging data can be subject to significant measurement errors (Holden and Horrod 1979, Stevens 1990), among others, because of the inherent variability of body weight. Thus, reported negative growth rates and two growth rates of mature males of 35 cm and 58 cm per year (Stevens 1990), considered questionable by the author, were excluded from the analysis. Moreover, outliers may lead to biased results, especially if the sample size is small. Due to large variability in annual growth among individuals, the absolute median deviation (MAD) was applied to detect and eliminate outliers, so that a representative growth sample of the majority of the individuals was obtained. MAD is defined as the median of the absolute differences of each data point to the median of the data (Hampel 2001). All annual growth rates that deviated more than three times the MAD were defined as outliers and excluded. Then, the von Bertalanffy growth parameters were estimated by the least residual sum of squares of predicted to observed growth, obtained via an iterative approach. This method requires an independent estimate of the asymptotic length L_∞. This was determined by the average of the three largest/heaviest specimens caught within the Northeast Atlantic and the Mediterranean Sea, sourced from the literature. The growth parameters were estimated in five steps:

1. Observed growth increment ΔL was obtained by:

$$\Delta L = L_r - L_c \tag{19}$$

where L_c is the length at capture and L_r is the length at recapture.

2. The age at the length of capture t_{Lc} was calculated by using an initial arbitrary value (e.g. 0.1) for the von Bertalanffy growth parameter k:

$$t_{Lc} = -LN(1 - \frac{L_c}{L_\infty})/k \tag{20}$$

3. The predicted length at recapture $\hat{L}_r$ was estimated:

$$\hat{L}_r = L_\infty(1 - e^{-k(t_{Lc}+dt)}) \tag{21}$$

where *dt* is the time at liberty in years.

4. The predicted growth increment $\widehat{\Delta L}$ can be obtained as:

$$\widehat{\Delta L} = \hat{L}_r - L_c \tag{22}$$

5. In the last step, *k* can be solved iteratively by minimizing the residual sum of squares of observed and predicted growth increments across all available recapture data. The standard deviation (*SD*) derived from residuals was used as a measure of uncertainty. *SD* was estimated from the single observed $k_{i,obs}$ values minus the predicted *k*. The observed von Bertalanffy growth parameter can be obtained via:

$$k_{i,obs} = \frac{\Delta L}{dt} / (L_\infty - (\frac{(L_r+L_c)}{2})) \tag{23}$$

SD is described by:

$$SD = \sqrt{\sum \frac{(k_{i,obs}-k)^2}{(n-2)}} \tag{24}$$

where *n* is the sample size. The estimated growth parameters were compared with those from other areas via the auximetric grid of Pauly et al. (1996). Based on length at maturity information (section 3.2) the growth parameters were used to calculate the age at maturity. Longevity is empirically related to the age at maturity (Froese and Binohlan 2000). Therefore, maximum age t_{max} was derived from its ratio to age at maturity t_m as described by Frisk et al. (2001) for elasmobranches:

$$t_{max} = t_m/0.38 \tag{25}$$

3.3.3 Results

In males, four individuals were excluded with an annual growth of 11 cm, 13 cm, 20 cm and 28 cm. In female sharks, five individuals were considered as outliers, one with an annual growth of 14 cm, two with an annual growth of 18 cm and two with an annual growth of 26 cm. The final dataset contained 16 male and 33 female sharks. The annual growth ranged from 1 cm to 12 cm in females (mean = 5.18 cm) and from 1 cm to 8 cm in males (mean = 3.3 cm).

Length ranged from 45 cm to 175 cm in females and 112 cm to 168 cm in males. In males, the shortest time at liberty was 10 weeks, the highest 10.9 years (mean 3.1 years). The time at liberty of females ranged from 7.3 weeks to 6.7 years (mean = 2.4 years). The maximum reported length of females was 200 cm from the Mediterranean Sea (Capapé and Mellinger 1988). The reported maximum weight for females in the southern North Sea was 37.4 kg (EFSA 2013) and 36.7 kg in Scottish waters (SSTP 2010). Stevens (1990) reported the heaviest male to be 22.3 kg in the Northeast Atlantic. These weights correspond to a length of 197 cm and 196 cm for females and 171 cm for males, respectively, derived from the length-weight relationship (section 3.1). Holden and Horrod (1979) found the largest male to be 168 cm in Irish waters and the largest male from Spanish waters was 184 cm (UK Shark Tagging Programme). The asymptotic length was calculated as the average of these catches and was 198 cm in females, 174 cm in males and 186 cm for both sexes combined. The obtained values for the von Bertalanffy growth function are given in Table 7 and are visualised in Figure 4 and 5.

Table 7: Von Bertalanffy growth parameter estimates for tope in the Northeast Atlantic. As a measure of uncertainty, the standard deviation (*SD*) derived from residuals was calculated from the observed minus the predicted *k*.

sex	L_∞	L_0	k	$SD\ k$	n
male	174	28	0.087	0.021	16
female	198	28	0.066	0.008	33
combined	186	28	0.074	0.009	49

On the basis of the von Bertalanffy growth parameters, age at 50% maturity was 21 years for females and 12 years for males. Longevity of tope in the Northeast Atlantic was estimated to be 55 years.
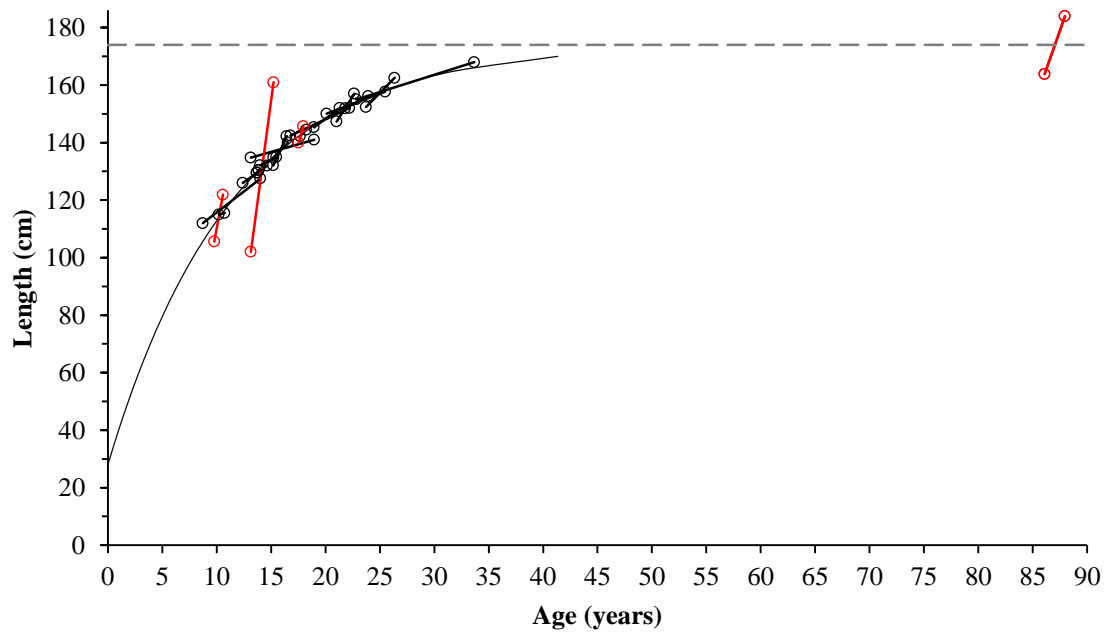
Figure 4: The figure shows the von Bertalanffy growth of male tope sharks within the Northeast Atlantic, estimated via an iterative approach: $L_{(t)} = 174-(174-28)e^{-0.087t}$. The black open circles represent the considered tagging data, the red open circles the outliers defined as exceeding three times the median absolute deviation (MAD). The grey dashed line indicates the asymptotic length.
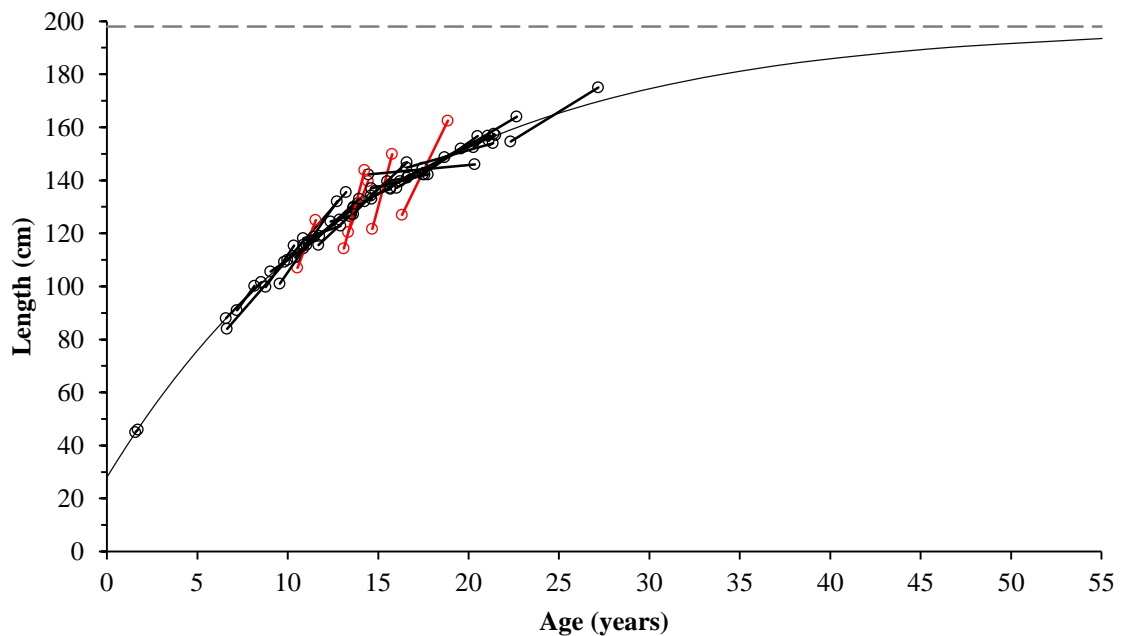
Figure 5: The figure shows the von Bertalanffy growth of female tope sharks within the Northeast Atlantic, estimated via an iterative approach: $L_{(t)} = 198-(198-28)e^{-0.066t}$. The black open circles represent the considered tagging data, the red open circles the outliers defined as exceeding three times the median absolute deviation (MAD). The grey dashed line indicates the asymptotic length.

3.3.4 Discussion

The maximum length observed in the Northeast Atlantic is similar to the Mediterranean Sea. When compared to other regions, the results indicated that female asymptotic length of 198 cm is larger than the 162 cm reported from south-eastern Australia (Grant et al. 1979), the 179 cm reported from New Zealand (Francis and Mulligan 1998) and the 163 cm from southern Brazil (Ferreira and Vooren 1991). Likewise, male asymptotic length of 174 cm was found to be larger than the 143 cm reported from New Zealand (Francis and Mulligan 1998), 154 cm from South Africa (McCord 2005), 152 cm from southern Brazil (Ferreira and Vooren 1991) and 158 cm from south-eastern Australia (Grant et al. 1979). However, if a 95% CL of ±10% is assumed, none of the maximum length estimates would be significantly different from the one found in this study, as indicated by overlapping confidence limits. The von Bertalanffy growth parameter k was found to be below that of all other regions (Grant et al. 1979, Ferreira and Vooren 1991, Moulton et al. 1992, Francis and Mulligan 1998, McCord 2005). If a 95% confidence limit of 20% is assumed, male growth would be significantly different from all areas, except southern Brazil. Female growth would be significantly different from South Africa and Australia, but not from New Zealand and southern Brazil. This is in accordance to the auximetric grid, where growth performance seems to be more closely related to New Zealand and southern Brazil stocks, than to Australian and South African stocks (Figure 6). The slope of all growth estimates combined is -2.3 and therefore close to the expected value of -2 (Pauly et al. 1996). Methods to derive growth parameters from tagging data have been developed previously (e.g. Gulland and Holt 1959, Fabens 1965, Francis 1988), but they can be sensitive to small sample sizes (Natanson et al. 2006). The Gulland and Holt method assumes no errors within the measurements and no growth variability (Campana 2001) and may fail if time at liberty is short (Simpfendorfer 2000). Simpfendorfer (2000) observed non reasonable results of Fabens method if sufficient data is lacking. The findings of this study suggest that the iterative approach can handle small sample sizes if outliers are excluded from the analysis. The calculated maximum age of 55 years is in agreement with the suggested maximum age of 53 years reported from Australia (Olsen 1984, Moulton et al. 1989) and 41 years from southern Brazil (Ferreira and Vooren 1991). The age at maturity found in this study is higher than the estimated 10 years in Australia (Olsen 1954), 16 years from southern Brazil (Peres and Vooren 1991) and the 13 to 15 years reported from New Zealand (Francis and Mulligan 1998). However, length at maturity was also higher in this study, therefore explains the difference.

The age at maturity of males is in agreement with that reported from southern Brazil (Peres and Vooren 1991) and New Zealand (Francis and Mulligan 1998), but higher than in South Africa (McCord 2005) and Australia (Olsen 1954). All life history information of *Galeorhinus galeus* from other regions are detailed in the Supplementary Information (Table 1). In summary, the growth performance of tope estimated in this study and shown in Table 7 is found to be reasonable and suitable for the Northeast Atlantic.

Figure 6: Auximetric grid showing the relationship of growth performance within tope species from different geographic areas. The different studies of tope are indicated by different colours. Growth parameters of females are displayed by circles, males by diamonds and combined sexes by triangles.

3.4 Natural mortality

3.4.1 Introduction

Natural mortality M is a key parameter in fisheries management. It is often estimated as adult natural mortality based on other life history parameters such as maximum age or growth parameters. Here, natural mortality is derived from empirical equations drawing on longevity, growth and environmental parameters. In tope sharks low natural mortality rates have been reported from Australia (Grant et al. 1979) and therefore, M is expected to be low.

3.4.2 Materials and methods

The empirical relationships of Hoenig (1983), Pauly (1980) and Jensen (1996) were applied, whenever observations of the required parameters were given.

The method of Hoenig (1983) relates the maximum age t_{max} to natural mortality:

$$LN(M) = 1.41 - 1.01 * LN(t_{\max}) \qquad (26)$$

Pauly (1980) proposed a relationship of the average water temperature T and the von Bertalanffy growth parameters k and L_∞ to natural mortality:

$$LOG(M) = -0.0066 - 0.279 * LOG(L_\infty) + 0.6543 * LOG(k) + 0.4634 * LOG(T) \qquad (27)$$

Jensen (1996) suggested two relationships. One is based on the von Bertalanffy growth parameter k:

$$M = 1.5 * k \qquad (28)$$

and the other is based on the age at maturity t_m:

$$M = 1.65/t_m \qquad (29)$$

The average water temperature of the Northeast Atlantic was set to 7 °C, obtained from Pauly (1980). The age at maturity was estimated via the von Bertalanffy growth function, based on length observations covered in the *Reproductive biology* sections. Only information other than empirically calculated were used as maximum age input. The remaining parameters have been treated in the corresponding species sections. For the purpose of this study, natural mortality was taken as the median across all applicable methods.

3.4.3 Results

The results of the life history approaches to estimate natural mortality are given in Table 8.

Table 8: Natural mortality rates of tope estimated from other life history traits. The median value is used for the purpose of this study. The 2.5 and 97.5 percentiles of natural mortality are 0.087 and 0.099, respectively.

method	Hoenig (1983)	Pauly (1980)	Jensen (1996) (age)	Jensen (1996) (growth)	median
input	---	$k = 0.066$, $L_\infty = 198$, $T = 7$	$t_m = 21$	$k = 0.066$	
natural mortality	---	0.094	0.079	0.099	0.094

3.4.4 Discussion

Although this study suggests a maximum age of 55 years for tope, it was based on an empirical theory that relies on an already empirically derived value and therefore the method of Hoenig (1983) was not applied.

The natural mortality of tope estimated for the Northeast Atlantic in this study is consistent with the natural mortality of 0.1 yr^{-1} reported from south-eastern Australia and obtained from tagging data (Grant et al. 1979), i.e. it is not significantly different if a 95% confidence limit of ±10% is assumed.

3.5 Habitat and distribution

3.5.1 Introduction

Niche modelling can help to identify areas that are most suitable for a given species. Here, the map produced by the AuqaMaps model was examined (Kaschner et al. 2013). Moreover, these maps can provide first indications of species hot spots. In the following, the results of the map are compared with the distribution information from the literature. Tope is expected to cover a wide range of the investigated area, because it is highly migratory, inhabiting continental seas and offshore regions (Compagno et al. 2005).

3.5.2 Materials and methods

The potential distribution of tope was modelled with AquaMaps (Kaschner et al. 2013). The depth range was adjusted by the maximum reported depth of the species, obtained from the literature. Ranges for temperature, salinity and primary production as suggested by the model were accepted.

3.5.3 Results

Although tope has been reported to a depth of 550 m in the Northeast Atlantic (Couto 2013), it has been recorded to 800 m in New Zealand (Walker 1999). Therefore, the maximum depth was set to 800 m. The potential distribution is shown in Figure 7 and the corresponding environmental parameters are detailed in Table 9.

Table 9: Environmental parameters used to model the suitable habitat of tope.

environmental envelopes	min	preferred min	preferred max	max
depth (m)	0	2	470	800
bottom water temperature (°C)	2	5.5	15	26
bottom salinity (psu)	22.5	35	38	39
primary production (mgC*m-2*day-1)	0	390	1459	3830
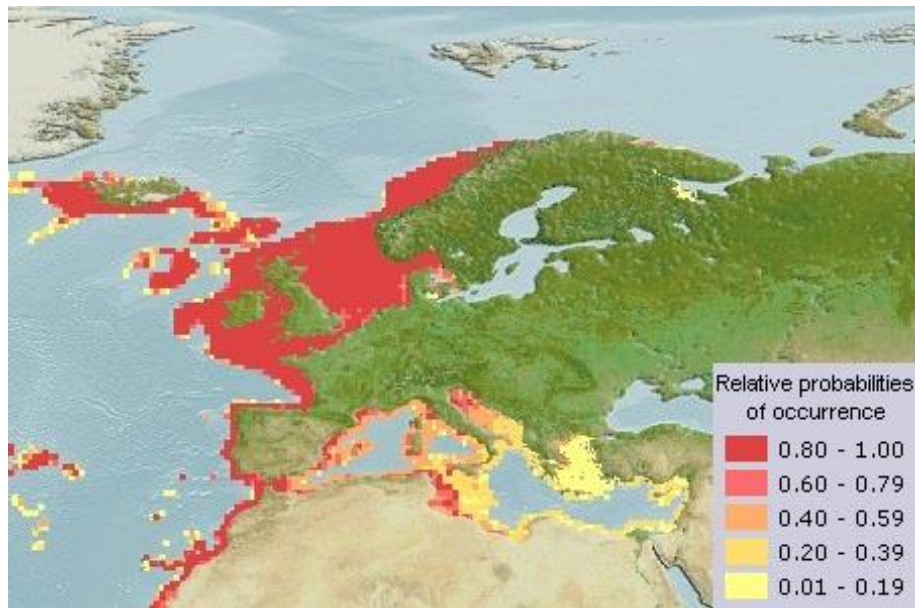
Figure 7: Potential distribution of tope in the Northeast Atlantic, obtained from AquaMaps, adjusted by depth.

3.5.4 Discussion

In accordance with the suitable habitat obtained from AquaMaps, the stock is considered to be distributed over a wide range covering ICES areas II to X, north-western Africa and the Mediterranean Sea (ICES 2009). Tope is highly migratory and long term movements have been reported from Scotland to Iceland (Little 1998), Portugal, Canary Islands, Algeria (Sutcliffe 1994, Little 1995, Little 1998) and the Bay of Biscay (SSTP 2011). Tope tagged at the Irish coast, moved as far as the Azores, Canary Islands, Bay of Biscay and into the Mediterranean Sea off Algeria and Spain (Fitzmaurice 1979). Long distance migrations from the British coast have been reported to the west coast of France, north of Spain, Portugal, the Atlantic region of Morocco and the Canary Islands (Holden and Horrod, 1979) and from English waters to Cadiz (Spain), Iceland and off Portugal (Stevens 1990). Whereas female tope sharks tagged in British waters were recaptured at the Azores, Madeira, the Spanish and Portuguese coast, including the Mediterranean Sea, males seem to be more stationary and have been recaptured in the Bay of Biscay and the northern coast of Spain (SSTP 2010). Similar to reports from other regions (Ripley 1946, Olsen 1984), segregation by sex occurs in the Northeast Atlantic. Males are predominant off the west of Scotland (Sutcliffe 1994, Little 1995, Little 1998) and along the west coast of Great Britain, whereas the abundance of females is higher in the North Sea, the English Channel (Holden and Horrod 1979) and off south-west England (Stevens 1990). Off southwest Scotland, large females can be found inshore from late July onwards (Little 1998). Little (1995) concluded that females might prefer shallow inshore areas whereas males prefer offshore habitats.

In agreement with this, Stevens (1990) suggested that there might be an inshore migration of mature females in spring. In Northern Ireland waters the highest numbers of tope sharks can be found from June to September, with large females predominant (Agri-Food & Biosciences Institute 2009). Furthermore, large females have been observed along the Netherlands coast in summer (Winter and van Oversee 2013). Information about mating locations is rare, but in Australia tope is believed to mate in deeper waters along the continental shelf (Olsen 1954). Several nursery areas have been proposed in the Northeast Atlantic. Ellis et al. (2012) suggested that these grounds are located inshore. Furthermore, juvenile tope sharks may stay in this nursery area for up to two years (Compagno et al. 2005). Greater abundances of juvenile tope have been observed in south-east England (Greater Thames Estuary), east Scotland (Firth of Forth), the Irish Sea, Bristol Channel, off north-western Scotland (Ellis et al. 2012) and the southern North Sea (Ellis et al. 2005a). In addition, the Solent straight, south of England, might serve as nursery ground (Ellis et al. 2012). In summary, tope covers a wide range of the investigated area with higher occurrence around the British Islands. According to the literature, critical habitats of mature individuals may be found along the coast of the Netherlands, the English Channel and south-west England, in the Irish Sea and off the west of Scotland. Nursery areas may occur around Scotland, the Bristol Channel and the Irish Sea, along the south-eastern coast of England and the southern North Sea.

3.6 Critical habitats

3.6.1 Introduction

Tope is a wide ranging species, yet certain areas seem to be important for critical life stages (Ellis et al. 2005a, Ellis et al. 2012). This species is mainly caught as bycatch, especially in the English Channel, the Western Approaches and the northern Bay of Biscay (Walker et al. 2006). Their life history renders the species extremely vulnerable to over-exploitation (see above). The fact, that bycatch is unregulated and unreported, raises the urgency to identify critical areas that can serve as refuges. Here, pupping and nursery grounds as well as aggregation sites for mature specimens in the Northeast Atlantic were investigated.

3.6.2 Materials and methods

The data was based on ICES surveys (section 2.1). Information about the different life history stages was taken from the *Reproductive biology* section. Early juveniles were defined by a length range of 33 cm to 50 cm, which corresponds approximately to an age up to 2 years. The dataset contained 1473 records of tope from 1984 to 2012.

Specimens were caught in all months, in depths ranging from 16 m to 460 m. Due to the limited amount of data, catches of the BT8 and GOV gear types were used to identify pupping grounds, assuming equal catchability of pups by these gear types. Moreover, investigation of critical areas was only possible on the basis of combined sexes.

3.6.3 Results

Pupping and nursery grounds were found in the Southern Bight and German Bight (Figure 8), especially at grounds off the Frisian Islands. In total, 38 pups were recorded in 6 different years, from 1991 to 2010. Pups were caught from July to October with a peak of abundance in the latter month. All catches were made in depths ranging from 23 m to 31 m. The results are summarised in Table 10. A higher number of early juveniles were caught regularly from 1988 to 2011 (n = 126), almost exclusively in the Outer Thames Estuary and the Frisian Islands (Figure 9). Most juveniles were caught in August.
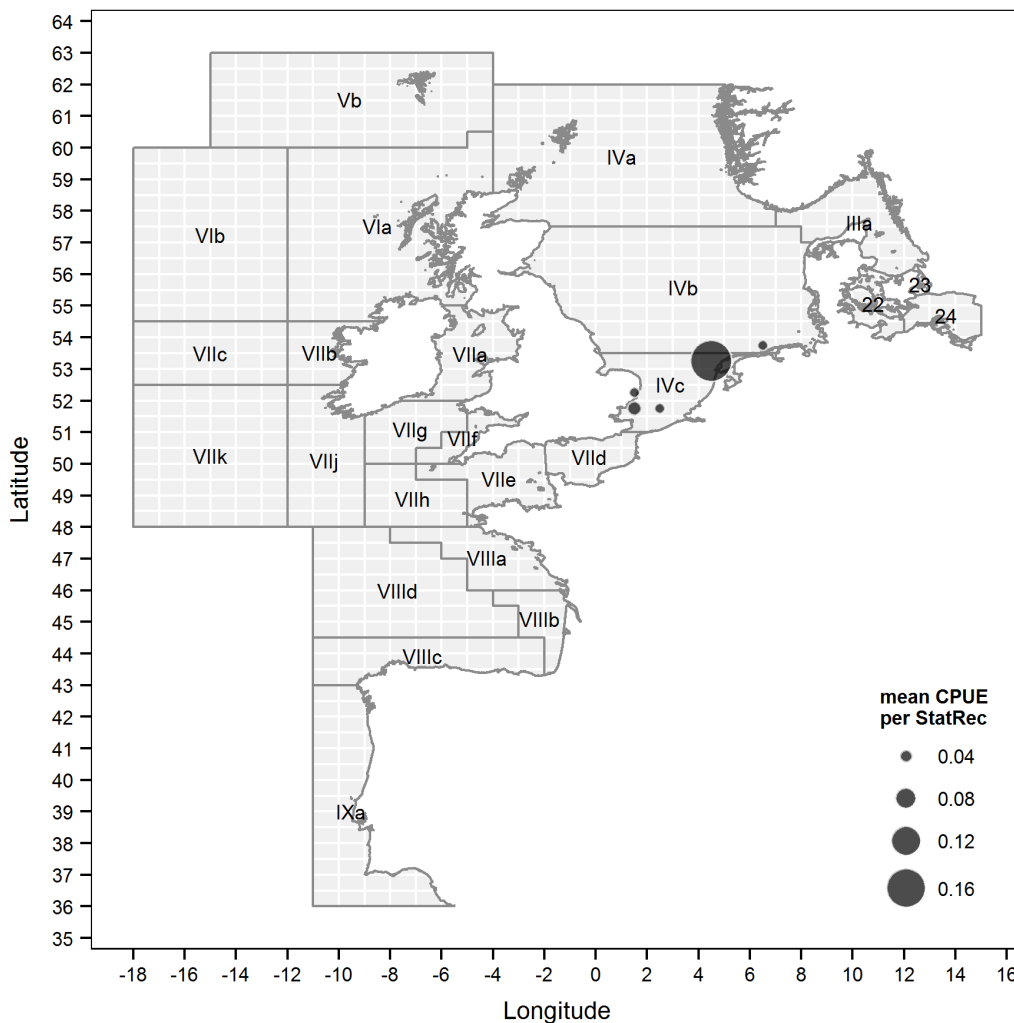
Figure 8: Records of tope pups (24 cm − 32 cm) from ICES surveys in the Northeast Atlantic. In total, the sample contained 38 individuals, reported in 6 different years from 1991 − 2010.

Figure 9: Records of early juvenile tope (33 cm − 50 cm), from ICES surveys in the Northeast Atlantic. In total, the sample contained 126 individuals, reported from 1988 − 2011.

Mature tope were caught in 22 different years from 1985 to 2012. Of the 364 mature tope recorded in total, 4 were females, 340 males and for 20 the sex was not given. They occurred in depth from 20 m to 300 m. Mature individuals were most abundant in the southern Irish Sea, the north coast of Ireland, the Vidal Bank region and off the east coast of England (Figure 10). Furthermore, catches were made in several years off south-west Ireland and in the southern Celtic Sea (Table 10). Females were only caught along the north coast of Ireland and the Frisian Islands, whereas specimens of unknown sex were mostly distributed at the southern Hebrides, the Frisian Islands, the Outer Thames Estuary and the east coast of England.
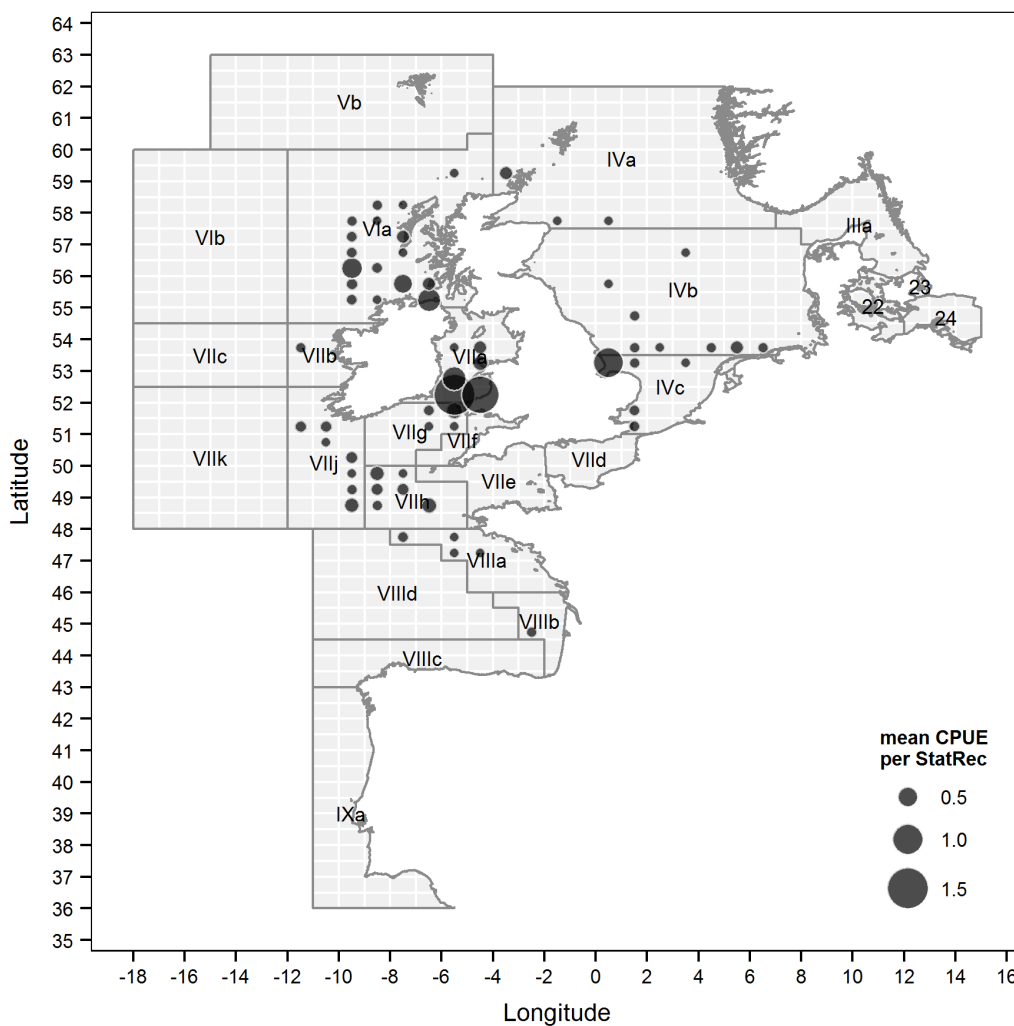
Figure 10: Records of mature tope (size of male $\geq$ 121 cm, size of female and unknown sex $\geq$ 155 cm) for combined sexes from ICES surveys in the Northeast Atlantic. In total, 364 mature individuals were recorded in 22 different years, from 1985 − 2012.

Table 10: Investigated areas of different life stages for tope in the Northeast Atlantic. Approximate bounding boxes are given by longitude and latitude. The total number caught is given for the time period when surveys were conducted. The mean *CPUE* refers to the mean catch per unit effort in this area, regardless of the area size. The highest catch per month was obtained by the mean number per month divided by the total effort in this month. In addition, it is indicated if this area is at least partly covered by a protected area (PA). This information was obtained from OSPAR (2013) and JNCC (2013). Areas determined as extremely important for tope are shown in bold.

life stage	ICES division	area name	long	lat	depth (m)	years caught	years investigated	period	number	mean CPUE	highest catch	inlcudes PA
pupping and nursery	IVc	Outer Thames Estuary	1, 2	51, 52.5	27-30	2	31	1982-2012	8	1.25	August	Yes
	IVc, IVb	**Broad Fourteens and Frisian Islands**	**3, 8**	**51, 54**	**23-31**	**3**	**41**	**1967-2012**	**28**	**2.39**	**October**	**Yes**
mature	**IVc, IVb**	**East coast of England**	**0, 3**	**53, 54**	**20-81**	**4**	**38**	**1967-2012**	**39**	**7**	**September**	**Yes**
	IVc	Outer Thames Estuary	1, 2	51, 52.5	29-45	3	31	1982-2012	8	1.11	January	Yes
	IVc, IVb	**Broad Fourteens and Frisian Islands**	**3, 8**	**51, 54**	**30-41**	**6**	**41**	**1967-2012**	**16**	**1.76**	**July**	**Yes**
	VIa	Mingulay	-8, -7 -7, -6	56.5, 57.5 55, 55.5	140-170	3	28	1985-2012	5	1.33	December	Yes
	VIa	**North coast of Ireland**	**-9, -7** **-10, -9**	**54, 56** **54, 55.5**	**56-259**	**7**	**28**	**1985-2012**	**137**	**2.99**	**October**	**Yes**
	VIa	Vidal Bank	-10, -9	55.5, 57	140-170	6	28	1985-2012	20	3.2	March	No
	VIIa	**Southern Irish Sea**	**-8, -4**	**52, 53**	**35-97**	**2**	**7**	**1997-2008**	**18**	**1.9**	**November**	**Yes**
	VIIa	North-west Anglesey Reef	-5, -4	53, 54	42-68	2	11	1996-2006	10	1.33	November	No
	VIIj	**Southwest of Ireland**	**-12, -9** **-9, -7**	**48, 52.5** **49.5, 50**	**126-214**	**7**	**23**	**1990-2012**	**16**	**1.47**	**November**	**Yes**
	VIIh	**Southern Celtic Sea**	**-9, -5**	**48, 49.5**	**123-151**	**10**	**18**	**1990-2012**	**26**	**0.90**	**November**	**Yes**

3.6.4 Discussion

The fact that pups and early juveniles were caught in the same areas indicates that the pupping grounds may serve also as nursery areas for tope. The nursery areas found here agree with those proposed in former studies (Ellis et al. 2005a, Ellis et al. 2012). Fewer locations were identified however, possibly due to the small sample size. Nevertheless, the Frisian Islands seem to be important, indicated as this area was used in different decades. The fact that pups were caught from July to October only, suggests that birth occurs in summer and autumn. This agrees with the temporal period proposed by others studies (Wheeler 1969, Little 1995, Nevell 1998, Walker 1999, Agri-Food & Biosciences Institute 2009), yet is later than reported from the Mediterranean Sea (Capapé and Mellinger 1988, Capapé et al. 2005). Interestingly, catches composed exclusively of males occurred in the southern Irish Sea, south-west of Ireland and the southern Celtic Sea. In the latter region it may be reasonable to assume females cross this area on their migrations from north to south (Fitzmaurice 1979, Holden and Horrod 1979, Stevens 1990, Sutcliffe 1994, Little 1995, Little 1998, SSTP 2011). This may be explained by seasonal sampling bias. On the other hand, females may encounter higher exploitation rates than males as reported from other areas (Olsen 1959). Due to the rarity of females, this study was unable to investigate sex segregation between the areas. Though, former studies found greater numbers of females in the North Sea (Holden and Horrod 1979, Stevens 1990) and large females have been reported along the coast of the Netherlands (Winter and van Oversee 2013) with length representing maturity. Likewise, the occurrence of large females were reported in the greater vicinity of the northern Irish coast (Little 1998, Agri-Food & Biosciences Institute 2009). The findings here, combined with information from the literature, indicate the Frisian Islands, the north coast of Ireland and possibly the east coast of England as critical habitats for female tope. Other areas where mature male tope aggregate were found in the Vidal Bank region, south-west Ireland, the southern Celtic Sea and the southern Irish Sea, including the marine protected area (MPA) in Cardigan Bay (OSPAR 2013, JNCC 2013). Although most areas were at least partly protected, and therefore reflect the importance of habitat protection for sharks, the entire area was seldom covered. Furthermore, some of the critical habitats are located within the Western Approaches, one of the main areas where tope is suffering from bycatch (Walker et al. 2006). Therefore, it is suggested to enlarge existing MPAs in the above mentioned areas, but in particular along the northern Irish coast and the Frisian Islands, to aid a healthy population structure by protecting spawners and early juveniles.

Especially within larger parts of the pupping and nursery grounds a strict fishing prohibition should be implemented to enhance recruitment, since juveniles may utilise these areas during the first two years of their life (Compagno et al. 2005). The Wadden Sea has undergone dramatic anthropogenic changes caused by exploitation, habitat alteration and pollution since the Middle Ages. Intensified fishing resulted in declines of several fish species (Lotze 2005, Lotze et al. 2005). The current fisheries is based offshore, although inshore fisheries of, inter alia, shrimp and flatfish still exist (Lotze et al. 2005). These fisheries are relatively unselective and are likely to affect juvenile tope. Therefore, tope is suffering from fishing pressure in its nursery grounds, followed by reduced habitat quality and reduced food availability. Based on the available data, new protected areas with great potential in tope conservation are proposed in the Central and Southern Celtic Sea, the southern Irish Sea, the east coast of England, the northern coast of Ireland, the Frisian Islands and the Vidal Bank region. However, these suggestions are based on limited data, thus future studies are recommended to support the results. The fact that such a small number of females were caught in the surveys raises questions regarding the sampling efficiency or exploitation rates, which was subsequently investigated in the next section.

3.6.5 Sampling bias or overfishing of mature females

3.6.5.1 Introduction

The sex distribution of tope showed an extremely skewed ratio (340 mature males, 4 mature females and 20 mature specimens with unknown sex) (section 3.6.3), raising the question whether females were heavily overfished or not sampled effectively. Surveys by the ICES are not capable of sampling large sharks representatively (ICES 2012). However, male tope sharks in these surveys were caught frequently measuring up to160 cm total length. Therefore, females of the same size should be sampled too, if in the area and if their behaviour is not distinct in a way that strongly reduces vulnerability. Here, the numbers of pups produced by the observed females was compared to the expected number of pups (back-calculated from early juveniles), to examine, if the number of expected pups could have been produced by the number of observed females. Overfishing of females would be indicated by a ratio of pups to females smaller or equal to 1. Ineffective sampling would be demonstrated by a ratio far exceeding 1. Furthermore, the abundance of females and early juveniles were investigated on the basis of *CPUE* values, to determine trends for both life history stages.

3.6.5.2 Materials and methods

Observed numbers of the single life stages were obtained from survey data. Only valid hauls were considered, as specified in DATRAS data. Juvenile age was obtained by applying the von Bertalanffy growth function (section 3.3). If sex was not determined, the parameters estimated for both sexes combined were used. For the purpose of this study, one year old juveniles ranged from age 0.5 to 1.49 and two year old juveniles from age 1.5 to 2.49. Furthermore, all mature specimens where sex was not determined were considered females as length at maturity for females was used, if sex was not given. It was assumed that all females caught in a specific year, would have produced all age one juveniles caught one year later. Due to limited data, age two juveniles (caught two years later than mature females) were used if age one juveniles were not present one year later. Assuming, a natural mortality of early juveniles twice the natural mortality of adults ($M_{juv} = 2*0.094$), the expected number of pups in a year N_0 can be obtained via:

$$N_0 = N_{juv} * e^{(M_{juv}*(0+t_{juv}))} \tag{31}$$

where N_{juv} is the number of juveniles in age class one or two and t_{juv} is the corresponding age. The possible number of pups produced by the females a year N_f was obtained by applying the length-fecundity relationship (section 3.2.3). The result was divided by 2, to account for a biennial reproductive cycle (section 3.3.3) and multiplied with the number of females caught that year. The total number of expected pups N_0 was divided by the total number of possible pups N_f. If the ratio is smaller or equal to 1, the females caught were capable of producing the expected number of pups. If the ratio was larger than 1, more pups would have been present than could have been produced by the observed number of females thus indicating sampling bias. Finally, the abundance trend of females and early juveniles was investigated by examining *CPUE* values across years. *CPUE* was calculated as described in section 2.6. Here, a three year moving average was used, because of the limited amount of data. Note that under this definition, the first and last estimates consist of two values only, due to border effects. A decreasing abundance trend for both life history stages would further indicate overfishing of mature females.

3.6.5.3 Results

In total, 24 mature females and 50 juveniles were caught in the surveys. The amount of pups produced by females exceeded the amount of expected pups. This is indicated by a ratio less than 1. A higher number of male sharks were caught during the same years (Table 11).

The abundance showed decreasing trends for both, early juveniles and mature females since 1992 (Figure 11). Furthermore, from the year 2000 until recently, the abundance was below the mean abundance of the considered time period.

Table 11: Mature tope females caught in the surveys, denoted as number of females. The corresponding years is given in the left column. The number of males caught in the same years is shown. The fecundity of mature females was obtained by the length-fecundity relationship (section 3.2.3) and divided by 2 to account for a biennial reproductive cycle. The result was multiplied with the number of females caught, to determine the total number of pups produced that year (N_f). The observed number of juveniles produced by these females was obtained from survey data and used to back-calculate the expected number of pups N_0. The ratio indicates if the observed number of females could have produced the expected number of pups. If the ratio is greater than 1, more pups than expected from the number of females would be present.

year	number females	number males	female length (cm)	fecundity	pups per female (N_f)	year juveniles	age group	number juveniles	expected pups (N_0)	ratio $\sum N_0/N_f$
1992	4	2	155	7.38	29.53	1993	1	20	24.14	
1993	2	18	163	8.31	16.63	1994	1	2	2.41	
1996	4	3	156 165	7.49 8.56	14.99 17.11	1997	1	6	7.24	
1997	2	10	160	7.96	15.91	1998	1	8	9.65	
1998	2	8	160	7.96	15.91	1999	1	4	4.83	0.33
2003	2	24	159	7.84	15.68	2004	1	4	4.83	
2004	2	22	160	7.96	15.91	2006	2	2	2.91	
2006	2	118	161	8.07	16.15	2008	2	2	2.91	
2010	4	4	155	7.38	29.53	2011	1	2	2.41	
$\sum$	24	209			187			50	61	
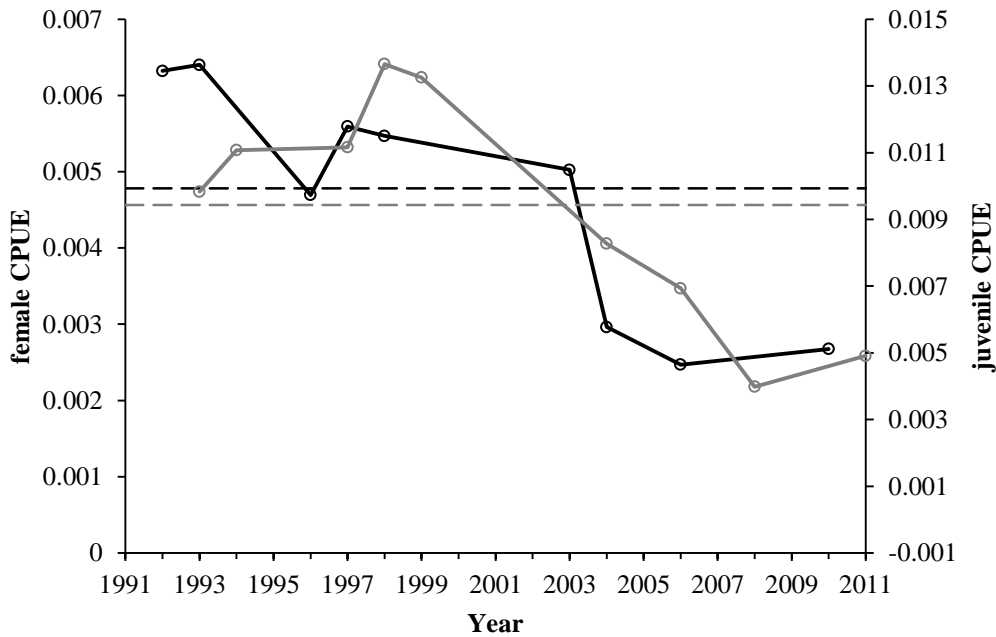
Figure 11: The abundance trends (*CPUE*) of observed mature tope females (black line) and early juveniles (grey line) caught in the surveys. The trends are shown as three year moving averages. Note that early juveniles in the years 2006 and 2008 consisted of age two individuals, whereas all others are represented by age one individuals. The black broken line indicates the mean *CPUE* of mature females and the grey broken line the mean *CPUE* of early juveniles.

3.6.5.4 Discussion

The number of observed females in this study could have produced the number of expected pups. Furthermore, the abundance of both life stages showed a decreasing trend. These results indicate that females are sampled proportionally compared to juveniles, yet females may well be heavily overfished. Males reaching a maximum size of 160 cm were caught frequently and one would expect females of the same size to be caught in similar proportions, if in the area and if the behaviour is not distinct from males. On the other hand, the number of mature males could not have been produced by the expected number of pups. Sampling is not made in all months in all areas and therefore may be another factor responsible for complicating the findings, because females and juveniles may inhabit areas subjected to less frequent sampling than males. However, investigation of such factors was beyond the scope of this study and uncertainty regarding representative sampling of both juveniles and females remains. Therefore, future research should use the current findings to address questions regarding sampling bias of males, females and juveniles. Nevertheless, in the areas where females and juveniles were sampled (central and southern North Sea), both life stages experienced a decline, post 1991.

3.7 Biological reference points for fishing mortality

3.7.1 Introduction

Tope has low productivity (Smith et al. 1998) and therefore the species' capacity to withstand fishing is low. Here, the theoretical fishing mortality producing the maximum sustainable yield was investigated.

3.7.2 Materials and methods

The methods applied to obtain proxies of maximum sustainable fishing mortality were covered in section 2.3. Maximum age was assumed at 55 years, age at maturity 21 years and natural mortality 0.094 yr^{-1}.

3.7.3 Results

The results of the life table approach are given in Table 12. The intrinsic rate of population increase was estimated as 0.062 yr^{-1}. The sustainable fishing mortality rate based on the intrinsic rate of population increase $F_{msy0.5r}$ was estimated at 0.031 yr^{-1}. The sustainable fishing mortality rate based on natural mortality $F_{msy0.5M}$ was estimated at 0.047 yr^{-1}.

3.7.4 Discussion

The intrinsic rate of population increase, as estimated in this study (section 2.3), is a function of natural mortality, fecundity at age, longevity and age of maturity. Here, late maturity and low fecundity at age, which was presumably underestimated if compared to observations from the Mediterranean Sea (Capapé and Mellinger 1988, Capapé et al. 2005), were the main factors causing a low value of *r*. However, the estimated intrinsic rate of population increase is higher than reported by Smith et al. (1998) for a population from the Pacific Ocean. Nevertheless, the results indicate low resilience of tope (Musick 1999) and confirm the low capacity to withstand fishing. To follow a precautionary approach, a value of 0.031 yr^{-1} should be utilised as reference point for the fishing mortality rate which produces maximum sustainable yield F_{msy}.

Table 12: Life table for tope from the Northeast Atlantic. The results are shown from age at maturity to maximum age. To account for sex ratio, resting stages and the complete reproductive cycle, the product of the proportion mature and litter size was multiplied with 0.25 to obtain the age specific fecundity (female pups per female) m_x. The annual reproductive rate per generation is the product of survival to age l_x and m_x. The intrinsic rate of population increase r was estimated at 0.062 yr^{-1}.

| length (cm)	age	% mature	litter size	m_x	l_x	$l_x m_x$
155	21	0.52	14.87	1.95	0.14	0.270
158	22	0.69	15.49	2.68	0.13	0.339
161	23	0.81	16.09	3.27	0.12	0.377
163	24	0.89	16.65	3.71	0.10	0.389
165	25	0.94	17.20	4.03	0.10	0.384
167	26	0.96	17.71	4.26	0.09	0.370
169	27	0.98	18.20	4.45	0.08	0.351
171	28	0.99	18.67	4.60	0.07	0.331
173	29	0.99	19.11	4.73	0.07	0.310
175	30	0.99	19.53	4.85	0.06	0.289
176	31	1.00	19.93	4.96	0.05	0.269
177	32	1.00	20.31	5.06	0.05	0.250
179	33	1.00	20.67	5.16	0.04	0.232
180	34	1.00	21.00	5.24	0.04	0.215
181	35	1.00	21.32	5.32	0.04	0.198
182	36	1.00	21.62	5.40	0.03	0.183
183	37	1.00	21.91	5.47	0.03	0.169
184	38	1.00	22.17	5.54	0.03	0.156
185	39	1.00	22.43	5.60	0.03	0.143
186	40	1.00	22.66	5.66	0.02	0.132
187	41	1.00	22.89	5.72	0.02	0.121
187	42	1.00	23.10	5.77	0.02	0.111
188	43	1.00	23.30	5.82	0.02	0.102
189	44	1.00	23.48	5.87	0.02	0.094
189	45	1.00	23.66	5.91	0.01	0.086
190	46	1.00	23.82	5.95	0.01	0.079
190	47	1.00	23.98	5.99	0.01	0.072
191	48	1.00	24.12	6.03	0.01	0.066
191	49	1.00	24.26	6.06	0.01	0.061
192	50	1.00	24.39	6.10	0.01	0.055
192	51	1.00	24.51	6.13	0.01	0.051
193	52	1.00	24.62	6.15	0.01	0.046
193	53	1.00	24.73	6.18	0.01	0.042
193	54	1.00	24.83	6.21	0.01	0.039
193	55	1.00	24.92	6.23	0.01	0.035

3.8 Total and fishing mortality

3.8.1 Introduction

Although tope is consumed in some countries, it is not a main target species of commercial fisheries in the Northeast Atlantic but, rather a bycatch species in mixed demersal and pelagic fisheries and important in recreational fisheries (Walker et al. 2006). Landings from recreational fishing are prohibited in Britain by the Tope (Prohibition of Fishing) Order (2008). The order further limits bycatches to 45 kg a day and only allows rod and line fisheries. Here, the total and fishing mortality rate of tope was investigated based on survey data.

3.8.2 Materials and methods

The method of estimating mortality from catch curves was described in detail in section 2.4. Catches were extracted from the survey data. Only valid hauls were considered, as specified in DATRAS data. The time period from 1992 to 2012 was selected, because not all age classes were present in earlier surveys (Supplementary Information, Figure 2). The length frequency distribution of the entire survey area showed an unrealistic small amount of juvenile specimens (Figure 12). Therefore, only the central North Sea (ICES division IVb) was used as a more representative area (Figure 13), due to the fact that it covers a large range and all life stages are present (section 3.6). The length frequency distributions of all sub-areas are given in the Supplementary Information (Figure 1). Age classes were obtained from length by applying the von Bertalanffy growth function. If sex was not given, the von Bertalanffy growth function of both sexes combined was used (section 3.3). Two total mortality rates were estimated, one for juveniles and one for adults, because of differences in the slopes. Finally, the average of both served as a proxy for total mortality of all ages. Fishing mortality was obtained from total mortality by assuming a constant natural mortality rate of 0.094 yr^{-1} (section 3.4).
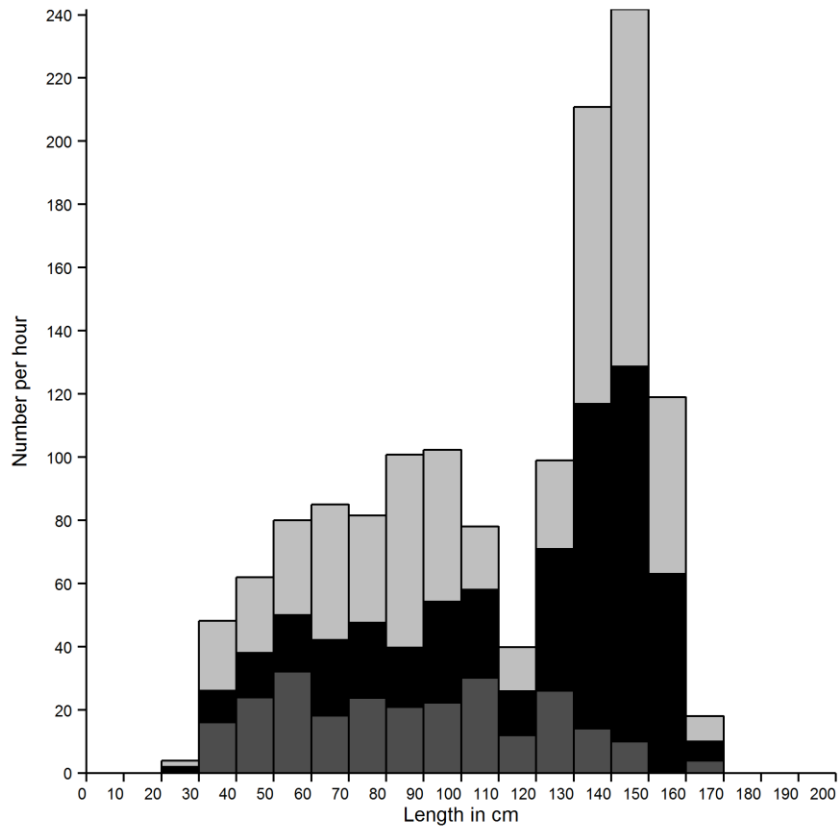
Figure 12: Length frequency distribution of tope in the Northeast Atlantic, with data pooled over the years 1992 − 2012. The dark-grey bars represent the number of females, the black bars the number of males and sex was not determined for the light-grey bars.
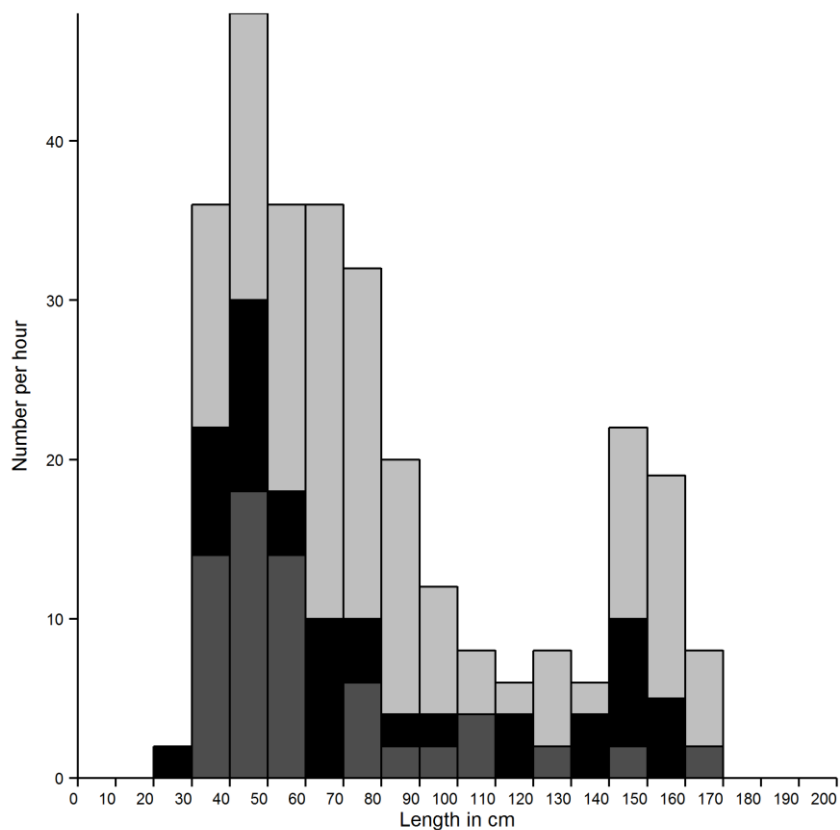
Figure 13: Length frequency distribution of tope in the central North Sea. The dark-grey bars represent the number of females, the black bars the number of males and sex was not determined for the light-grey bars.

3.8.3 Results

The results of the catch curve are presented in Figure 14. The total mortality estimated for ages 1 to 16 is 0.25 yr^{-1} ($r^2 = 0.89$, $p < 0.001$). The total mortality estimated for age 17 to age 26 is 0.16 yr^{-1} ($r^2 = 0.47$, $p < 0.05$). Therefore the total instantaneous mortality rate of tope in the Northeast Atlantic is at 0.21 yr^{-1} for all ages. Subtracting natural mortality of 0.094 yr^{-1} resulted in a fishing mortality of 0.116 yr^{-1}. Adult fishing mortality is 0.07 yr^{-1}, obtained from adult total mortality of 0.16 yr^{-1} minus natural mortality. It follows that the natural mortality of juveniles is suggested twice that of adults ($M_{juv} = 0.18$ yr^{-1}), estimated from the total juvenile mortality rate of 0.25 yr^{-1} minus the adult fishing mortality rate of 0.07 yr^{-1}.
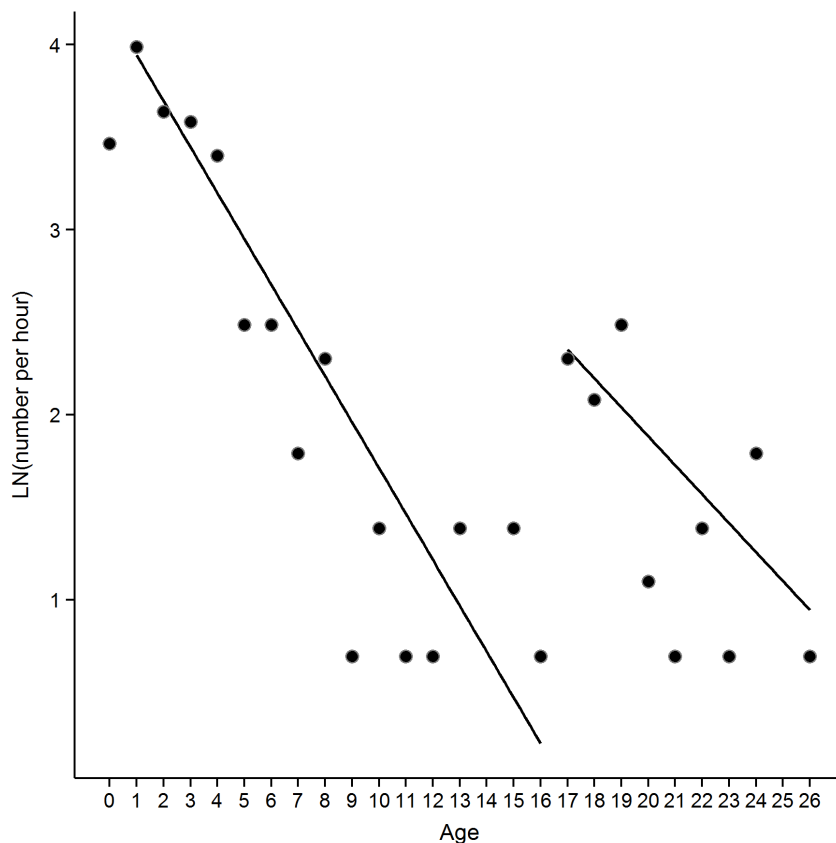
Figure 14: Catch curve used to estimate the total mortality of tope in the Central North Sea. The numbers were pooled from 1992 to 2012. The slope of the left regression accounts for the ages 1 to 16 and was estimated at 0.25 ($r^2 = 0.89$, $p < 0.001$, 95% confidence limits = 0.2 − 0.3). The slope of the right regression line accounts for the ages 17 to 26 and was estimated at 0.16 ($r^2 = 0.47$, $p < 0.05$, 95% confidence limits = 0.04 − 0.28). The regression analysis was weighted by number caught per hour.

3.8.4 Discussion

The bimodal length frequency distribution might be an artefact of sampling bias. However, the fact that all areas exhibit such bias (Supplementary Information, Figure 1) makes it more likely, that the higher amount of large specimens is explained by remnants from the past, where fishing mortality was lower. Although large sharks may not be sampled effectively in the ICES survey due to strong swimming capacity and offshore occurrence (ICES 2009), large males were frequently caught (Figure 12). According to this, the low amount of juveniles indicates recruitment failure in recent years. This pattern has been observed in other regions due to exploitation (Olsen 1959). The second hypothesis is further supported by the findings that the adult fishing mortality is lower than the juvenile fishing mortality. The fishing morality rate for all ages combined was between two to four times above F_{msy}, although it is not a commercially important species in the Northeast Atlantic Ocean (Walker et al. 2006). Therefore, the majority of the mortality rate can be reduced to bycatch mortality. Furthermore, the uncertainty of the estimates indicated by the 95% confidence limits makes a total mortality at 0.29 yr^{-1} possible, which would result in a fishing mortality at 0.2 yr^{-1}. This would suggest the current exploitation six times above sustainability and the stock might be in serious danger to collapse, especially if exploitation was unsustainable over several years. The current findings are an alarming signal. Due to its low potential to withstand fishing, which is even lower in the Northeast Atlantic than in areas where tope did not recover after depletion (Camhi et al. 1998, Walker 1998, Walker 1999), suggests the urgent need for management actions. However, precautionary management would have to assume the upper 95% confidence limits of Z and F and the lower estimate of F_{msy} at 0.031 yr^{-1}. In addition, the results support the assumption made in section (3.6.5), that the natural mortality of juveniles is twice the natural mortality of adults. The exploitation levels of females should be addressed in future studies, due to the findings in section (3.6.5), which indicated that females may have experienced severe depletion.

3.9 Exploitation rate

3.9.1 Introduction

Although the fishing mortality of tope appears to be above sustainable levels (section 3.8), data was too limited to identify temporal trends of F. Therefore, an index based assessment model (NEFSC 2002) was used to evaluate the historical exploitation levels.

3.9.2 Materials and methods

The method is presented in detail in section 2.5. All species specific landings of tope were extracted from ICES catch data for the Northeast Atlantic (ICES 2013). Data was available from 1992 to 2011. For the calculation of the survey biomass index, only the time period from 1992 to 2011 was considered, because of the absence of some age classes before 1992 (Supplementary Information, Figure 2). Furthermore, only valid hauls were used, as specified in DATRAS data.

3.9.3 Results

Tope landings have increased since 1992 with a peak in 2005. Thereafter, landings decreased. This trend is supported by the pattern visible in the survey biomass index (Figure 15). Since 1997, both lines followed the same trend, making the analysis possible from this year to 2012. The exploitation ratio which would allow the stock to replace itself (NEFSC 2002) was estimated to be 5.4 (Figure 16). Figure 17 shows that this value was far exceeded many times since 1997.
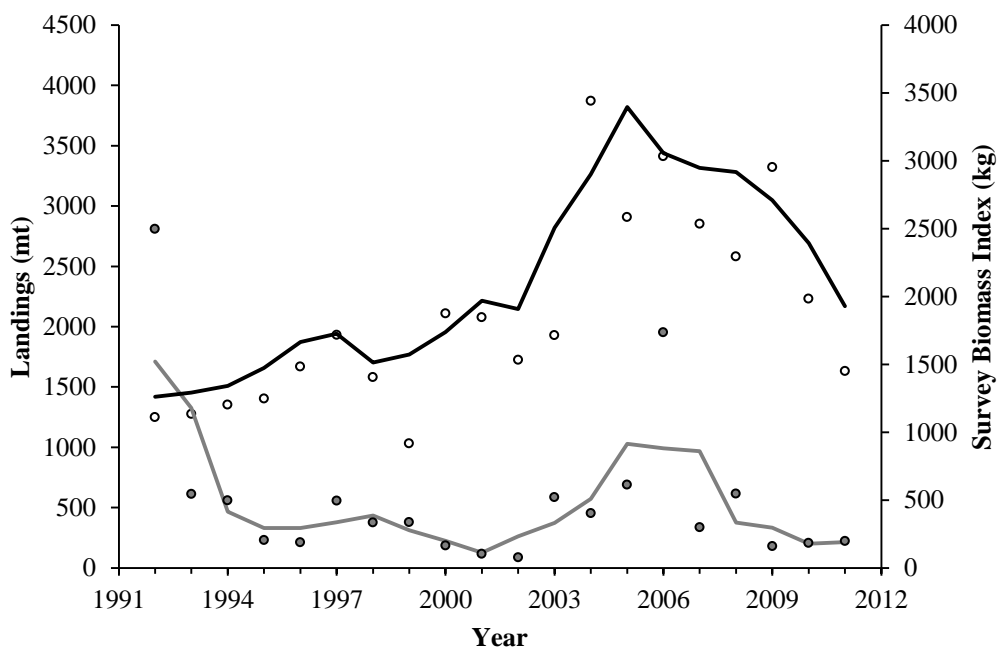
Figure 15: Official landings of tope in the Northeast Atlantic (open circles, black line) and the survey biomass index (filled circles, grey line). The lines are shown as three years moving average. Note that the first and last estimates consist only of two values.
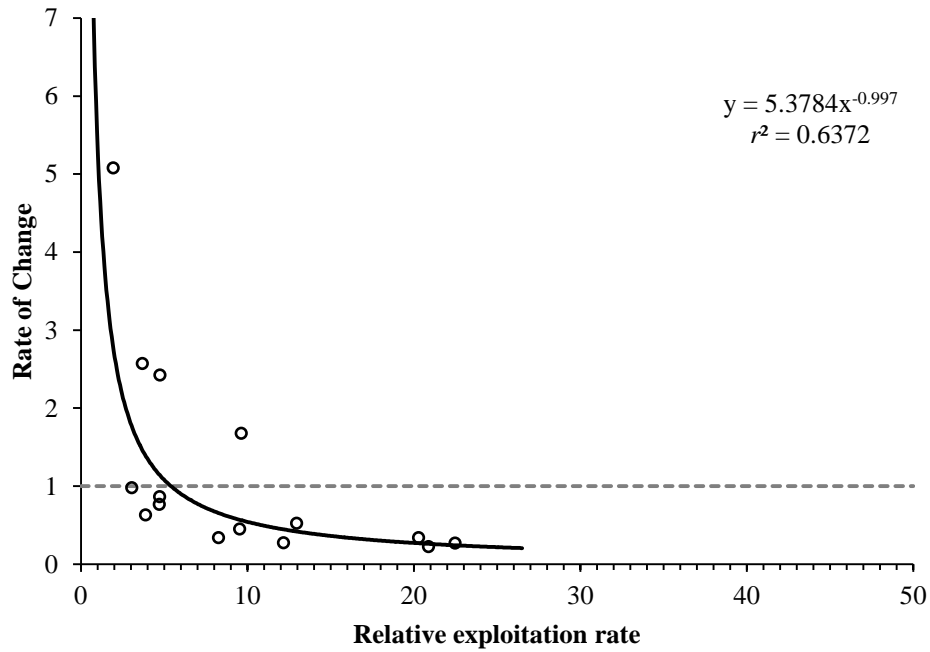
Figure 16: Rate of change regressed over the relative exploitation rate of tope in the Northeast Atlantic. The grey dashed line indicates a replacement ratio of 1:1. Therefore, stock replacement would be achieved if the exploitation ratio equals 5.4.
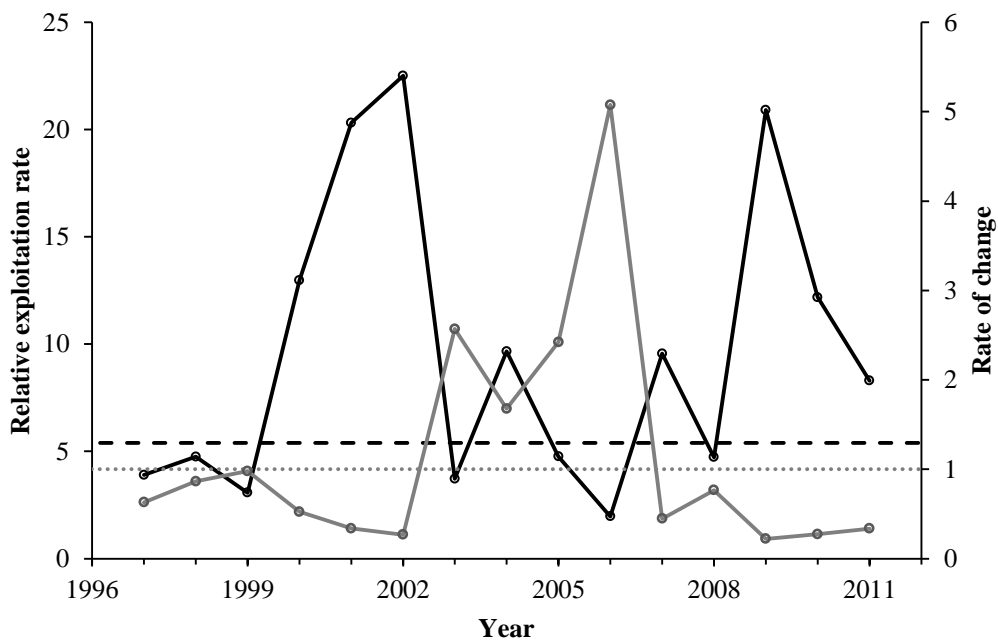
Figure 17: Relative exploitation ratio of tope in the Northeast Atlantic (black line) and the rate of change (grey line). The black dashed line indicates an exploitation rate at which the stock can replace itself. The dotted grey line indicates a rate of change that equals 1. If the exploitation ratio is below the replacement proxy, a positive rate of change (> 1) occurs, i.e. the population would grow.

3.9.4 Discussion

Official landing data of sharks are usually incomplete (Bonfil 1994) and tope is often reported in generic groups (ICES 2012). Most likely true landings are higher than indicated by the data used here. This means, that true exploitation rates may also be higher and the results presented in this study may display an optimistic picture. Even though, since 1997 the exploitation rate was almost consistently at levels which did not allow the stock to replace itself. Combining the findings of this section with those of section 3.8, tope might have experienced large declines over the past 15 years. Similar patterns have been observed in other areas (Ripley 1946, Olsen 1959), where the stocks eventually collapsed. A well-known example is the California tope fishery, where the population suffered a collapse during the late 1940's (Ripley 1946, Stevens et al. 2000). Today, it is still unclear if the population recovered, although intensive fishing only sustained eight years (Camhi et al. 1998, Walker 1999). This raises further concern due to similar biology and life history traits among this region and the Northeast Atlantic stock. In addition, tope was among the third most important species in commercial shark catches of France in the late 1980's, where catches were already declining (Bonfil 1994). Therefore, it is likely that historical exploitation already depleted the stock, as suggested in the present results, yet current unselective and unmanaged bycatch has further severely decreased the population.

3.10 Abundance trends

3.10.1 Introduction

Tope has experienced serious declines in abundance in parts of the Mediterranean Sea (Ferretti et al. 2005). In the Northeast Atlantic, declines of mean density have been reported from the English Channel (Martin et al. 2010), whereas a slight increase was reported from the Celtic Sea (Ellis et al. 2005b). Due to the unsustainable exploitation of tope in the Northeast Atlantic (section 3.8 and 3.9), it is expected that the abundance in the available survey data decreased over the last years. Here, catch per unit effort (*CPUE*) data was used, to investigate the abundance of tope over the last two decades.

3.10.2 Materials and methods

The method applied to investigate the abundance trends was presented in detail in section 2.6. The catches were extracted from the survey data. Only valid hauls were considered, as specified in DATRAS data.

The time period from 1992 to 2012 was selected, because not all age classes were present in the early surveys (Supplementary Information, Figure 2).

3.10.3 Results

An exponential curve fitted to the abundance data from 1992 to 2012 accounted for 32% of the observed variability, with a negative slope of -0.0633 (r^2 = 0.32, p = 0.007, 95% confidence limits = -0.105 − -0.022) (Figure 18). Accordingly, the *CPUE* was 0.193 in 1992 and 0.054 in 2012. Trend analysis revealed that the population declined by 72% since 1992 in the Northeast Atlantic. Furthermore, it is consistently below the mean *CPUE* since 2006. An investigation of the different surveys revealed that tope catches decreased by 85% in the North Sea survey (r^2 = 0.25, p = 0.026, slope = -0.0992, 95% confidence limits = -0.179 − -0.019, intercept = 195.83, 95% confidence limits = 35.92 − 355.75), whereas no trend was shown by the other surveys, because of few data and high scatter ($p > 0.05$) (Figure 19).
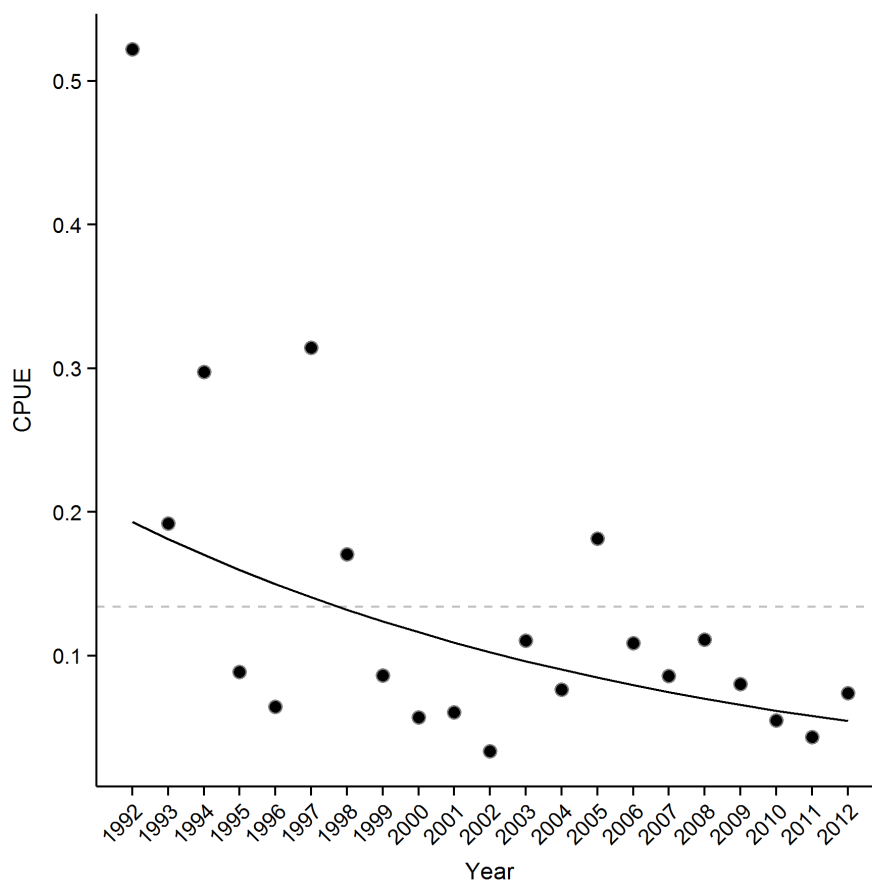
Figure 18: Abundance trends of tope in the Northeast Atlantic from 1992 to 2012. The decrease is explained by an exponential model (r^2 = 0.32, p = 0.007, slope = -0.0633, 95% confidence limits = -0.105 − -0.022, intercept = 124.49, 95% confidence limits = 41.68 − 207.3). The dashed line indicates the mean catch per unit effort (*CPUE*) of 0.134 from 1992 to 2012.
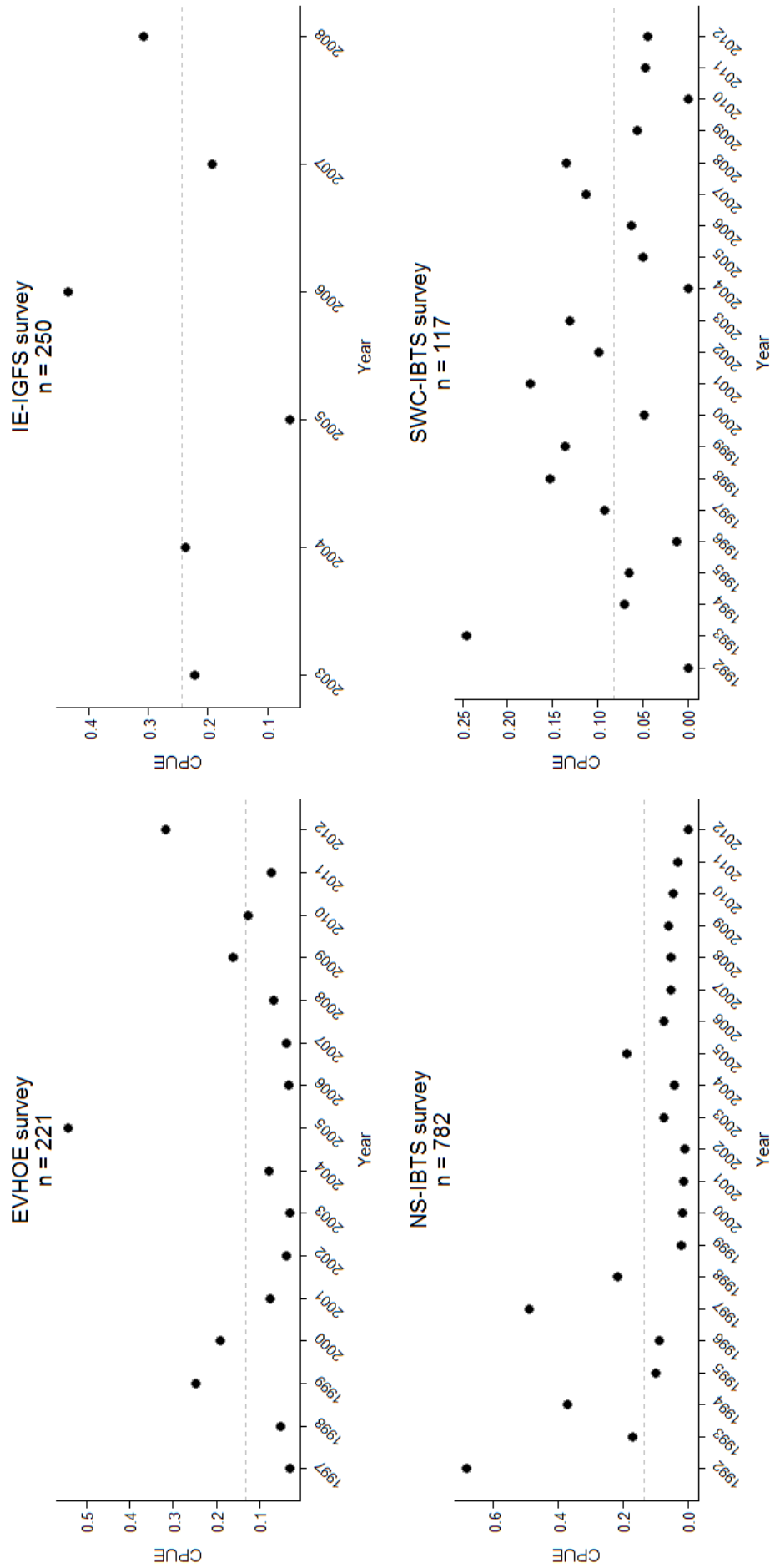
Figure 19: Abundance estimates of tope across the single surveys. The grey dashed line indicates the mean *CPUE* over the time period. The abbreviation *n* gives the total number of individuals caught in this survey and time period.

3.10.4 Discussion

Due to the strong swimming ability and large size of adults, ICES surveys do not effectively sample tope sharks (ICES 2009) and the ICES (2012) states that the analysis of *CPUE* data has been undertaken carefully. However, the efficiency of catching this species should not change over time if the same gear is used. Moreover, the strong decrease, together with the possible lack of females and juveniles, suggest that tope has been seriously depleted in the Northeast Atlantic. Likewise, the abundance estimates were far below the mean *CPUE*, since recently. As it take long periods of time for this species to recover, even in areas where maturity is earlier and productivity higher (Punt et al. 2005), the results demonstrate the urgent need for appropriate management of tope in the Northeast Atlantic.

3.11 Length and age at first capture

3.11.1 Introduction

Froese et al. (2008) showed the importance of including size in management plans. They found that if fishes are caught after a certain length, cohort biomass is much less affected by fishing pressure. Likewise, Colloca et al. (2013) investigated the effect of size under sustainable fishing of teleosts and crustaceans and supported that length must be considered to maximise yield and biomass. Here, the effect of length and age at first capture on female cohort biomass was investigated under different fishing scenarios, to evaluate the importance of including size at first capture in shark management plans. Tope served as reference species, because of its late maturity of 21 years and its longevity of 55 years (section 3.3). Thus, the length at first capture is expected to play a crucial role in sustainable exploitation of this species.

3.11.2 Materials and methods

The method was explained in detail in section 2.7. The change in cohort biomass was investigated for three different fishing scenarios ($F_{msy0.5r}$, $F_{msy0.5M}$ and $F_{current}$) obtained from the above sections. The results were compared to an unfished population ($F = 0$). Age at first capture was set to age 1 and age 15. In accordance to the von Bertalanffy growth function, this translates into sizes of approximately 40 cm and 135 cm, respectively. The latter refers to the optimum length calculated for tope.

3.11.3 Results

If age at first capture was one year, the total cohort biomass was only 15% of that from an unfished population under the current fishing mortality (Figure 20). Moreover, under the current fishing mortality, the cohort biomass at maturity decreases by 90%. The total cohort biomass and the percentage reaching maturity are at half of the virgin biomass under $F_{msy0.5r}$, but remain below 50% under $F_{msy0.5M}$. Considering F_{msy} and an optimum age at first capture, the total cohort biomass is approximately 25% below the total cohort biomass of an unfished population. This decreases to half of the unexploited cohort biomass under the current fishing mortality rate. If the cohort would not experience fishing before reaching the optimum age, more than 75% would reach maturity under F_{msy} compared to the virgin cohort biomass, whereas under the current fishing mortality rate this would still be below 40%.
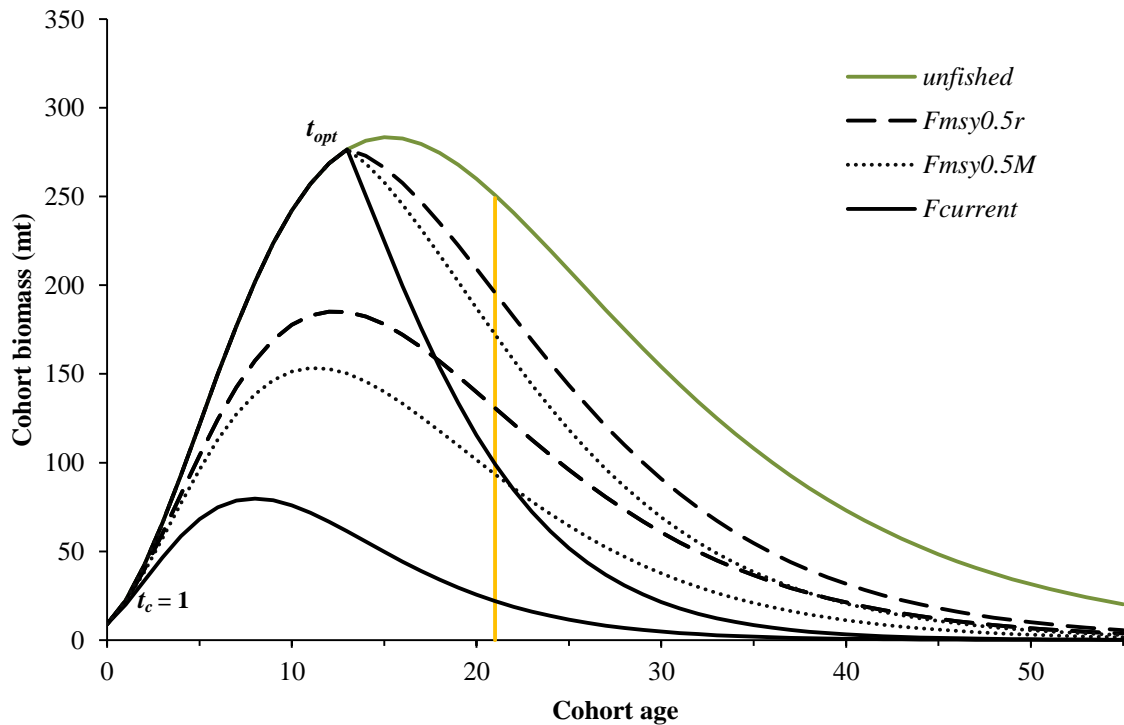
Figure 20: The effect for different scenarios of fishing mortality rates ($F = 0$, $F_{msy0.5r} = 0.031$ yr^{-1}, $F_{msy0.5M} = 0.047$ yr^{-1}, $F_{current} = 0.116$ yr^{-1} and ages at first capture t_c ($t_c = 1$, $t_c = 15$) on the cohort biomass of tope. The orange vertical line represents the age at maturity of females ($t_m = 21$).

3.11.4 Discussion

The results demonstrate the importance of size in the management of slow growing, late maturing and long lived sharks. There was a significant increase in cohort biomass if the age at first capture was at optimum age. This is in agreement with findings for teleosts, where harvesting at optimum size increases cohort biomass (Froese et al. 2008, Colloca et al. 2013).

However, under the current fishing mortality rate, the spawning stock was only at 15% of the virgin biomass. This means that even with an age at first capture of 15 years (or 135 cm), sustainable exploitation is unrealistic. Due to the destructive and unselective fishery in the nursery ground of tope (section 3.6), one year as age of first capture (or 40 cm) seems to be a reasonable assumption. Considering the long history of fishing in this area (Lotze 2005, Lotze et al. 2005) and the low percentage of females reaching maturity under these conditions, the findings strongly support those of section 3.6, 3.8, 3.9 and 3.10. According to Ricker (1975), maximum sustainable yield is achieved at half of the unexploited biomass. Therefore, even under apparent sustainable exploitation, i.e. assuming F_{msy} to occur at half the natural mortality rate, maximum sustainable yield is not produced if the age at first capture is one year. Only if sustainable exploitation is assumed to occur at half the intrinsic rate of population increase, maximum sustainable yield can be achieved independently from size. This is presumably caused by the low value of $F_{msy0.5r}$. The findings of this study support that low productive shark species are highly vulnerable to already light fishing pressure (Myers and Worm 2005, Ward-Paige et al. 2012). Furthermore, tope should not be caught before reaching maturity, to allow recovery of the population and sustainable exploitation.

4. Biology and life history of *Mustelus asterias*

Starry smoothhound (*Mustelus asterias*) (Figure 21) belongs to the family of houndsharks (*Triakidae*). The genus *Mustelus* is the largest within this family, containing more than half of all species. The species is distributed in the Northeast Atlantic, the Mediterranean Sea and along the north-western coast of Africa, down to Mauritania. It is the only white spotted smoothhound species in Europe. Unlike the opportunistic tope or spurdog, this species feeds primarily on crustaceans (Compagno 1984b, Compagno et al. 2005). In the following, aspects of its biology and life history as needed to examine the status, trends and conservation opportunities are presented. The findings are summarised in the Supplementary Information (Table 3).
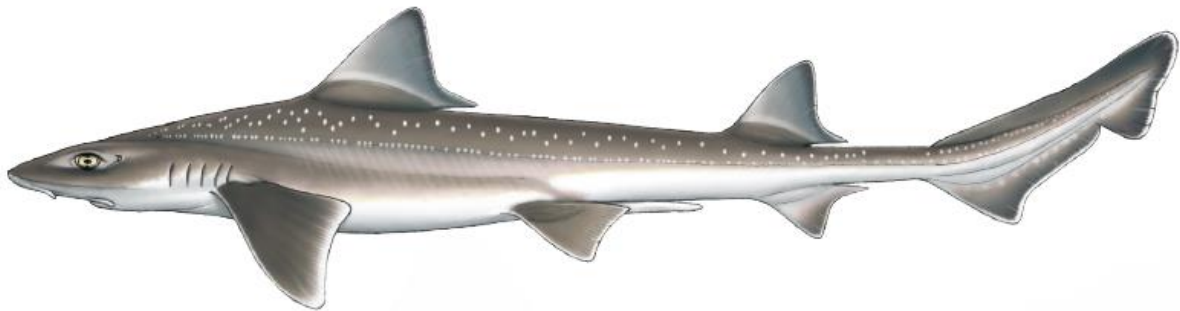
Figure 21: Illustration of *Mustelus asterias*, modified and taken from www.sharktrust.org.

4.1 Length-weight relationship

4.1.1 Introduction

The starry smoothhound has a rather slender body (Figure 21). Therefore it is expected that the shape parameter a is between 0.01 and 0.001, if growth is isometric (Froese 2006).

4.1.2 Materials and methods

Information on the length-weight relationship was taken from Farrell et al. (2010a) and Greenstreet et al. (2007). The parameters for both sexes combined were obtained by treating males and females as two different studies. Then, the relationship can be summarised by the geometric mean of a and the arithmetic mean of b (Froese 2006).

4.1.3 Results

The length-weight relationships of males, females and both sexes combined for the Northeast Atlantic are presented in Table 13. Total length is given in cm and weight is given in grams.

Table 13: Length-weight relationship of starry smoothhound for the Northeast Atlantic. The summarised parameters are shown in bold. The 95% confidence limits are given in parentheses.

sex	*a*	*b*	n	length range (cm)	r^2	source
male	0.0030	3.05	304	28 − 104	0.98	Farrell et al. (2010a)
female	0.0010	3.27	424	30 − 124	0.98	Farrell et al. (2010a)
combined	0.0020	3.12	---	---	---	Greenstreet et al. (2007)
	0.0018 (0.014 − 0.024)	**3.15** (3.09 − 3.21)	**---**	**---**	**---**	this study, summarised from above

4.1.4 Discussion

Although the exponent of females is larger than 3, it is still in the expected range from 2.7 to 3.4 as reported for most fish, but indicates a positive allometric growth (Froese 2006). Thus, females will become more rotund as they grow. The parameter *a* of males and females falls within the expected ranges for slender fishes, and indicates this species is being between an eel-like and elongated form (Froese 2006). Therefore, the results reflect the slender body shape of this species (Figure 21).

4.2 Reproductive biology:

4.2.1 Introduction

The reproductive biology of starry smoothhound for the Northeast Atlantic has been described recently by Farrell et al. (2010b). Here, all information is summarised with respect to the latter examination of species status, exploitation trends and critical habitats.

4.2.2 Materials and methods

Information on reproductive biology was extracted from Farrell et al. (2010b) and Ebert and Stehmann (2013).

4.2.3 Results

The size at maturity of the starry smoothhound for the Northeast Atlantic is given in Table 14.

Table 14: Maturity stages of starry smoothhound in the Northeast Atlantic.

sex	length at matruity (cm)			region	source
	first	50%	100%		
male	72	78	86	NE Atlantic	Farrell et al. (2010b)
female	83	87	92	NE Atlantic	Farrell et al. (2010b)

The proportion of females mature p has been described by (Farrell et al. 2010b):

$$p = 1/(1 + e^{-(-48.596+0.561*TL)}) \tag{30}$$

where *TL* is the maternal total length in cm. The average size at birth is 30 cm and ranges from 28 to 32 cm Farrell et al. (2010b).

The litter size increases with maternal length and is described by (Farrell et al. 2010b):

$$litter\ size = 0.00004 * TL^{2.64}\ (r^2 = 0.39) \tag{31}$$

The sex ratio at birth is 1:1 (Farrell et al. 2010b). The gestation period lasts for 12 months and breeding takes place every other year, resulting in a biennial reproductive cycle (Farrell et al. 2010b). Pupping occurs from April to July in shallow waters (Farrell et al. 2010b). Mating is thought to occur soon after parturition (Ebert and Stehmann 2013), possibly in October (Farrell et al. 2010b).

4.2.4 Discussion

The size at 50% maturity of females suggested by Farrell et al. (2010b) agrees with the findings of Henderson et al. (2003). They examined three females, the smallest 87 cm, and found all to be mature. However the size at maturity is smaller than determined for Mediterranean specimens (Capapé 1983). The variations in the size at maturity among the two regions have been discussed by Farrell et al. (2010b) as possible differences in methodology, higher growth rates, limited food availability in the Mediterranean, or a response of fishing pressure. Fecundity is mainly a function of body weight (Froese and Luna 2004) and therefore, the exponent of the fecundity-length relationship would be expected close to 3 (Froese 2006). The slightly lower exponent suggests that larger females produce slightly larger pups. Furthermore, fecundity was found to be lower than in the Mediterranean Sea (Capapé 1983). The suggested time of mating should be viewed with caution, because egg fertilization might happen after a period of sperm storage and mating can may happen before the females reach sexual maturity (Farrell et al. 2010b).

4.3 Age and growth:

4.3.1 Introduction

Growth of starry smoothhound from the Northeast Atlantic has been investigated in detail by Farrell et al. (2010a). Thus most information has been summarised based on their study.

4.3.2 Materials and methods

Growth parameters of the starry smoothhound for the Northeast Atlantic have been described in the literature based on sectioned vertebrae (Farrell et al. 2010a) and modelled for combined sexes (Greenstreet et al. 2007). For the purpose of this study, the parameters for both sexes combined were estimated as the geometric mean of all available studies.

4.3.3 Results

The von Bertalanffy growth parameters are given in Table 15.

Table 15: Von Bertalanffy growth parameters of starry smoothhound from the Northeast Atlantic. The summarised parameters are shown in bold. The 95% confidence limits are given in parentheses.

sex	L_∞	k	L_0	region	source
male	103.7	0.195	38.1	NE Atlantic	Farrell et al. (2010a)
female	123.5	0.146	34.9	NE Atlantic	Farrell et al. (2010a)
combined	105.4	0.118	---	North Sea	Greenstreet et al. (2007)
	111 (105 − 116)	**0.150** (0.13 − 0.17)	**36.5** (34.9 − 38)	NE Atlantic	this study, geometric mean of above

The maximum size given by Farrell et al. (2010a) is 104 cm for males and 133 cm for females, yet these may reach 140 cm (Ebert and Stehmann 2013). The maximum age based on the time needed to reach 95% of the asymptotic length (Taylor 1958) is 18.3 years for females and 13 years in males (Farrell et al. 2010a). The age at 50% maturity based on the von Bertalanffy growth function is 5 years in males and 6 years in females (Farrell et al. 2010b).

4.3.4 Discussion

The female growth rate found by Farrell et al. (2010a) is about half of that reported for specimens from the Mediterranean Sea (Francis 1981). Large differences between the two areas have been suggested by Henderson et al. (2003), based on three specimens from western Ireland. Thus, the age at maturity of females is higher than the previously estimated 2.3 to 2.5 years from the Mediterranean Sea (Francis 1981).

4.4 Natural mortality

4.4.1 Introduction

No information of the natural mortality for starry smoothhound are described in the literature, however, based on its life history it is expected to have a higher mortality rate than spurdog or tope.

4.4.2 Materials and methods

Natural mortality of starry smoothhound was estimated from empirical equations, see *Natural mortality* for tope (section 3.4)

4.4.3 Results

The results of the life history approaches to estimate natural mortality are given in Table 16.

Table 16: Natural mortality rates of starry smoothhound estimated from life history. The median value is used for the purpose of this study. The 2.5 and 97.5 percentiles of natural mortality are 0.199 and 0.272, respectively.

method	Hoenig (1983)	Pauly (1980)	Jensen (1996) (age)	Jensen (1996) (growth)	median
input	---	$k = 0.146$, $L_\infty = 123.5$, $T = 7$	$t_m = 6$	$k = 0.146$	
natural mortality	---	0.180	0.275	0.219	0.219

4.4.4 Discussion

Although Farrell et al. (2010a) suggested a maximum age above 18 years for starry smoothhound, this was based on the assumption that the time needed to reach 95% of the asymptotic length equals longevity and therefore the method of Hoenig (1983) was not applied. The estimate of natural mortality derived with the remaining empirical methods for starry smoothhound is similar to the natural mortality of rig (*Mustelus lenticulatus*), a species with comparable life history traits (Francis and Maolagáin 2000, Compagno et al. 2005) and with *M* estimated to be in the range of 0.2 yr^{-1} to 0.3 yr^{-1} (Francis and Francis 1992).

4.5 Habitat and distribution

4.5.1 Introduction

The potential distribution of starry smoothhound was examined via AquaMaps (Kaschner et al. 2013). The species is commonly found along continental and insular shelves (Compagno et al. 2005). Therefore starry smoothhound is expected to cover a broad range of the study area.

4.5.2 Materials and methods

Potential distributions were investigated as described under *Habitat and distribution* of tope (section 3.5).

4.5.3 Results

The starry smoothhound occurs to depth of 350 m (Serena et al. 2009). The potential distribution is given in Figure 22 and the environmental parameters are detailed in Table 17.
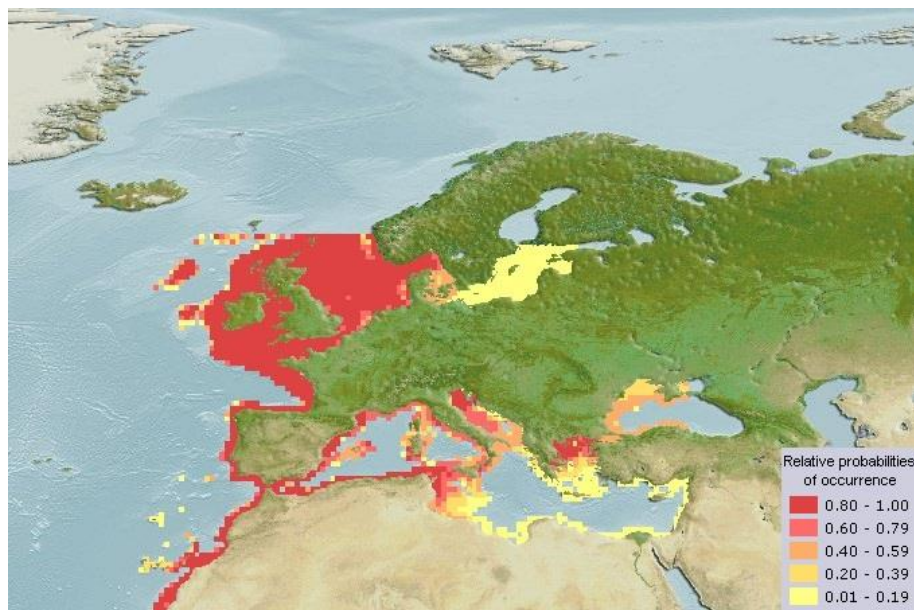
Figure 22: Potential distribution of the starry smoothhound in the Northeast Atlantic, obtained from AquaMaps, adjusted by depth.

Table 17: Environmental parameters used to model the potential distribution of starry smoothhound in the Northeast Atlantic.

environmental envelopes	min	preferred min	preferred max	max
depth (m)	1	41	162	350
bottom water temperature (°C)	4.7	9.8	20	22.5
bottom salinity (psu)	5.6	34.2	37.5	39.3
primary production (mgC*m-2*day-1)	306	457	1729	3781

4.5.4 Discussion

Although its habitat preferences are narrower than the tope shark's, the starry smoothhound covers potentially most areas investigated in this study. The starry smoothhound seems to be highly migratory, indicated by recent tagging results. Of several sharks tagged in summer in the southern North Sea, one female was recaptured in the Bay of Biscay, one male at the coast of Norway and another male at the east coast of Scotland.

All recaptures were made during winter and specimens have been at liberty for less than 17 months (Winter and van Oversee 2013). In addition, first tagging results from other areas support that *Mustelus asterias* is wide ranging, indicated by one female tagged in Wales and recaptured in the Bay of Biscay after 257 days at liberty (Farrell et al. 2010b). Therefore, starry smoothhound was considered to be a single stock unit covering the Northeast Atlantic. It was speculated that breeding grounds may exist in the Irish Sea and female feeding grounds in the Bay of Biscay (Farrell et al. 2010b). Areas with higher abundances of juveniles have been observed inshore off southern England, the Bristol Channel and the Outer Thames Estuary (Ellis et al. 2005a). Furthermore, Farrell (2010) reported juveniles from the south-east coast of Ireland. Mature females have been observed in the waters of northwest Wales in May (Farrell 2010). Both sexes with length larger than 50% at maturity have been observed in the southern North Sea in summer (Winter and van Oversee 2013). In conclusion, starry smoothhound covers a major part of the investigated area. Critical areas for adults may occur in the Irish Sea, the Bay of Biscay and the southern North Sea. Nursery grounds may be found all along the south-eastern to the south-western coast of England and the Irish Sea.

4.6 Critical areas

4.6.1 Introduction

Landings of the starry smoothhound have been increasing recently, possibly as the fishery compensate for the depleted spurdog (ICES 2012). Therefore, it is crucial to identify areas where this species can recover from fishing pressure. Here, pupping and nursery grounds as well as grounds important for mature specimens in the Northeast Atlantic were investigated based on *CPUE* data.

4.6.2 Materials and methods

The data was based on ICES surveys (section 2.1). Information about the different life history stages was taken from the *Reproductive biology* section. Early juveniles were defined by a length range of 33 cm to 50 cm, which would approximately correspond to an age of up to 2 years. Analysis of critical habitats for mature specimens were made for males and females separately. The individuals where sex was not determined were included in the female dataset. The dataset contained 8066 records of starry smoothhound, caught from 1971 to 2012. Specimens were present in all months and depth ranged from 10 m to 320 m.

4.6.3 Results

Pupping and nursery grounds were found in the Southern Bight and the Bristol Channel (Figure 23). Catches in the latter region occurred only in one year. In total, 83 pups were recorded within 13 different years in a period from 1992 to 2012. The highest numbers of pups occurred in August. However, pups were also caught in November, January, February and May. All catches were made in depths ranging from 11 m to 85 m. The results are summarised in Table 18. A higher number of early juveniles covering a broad range were caught fairly regularly from 1990 to 2012 (n = 2271) (Figure 24). Their abundance was highest in November.
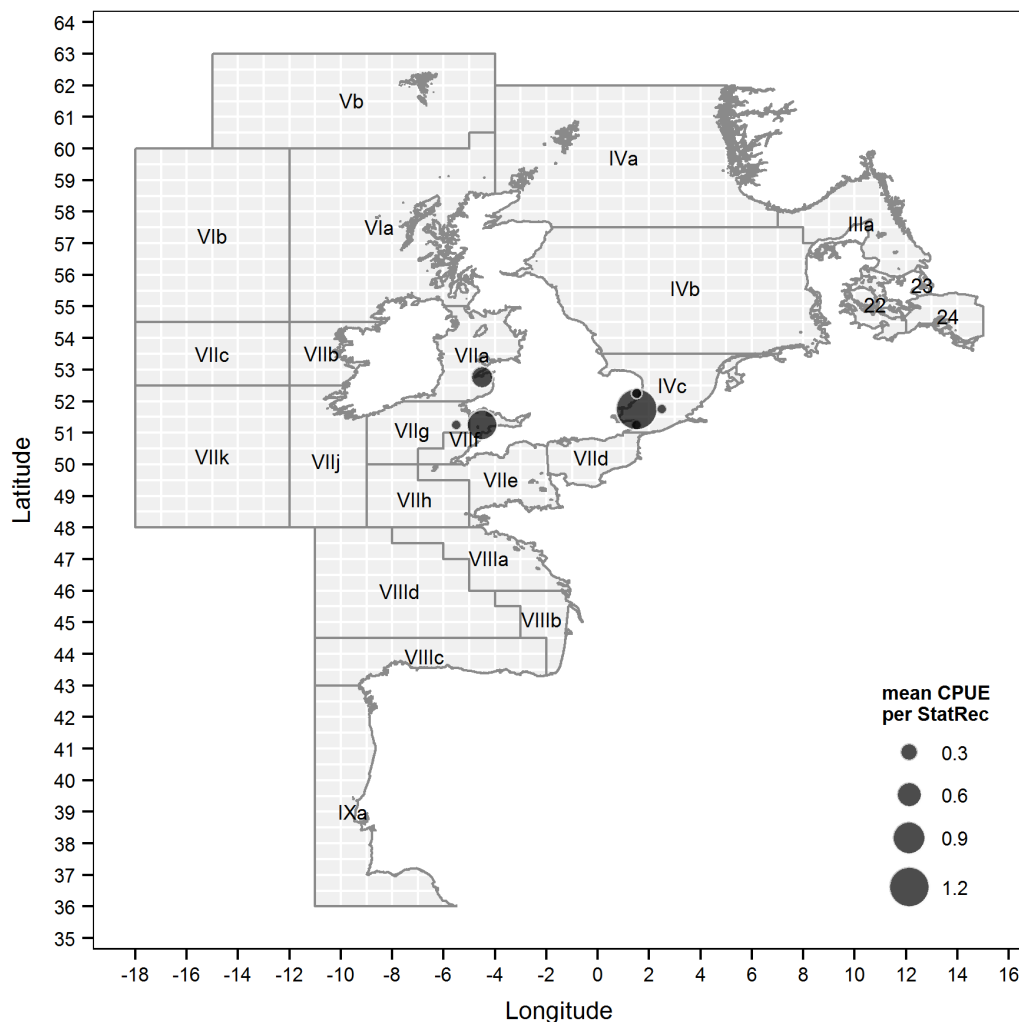
Figure 23: Records of starry smoothhound pups (28 cm − 32 cm) from ICES surveys in the Northeast Atlantic. In total, the sample contained 83 individuals, reported in 13 different years from 1992 − 2012.
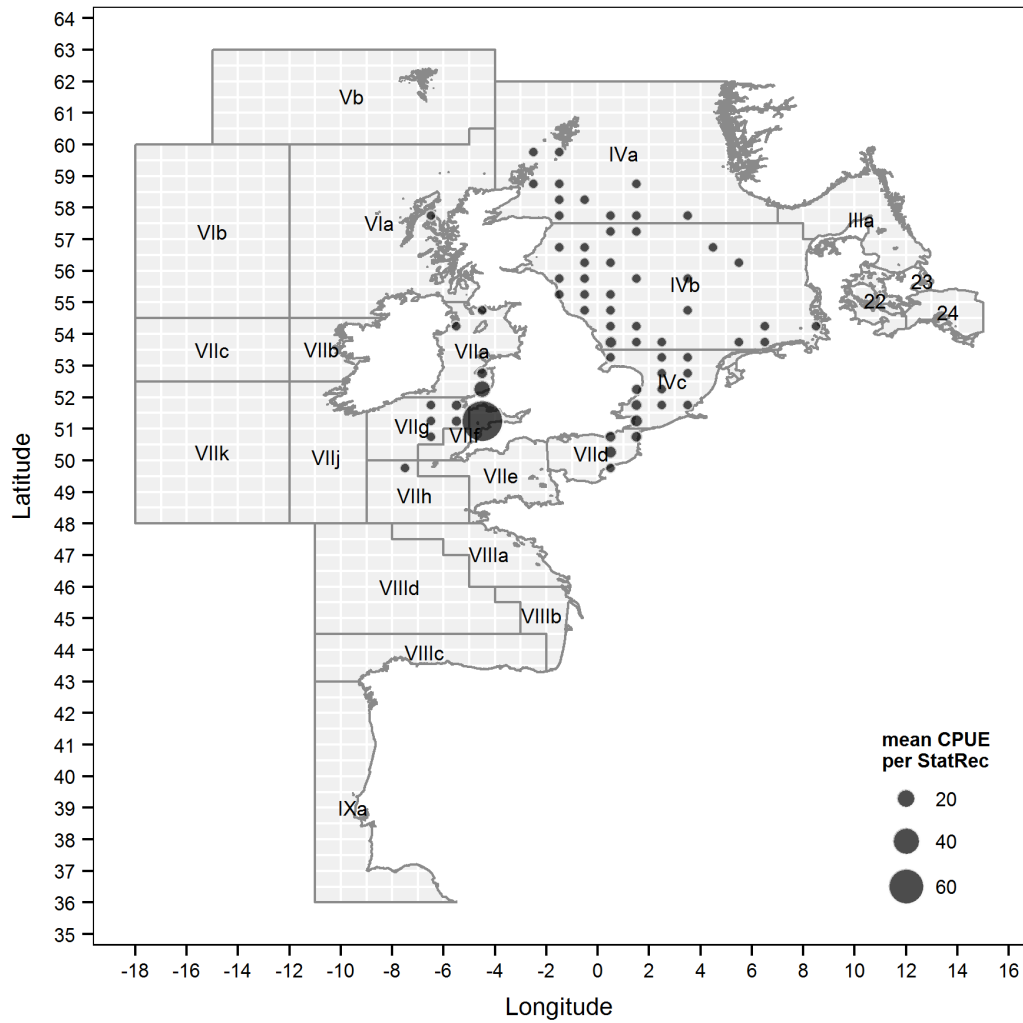
Figure 24: Records of early juvenile starry smoothhound (33 cm − 50 cm), from ICES surveys in the Northeast Atlantic. In total, the sample contained 2271 individuals, reported from 1990 − 2012.

Mature specimens were recorded in 23 different years, from 1989 to 2012. The total number caught was 1731 individuals of which 468 were females, 1093 males and for 170 the sex was not determined. The depth ranged from 15 m to 298 m. The highest abundance of males was found in the southern Irish Sea, followed by the Bristol Channel (Figure 25). In both areas the highest *CPUE* occurred in November (Table 18). Males were also frequently caught in the Outer Thames Estuary, especially in August. In February, the males *CPUE* was highest in the northern North Sea. Females were most numerous off the east coast of England and in the northern Bay of Biscay (Figure 26). In the latter region, catches of the species have been reported in every year of investigation, with highest abundance in December (Table 18). Furthermore, both sexes were caught regularly in the southern Celtic Sea.
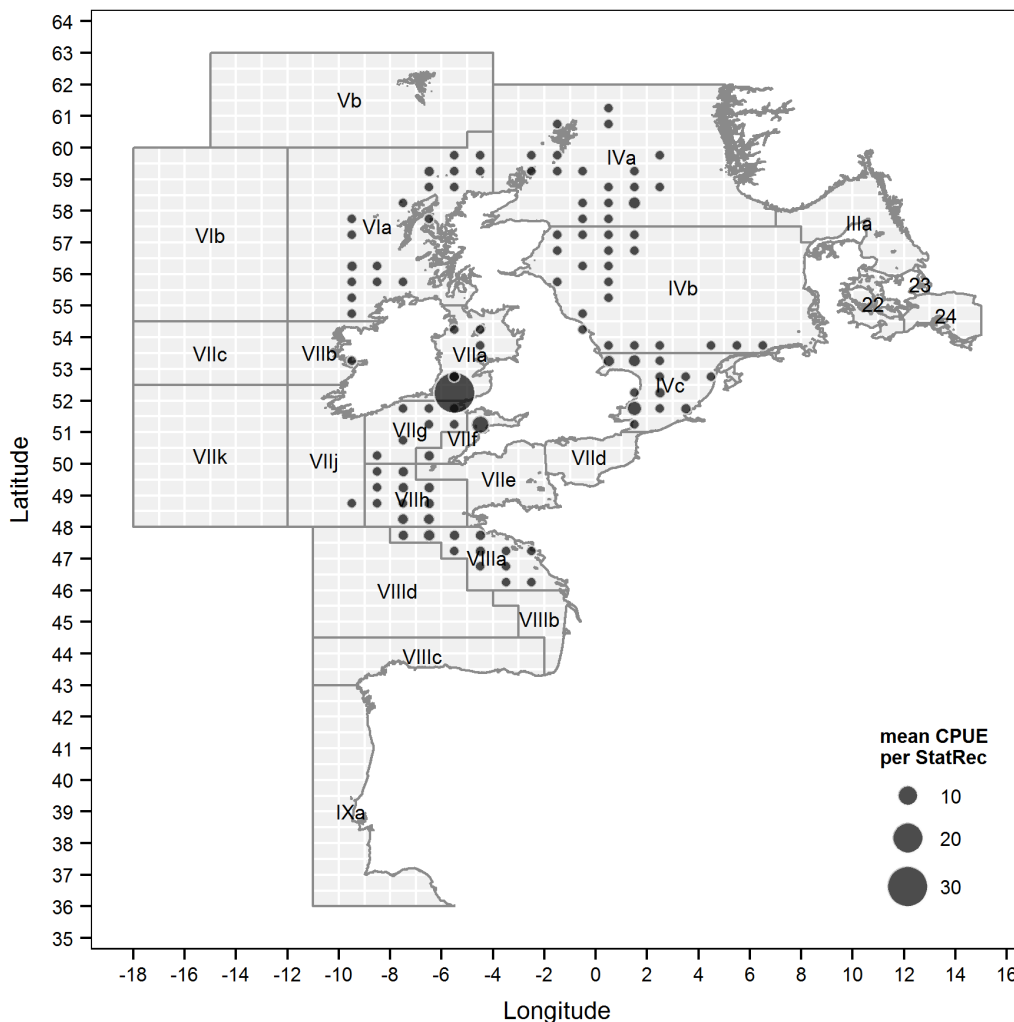
Figure 25: Records of mature starry smoothhound (size of male ≥ 78 cm, size of female and unknown sex ≥ 87 cm) for combined sexes from ICES surveys in the Northeast Atlantic. In total, 1731 mature individuals were recorded in 23 different years, from 1989 − 2012.

Figure 26: Distribution of mature starry smoothhounds (size ≥ 87 cm) with males excluded, i.e. presumably females, from ICES surveys in the Northeast Atlantic. In total, 638 mature individuals were recorded.

Table 18: Investigated areas of different life stages for starry smoothhound in the Northeast Atlantic. Approximate bounding boxes are given by longitude and latitude. The total number caught is given per sex and the time period when surveys were conducted. The mean *CPUE* refers to the mean catch per unit effort in this area, regardless of the area size. The highest catch per month was obtained by the mean number per month divided by the total effort in this month. In addition, it is indicated if this area is at least partly covered by a protected area (PA). This information was obtained from OSPAR (2013) and JNCC (2013). Areas determined as extremely important for starry smoothhound are shown in bold.

life stage	ICES division	area name	long	lat	depth (m)	years caught	years investigated	period	number			mean CPUE	highest catch	includes PA
									females	males	unknown			
pupping and nursery	IVc	**Outer Thames Estuary**	**1, 2**	**51, 52.5**	**22-46**	**11**	**31**	**1982-2012**	**33**	**31**	**8**	**3.15**	**August**	**Yes**
	VIIf	Bristol Channel	-5, -4	50.5, 52	61	1	6	1999-2012	0	5	0	4.8	November	Yes
	VIIa	Cardigan Bay	-5, -4	52, 53	11	1	2	2003, 2004	2	0	0	1	November	Yes
mature	IVa	**Fladen Ground**	**-1, 2**	**58, 59.5**	**110-151**	**9**	**40**	**1971-2012**	**18**	**190**	**19**	**8.73**	**February**	**Yes**
	IVb	East Scotland	-2, 1	55.5, 57.5	63-96	11	42	1967-2012	8	29	5	1.33	January	Yes
	IVc, IVb	**East coast of England**	**0, 3**	**53, 54**	**15-90**	**16**	**38**	**1967-2012**	**78**	**46**	**63**	**4.86**	**August**	**Yes**
	IVc	**Outer Thames Estuary**	**1, 2**	**51, 52.5**	**23-44**	**18**	**31**	**1982-2012**	**10**	**242**	**22**	**7.04**	**August**	**Yes**
	VIa	Northwest of Scotland	-7, -5 / -7, -6	57.5, 59.5 / 55, 55.5	100-161	6	25	1985-2012	10	38	2	3.04	February	Yes
	VIa	North coast of Ireland	-9, -7 / -10, -9	54, 56 / 54, 55.5	70-150	7	28	1985-2012	17	7	3	1.64	February	Yes
	VIa	Vidal Bank	-10, -9	55.5, 57	141-180	4	28	1985-2012	8	9	0	4.25	March	No
	VIIa	**Southern Irish Sea**	**-8, -4**	**52, 53**	**72-97**	**2**	**7**	**1997-2008**	**4**	**126**	**0**	**21.76**	**November**	**Yes**
	VIIa	North-west Anglesey Reef	-5, -4	53, 54	42-68	2	11	1996-2006	6	4	0	2.17	November	No
	VIIf	**Bristol Channel**	**-5, -4**	**50.5, 52**	**57-61**	**4**	**6**	**1999-2012**	**4**	**43**	**0**	**11.73**	**December**	**Yes**
	VIIj	Southwest of Ireland	-12, -9	48, 52.5	169	2	23	1990-2012	0	4	0	1.5	November	Yes
	VIIh	**Southern Celtic Sea**	**-9, -7 / -9, -5 / 1, -5**	**49.5, 50 / 48, 49.5 / 46, 47**	**119-180**	**15**	**18**	**1990-2012**	**78**	**93**	**2**	**2.19**	**October**	**Yes**
	VIIIa	**Northern Bay of Biscay**	**-2, -6 / -3, -8**	**47, 47.5 / 47.5, 48**	**37-298**	**16**	**16**	**1997-2012**	**181**	**83**	**2**	**1.94**	**December**	**Yes**

4.6.4 Discussion

The fact that pups were caught in all months might be an artefact of net abortion or of length variability at birth. However, the observed abundance peak of pups in August agrees with reported time of birth from April to July (Farrell et al. 2010b). The distribution of pups and early juveniles was overlapping and thus indicated that the pupping grounds serve also as nursery grounds. The Outer Thames Estuary seems to be the most important nursery area of those identified here, indicated by its use over several years. This is supported by a higher number of juveniles found in this area in former studies (Ellis et al. 2005a). Though not all proposed nursery areas could be identified here (Ellis et al. 2005a, Farrell 2010), because of the small sample size. In addition, the high number of juveniles along the east coast of Britain may reflect another nursery ground. Areas where both sexes occur have the potential to display mating grounds. Mating has been suggested to occur in October (Farrell et al. 2010b). This would indicate the east coast of England, the southern Celtic Sea and the northern Bay of Biscay as most likely mating grounds. Off the east coast of England, both sexes were present in August and September, in the southern Celtic Sea both sexes were present in November, and in the northern Bay of Biscay males and females were present from October to December. Note that there is a high degree of uncertainty in the occurrence of both sexes in other months or areas, due to the lack of sex determination and seasons without any sampling effort. However, in the two southern areas sex was identified for most individuals and annual catches were made regularly. Farrell et al. (2010b) suggested female feeding grounds to exist in the Bay of Biscay. Accordingly, the southern Celtic Sea would possibly represent an important site, where females on their migration from the northern pupping grounds to the Bay of Biscay meet with males to mate. Male feeding grounds may be located in the southern Irish Sea and the northern North Sea. This agrees with tagging results from the Netherlands, where males migrated from the southern North Sea in summer to the northern North Sea in winter (Winter and van Oversee 2013). Although a refuge for sharks, due to less fishing intensity, have been proposed by Shephard et al. (2012) in the north eastern Celtic Sea, the southern Celtic Sea seems to be another important location for the establishment of a protected area. Only a minimal area is covered by an MPA in the south-east (OSPAR 2013, JNCC 2013). Further areas of high protective value for starry smoothhound exist in the northern Bay of Biscay and the Outer Thames Estuary. In addition, the northern coast of Ireland and the Vidal Bank region have potential as conservation areas.

4.7 Biological reference points for fishing mortality

4.7.1 Introduction

There is no information about the intrinsic rate of population increase of starry smoothhound. However, members of the genus *Mustelus* have been suggested to belong to the species of sharks with higher rebound potentials (Smith et al. 1998). Therefore its capacity to withstand fishing may allow sustainable use. Here, the theoretical fishing mortality producing the maximum sustainable yield was investigated.

4.7.2 Materials and methods

The methods applied to obtain proxies of maximum sustainable fishing mortality were covered in section 2.3. Maximum age was assumed at 18 years (Farrell et al. 2010a), age at maturity at 6 years (Farrell et al. 2010b) and natural mortality at 0.219 yr^{-1} (section 4.4).

4.7.3 Results

The results of the life table approach are given in Table 19. The intrinsic rate of population increase was estimated as 0.079 yr^{-1}. The sustainable fishing mortality rate based on the intrinsic rate of population increase was estimated at 0.04 yr^{-1}. The sustainable fishing mortality rate based on natural mortality was estimated at 0.11 yr^{-1}.

Table 19: Life table for starry smoothhound from the Northeast Atlantic. The results are shown from age at maturity to maximum age. To account for sex ratio, resting stages and the complete reproductive cycle, the product of the proportion mature and litter size was multiplied with 0.25 to obtain the age specific fecundity (female pups per female) m_x. The annual reproductive rate per generation is the product of survival to age l_x and m_x. The intrinsic rate of population increase r was estimated at 0.079 yr^{-1}.

length (cm)	age	% mature	litter size	m_x	l_x	$l_x m_x$
87	6	0.50	5.21	0.65	0.269	0.174
92	7	0.94	6.05	1.43	0.216	0.308
96	8	0.99	6.83	1.70	0.173	0.295
100	9	1.00	7.56	1.89	0.139	0.263
103	10	1.00	8.22	2.06	0.112	0.230
106	11	1.00	8.83	2.21	0.090	0.198
108	12	1.00	9.37	2.34	0.072	0.169
110	13	1.00	9.85	2.46	0.058	0.143
112	14	1.00	10.29	2.57	0.047	0.120
114	15	1.00	10.67	2.67	0.037	0.100
115	16	1.00	11.01	2.75	0.030	0.083
116	17	1.00	11.30	2.83	0.024	0.068
117	18	1.00	11.56	2.89	0.019	0.056

4.7.4 Discussion

The estimated intrinsic rate of population increase is lower than in other species of the genus, but in agreement with species having similar life history traits (Smith et al. 1998). Furthermore, the result indicates low resilience (Musick 1999). *Mustelus antarcticus*, a species with similar life history traits, is one of the few examples of sustainable exploitation in sharks, according to Walker (1998). Therefore, sustainable exploitation of starry smoothhound may be possible under appropriate management measures. To follow a precautionary approach, a value of 0.04 yr^{-1} should be utilised as reference point for the fishing mortality rate which produces maximum sustainable yield F_{msy}.

4.8 Annual fishing mortality

4.8.1 Introduction

At present, there is no assessment of the exploitation status of starry smoothhound in the Northeast Atlantic. Serious declines (Ferretti et al. 2005) and local extinctions have been suggested in the Mediterranean Sea (Serena 2005), whereas starry smoothhound is only of limited market value in the Northeast Atlantic (Serena et al. 2009). The species is taken in trawl, gillnet and longline fisheries as bycatch (ICES 2012), where it is often discarded (Serena et al. 2009, ICES 2012). Nevertheless, starry smoothhound is relatively important in recreational fisheries and commercial fisheries for this species may have expanded, possibly because it is targeted instead of the depleted spurdog (ICES 2012). However, an appropriate management plan is missing and information on mortality rates does not exist. Therefore, the current and historical development of annual fishing mortalities was examined here. Fishing mortality was obtained from total mortality based on pooled catch at age ratio.

4.8.2 Materials and methods

The method of estimating mortality via pooled catch at age ratios, i.e. the decrease in total numbers from age at recruitment to maximum age to the decrease in total numbers one age older, was described in detail in section 2.4. Catches were obtained from the survey data. Only valid hauls were considered, as specified in DATRAS data. The time period from 1992 to 2012 was selected, as not all age classes were present in early surveys (Supplementary Information, Figure 3). The log-normal length frequency distribution of the whole survey area allowed the analysis of all available data (Figure 27). On this basis, age classes were obtained from length by applying the von Bertalanffy growth function.

If sex was not given, the von Bertalanffy growth function of both sexes combined was used (section 4.3). In most years a peak was visible at age 5 with decreasing numbers until age 13. Therefore, age recruitment was set to 5 and maximum age to 13. Fishing mortality was obtained from total mortality by assuming a constant natural mortality at 0.219 yr^{-1} (section 4.4).

4.8.3 Results

Annual fishing mortality rates ranged from 0.011 yr^{-1} to 0.261 yr^{-1} (Figure 28). Fishing mortality decreased most rapidly at the end of the 1990's and fluctuated thereafter. In total, three main periods of increasing fishing mortality are visible, followed by three decreasing periods. The majority of exploitation was at levels above F_{msy}.
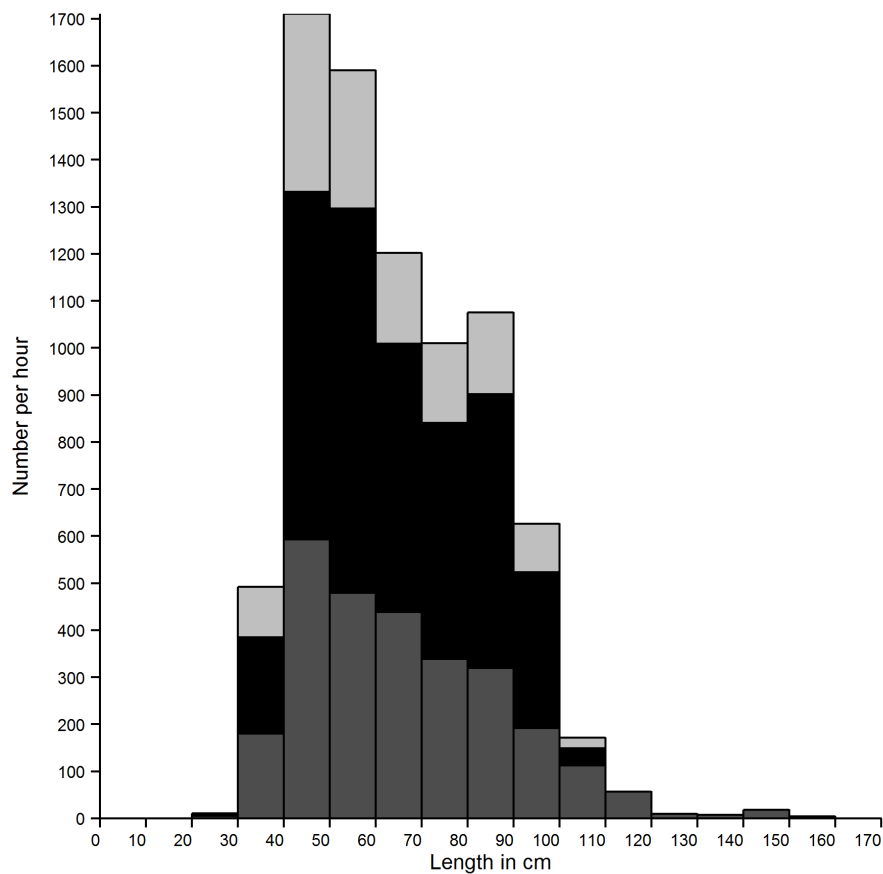
Figure 27: Length frequency distribution of starry smoothhound in the Northeast Atlantic, with data pooled over the years 1992 − 2012. The dark-grey bars represent the number of females, the black bars the number of males and sex was not determined for the light-grey bars.
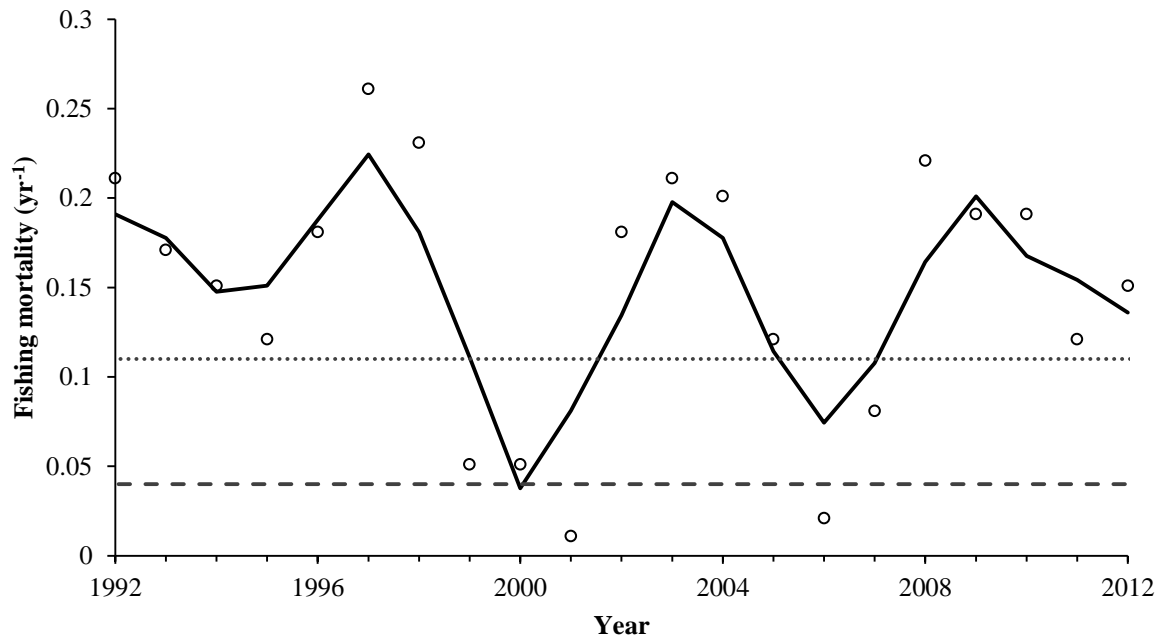
Figure 28: Annual fishing mortality rates of starry smoothhound in the Northeast Atlantic (open circles). The bold line represents the three years moving average. Note that the first and last year only consist of two values, because of border effects. The grey dashed line shows the fishing mortality that would produces maximum sustainable yield F_{msy} estimated from the intrinsic rate of population increase ($F_{msy0.5r} = 0.04$ yr^{-1}), the grey dotted line shows F_{msy} estimated from natural mortality ($F_{msy0.5M} = 0.11$ yr^{-1}).

4.8.4 Discussion

The fishing morality rates had several ups and downs, whereas official landings show an increasing pattern since 1992 (ICES 2013). Though this species is of little market value in the Northeast Atlantic (Serena et al. 2009), it is predominantly caught as bycatch (ICES 2012). Thus, the observed fluctuations might be explained accordingly: as the abundance increases, more individuals are caught accidently, which in turn, decreases the stock size. Thereafter, the stock may recover, as it is not of direct target. One may further argue that in former times, starry smoothhound bycatch was more often discarded at sea, but more recently it is landed due to a higher demand in shark products (Clarke 2004, Hareide et al. 2007). As a result, landings would increase. Under these circumstances, however, the population will decrease in the long term, due to exploitation levels above sustainability. Although this species might not be of direct target and the fishing mortality rates seem to have decreased since 1992, they exceeded sustainable levels the majority of time. Thus, the results confirm the urgent need of appropriate management measures.
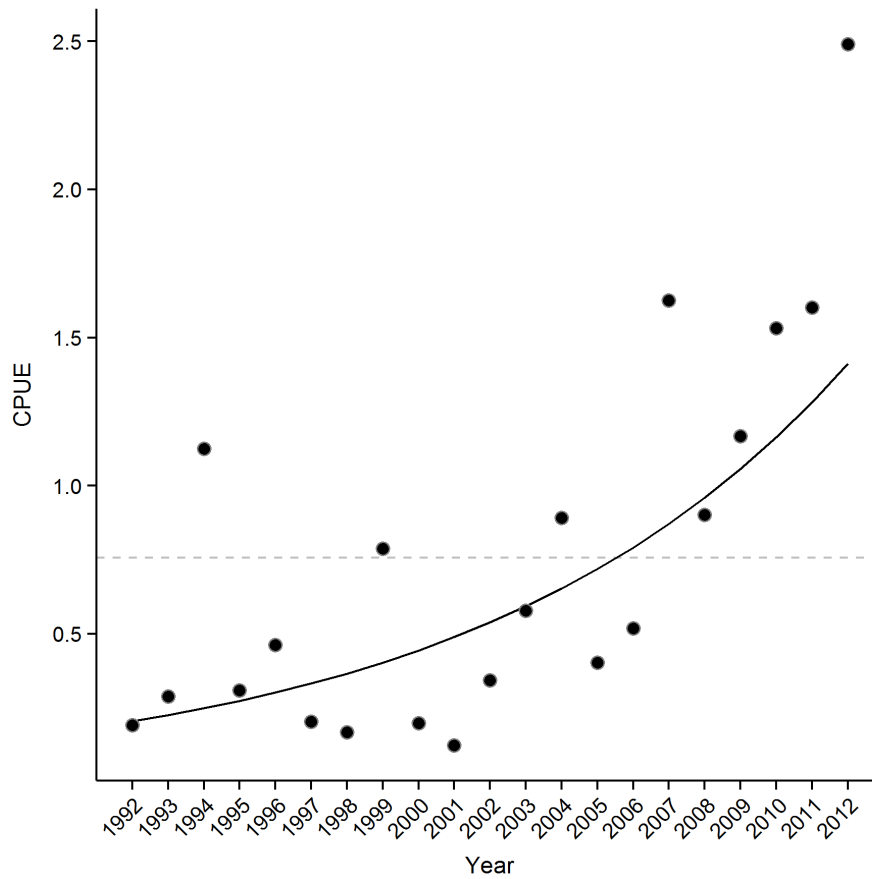
4.9 Abundance

4.9.1 Introduction

Increasing abundance trends have been reported from various regions for starry smoothhound in the Northeast Atlantic (Ellis et al. 2005b, Martin et al. 2010, ICES 2012). Furthermore, total landings increased from 1992 to 2009 and decreased slightly thereafter (ICES 2013). Similar, landings decreased in Portuguese waters (Correia and Smith, 2003). However, the interpretation of landing data is unreliable as this species is commonly reported in aggregated categories (ICES 2012). Here, the abundance trend of starry smoothhound from 1992 to 2012 in the Northeast Atlantic was examined on the basis of mean *CPUE* to investigate its status on the larger geographic scale.

4.9.2 Materials and methods

The method applied to investigate the abundance trends was described in detail in section 2.6. The catches were extracted from the survey data. Only valid hauls were considered, as specified in DATRAS data. The time period from 1992 to 2012 was selected, because not all age classes were present in the early surveys (Supplementary Information, Figure 3).

4.9.3 Results

The abundance of starry smoothhound increased rapidly from the beginning of this century and is far above the mean *CPUE* in 2012 (Figure 29). The greatest change was observed in the French surveys and all surveys except the Irish followed the overall trend, with *CPUE* values above the mean in recent years (Figure 30). The decrease in IE-IGFS survey was not significant ($p > 0.05$), whereas the increase in all other surveys was ($p < 0.05$). An exponential model was fitted from 1992 to 2012 ($r^2 = 0.47$, $p < 0.001$, slope = 0.0965, 95% confidence limits = 0.05 − 0.14, intercept = -193.73, 95% confidence limits = -285.87 − -101.60), which suggests an increase of nearly seven times since 1992.

Figure 29: Abundance trends of starry smoothhound in the Northeast Atlantic from 1992 to 2012. The increase is explained by an exponential model ($r^2 = 0.47$, $p < 0.001$, slope = 0.0965, 95% confidence limits = 0.05 − 0.14, intercept = -193.73, 95% confidence limits = -285.87 − -101.60). The dashed line indicates the mean catch per unit effort (*CPUE*) of 0.757 from 1992 to 2012.
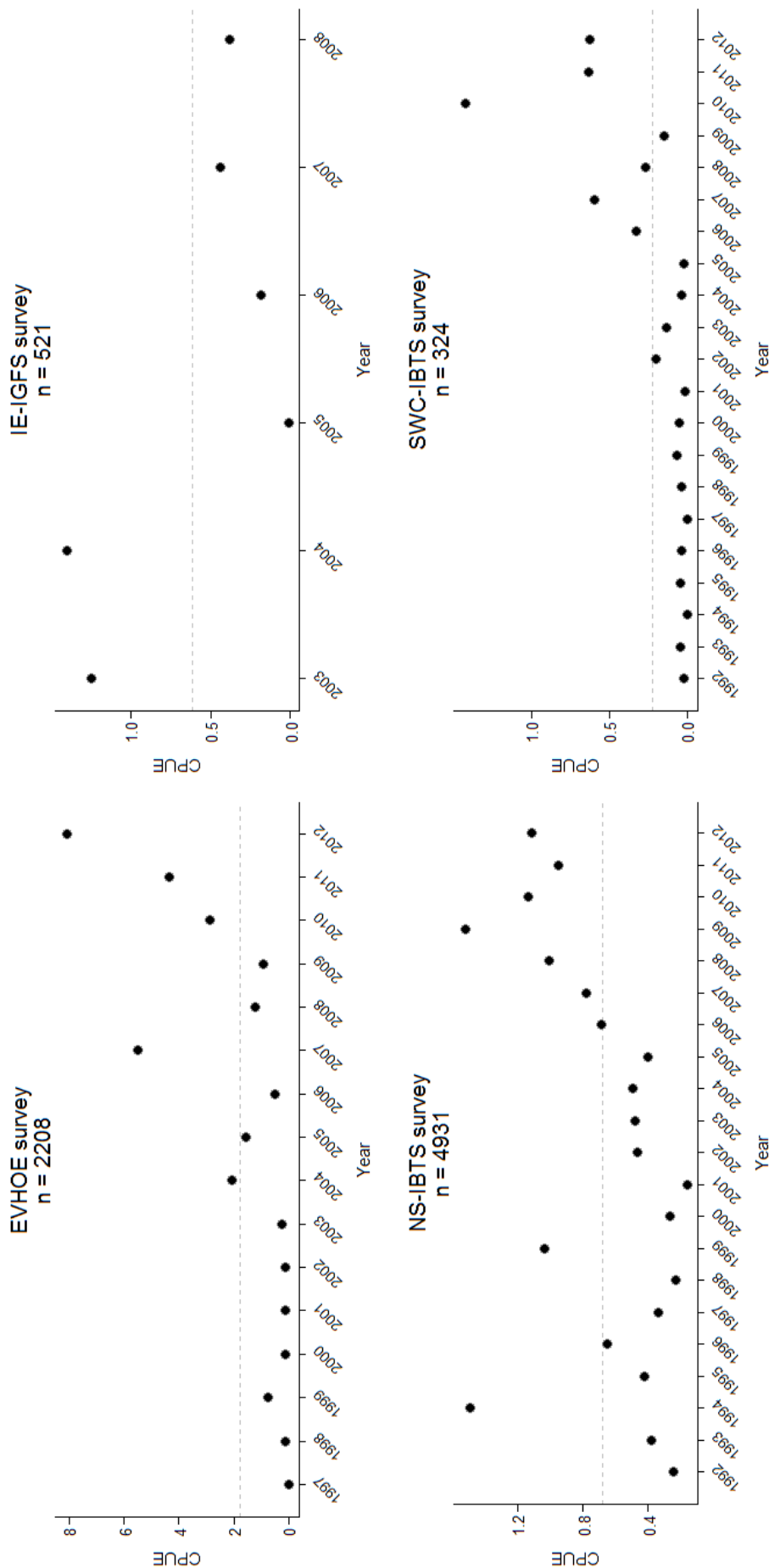
**Figure 30:** Abundance estimates of starry smoothhound across the single surveys. The grey dashed line indicates the mean *CPUE* over the time period. The abbreviation *n* gives the total number of individuals caught in this survey and time period.

4.9.4 Discussion

The results of the present study are in agreement with findings from others (Ellis et al. 2005b, Martin et al. 2010, ICES 2012), yet such a strong increase in only 20 years seems questionable. The main increase in abundance was observed in the French survey. Shephard et al. (2012) found high biomass of starry smoothhound in a north-east Celtic Sea refuge, created by less fishing effort in this region. It has been shown, that the Celtic Sea is a critical habitat for mature specimens, possibly relevant for mating (section 4.6). These observations indicated that the recent increase in abundance may be due to a higher number of adults in the Northeast Atlantic. In accordance, the abundance started to increase after the year of lowest rate of exploitation (section 4.8). These circumstances may have allowed for stronger recruitment. However, the results presented here should be interpreted with caution, because the virgin biomass is unknown. Furthermore, the results suggest a strong increase in abundance, although the fishing mortality is above F_{msy} (section 4.8). On the one hand, this would mean that the abundance increase will not result in a biomass which produces the maximum sustainable yield. On the other hand, the mortality estimates did not include all age classes (< age 5 and > age 13), whereas the abundance analysis did. Therefore, the increase may be caused by early juveniles, which are not represented in the fishing mortality rates. In addition, this study utilised proxies of F_{msy} and thus, cannot completely replace a full analytical assessment. Future, studies should investigate the fishing mortality rates of early juveniles and address possible reasons for the abundance increase, e.g. if predators or competitors may have declined or food resources have increased.

5. Biology and life history of *Squalus acanthias*

The spurdog (*Squalus acanthias*) (Figure 31), also often referred to as piked dogfish, belongs to the order of dogfish sharks (Squaliformes). The genus includes at least 18 different species. Spurdog is one of the most abundant shark species and its distribution ranges worldwide, although absent from the polar regions and tropical waters. They have been reported to aggregate in large schools at feeding grounds. Spurdog has the longest gestation period of any shark species. Although they are slow growing, late maturing and long living, it was one of the most important species in commercial shark fisheries (Compagno 1984a, Compagno et al. 2005). In the following, the species biology and life history traits required to examine the status, trends and conservation opportunities are presented. The findings are summarised in the Supplementary Information (Table 4).
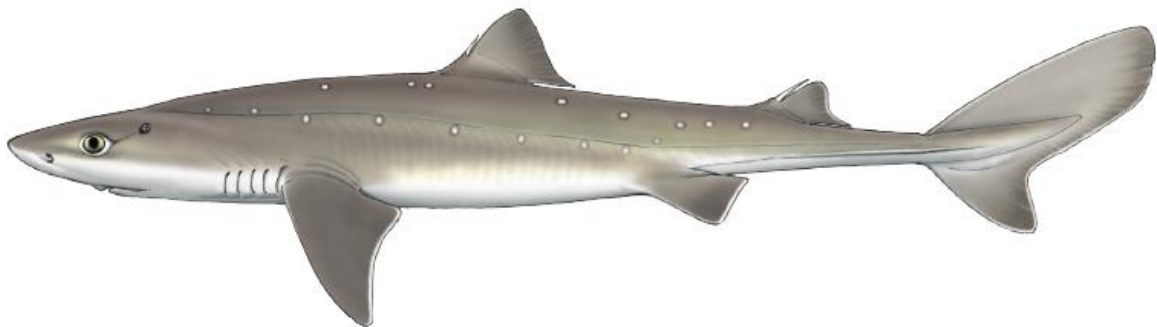
Figure 31: Illustration of *Squalus acanthias*, modified and taken from www.sharktrust.org.

5.1 Length-weight relationship

5.1.1 Introduction

Spurdog has a fairly slender body shape (Figure 31). Thus, the shape parameter a would be expected between 0.01 and 0.001, if growth is isometric (Froese 2006).

5.1.2 Materials and methods

Information on length-weight relationships of spurdog have previously been investigated in other studies and were obtained from the literature. Parameters were summarised by the geometric mean of a and the arithmetic mean of b (Froese 2006). The relationship of both sexes combined was determined in the same way.

5.1.3 Results

The length-weight relationships of male, female and both sexes combined for the Northeast Atlantic are given in Table 20. Total length is given in cm and weight is given in gram.

Table 20: Length-weight relationship of spurdog for the Northeast Atlantic. In bold are the mean values used in this study. The 95% confidence limits are given in parentheses.

sex	*a*	*b*	n	region	source
male	0.0058	2.89	---	NE Atlantic	Coull et al. (1989)
	0.0032	3.04	508	North Sea	Sosinski (1978)
	0.0043 (0.003 − 0.006)	**2.96** (2.77 − 3.53)	---	NE Atlantic	this study, mean of Sosinski (1978) and Coull et al. (1989)
female	0.0011	3.30	---	NE Atlantic	Coull et al. (1989)
	0.0060	2.89	---	NE Atlantic	Coull et al. (1989)
	0.0013	3.27	743	North Sea	Sosinski (1978)
	0.0020 (0.001 − 0.003)	**3.15** (2.66 − 3.64)	---	NE Atlantic	this study, mean of Sosinski (1978) and Coull et al. (1989)
combined	**0.0028** (0.002 − 0.004)	**3.07** (2.73 − 3.57)	---	NE Atlantic	this study, summarised from above

5.1.4 Discussion

The results indicate that females increase more in weight than predicted by their length, possibly because of extended periods of pregnancy above length at maturity. The slender body shape of this species (Figure 31) is reflected by parameter *a* falling between 0.01 and 0.001 (Froese 2006).

5.2 Reproductive biology

5.2.1 Introduction

Several studies investigated the reproductive biology of spurdog from the Northeast Atlantic. These findings have been summarised to obtain a single value for the different parameters.

5.2.2 Materials and methods

Available information has been extracted from the literature. The proportion of mature female spurdogs was estimated as described for the tope shark (section 3.2). However, findings about the size at different maturity stages varied significantly among studies. Therefore, the median length was calculated instead of the mean. Moreover, the median length of 25% and 75% mature was calculated, to estimate the proportion of maturity in females. The data was partly extracted from charts and in the case of Henderson et al. (2002), calculated from their logistic model.

5.2.3 Results

The median length at 50% maturity is 60 cm in males and 82 cm in female spurdogs. The minimum length at first maturity is 64 cm in females and 55 cm in males. The maximum length where all specimens are mature is 99 cm for females and 69 cm for males (Table 21). The length at birth ranges from 19 cm (Gauld 1979) to 31 cm (Ford 1921) with a mean length at birth of 26 cm, pooled from different sources (Ford 1921, Hickling 1930, Holden and Meadows 1962, Sosinski 1978, Gauld 1979).

Table 21: Maturity stages of spurdog in the Northeast Atlantic**.** In bold are the median values used in this study. The 2.5 and 97.5 percentiles are given in parentheses.

sex	length at maturity (cm)			region	source
	first	50%	100%		
male	59	64	69	north and west Scottish coast	Holden and Meadows (1962)
	55	57.5	62	west coast of Ireland	Henderson et al. (2002)
	55	59.5	64	Ireland	Hickling (1930)
	59	---	---	England	Ford (1921)
	55	**60** (58.5 − 63.8)	**69**	Northeast Atlantic	this study [1]
female	75	85	95	north and west Scottish coast	Holden and Meadows (1962)
	69	74	86	south west Ireland	Fahy (1989)*
	72	82	96	Scotland	Holden and Meadows (1964)*
	70	78.5	88	west coast of Ireland	Henderson et al. (2002)*
	86	92.5	99	North Sea	Sosinski (1978)
	64	81	---	Ireland	Hickling (1930)*
	72.8	84.5	98	England	Ford (1921)
	71	83	94	Northeast Scotland	Gauld (1979)*
	76	81	88	Norway Oslofjord	Jones and Ugland (2001)
	73	77	90	Skagerrak	Stenberg (2005)
	64	**82** (79.1 − 90.8)	**99**	Northeast Atlantic	this study [1]

[1] mean length at 50% maturity and minimum or maximum length at first and 100% maturity, respectively.

* Studies used to determine the length at 25% and 75% of females.

The curve describing the proportion of mature females is given in Figure 32. The number of pups increases with maternal length (Ford 1921, Holden and Meadows 1964, Gauld 1979, Fahy 1989, Jones and Ugland 2001, Ellis and Keable 2008). Fahy (1989) described this relationship based on approximately 50 specimens investigated per month from April 1987 to March 1988 as follows:

$$litter\ size = 0.000034 * TL^{2.72}\ (r^2 = 0.58) \tag{32}$$
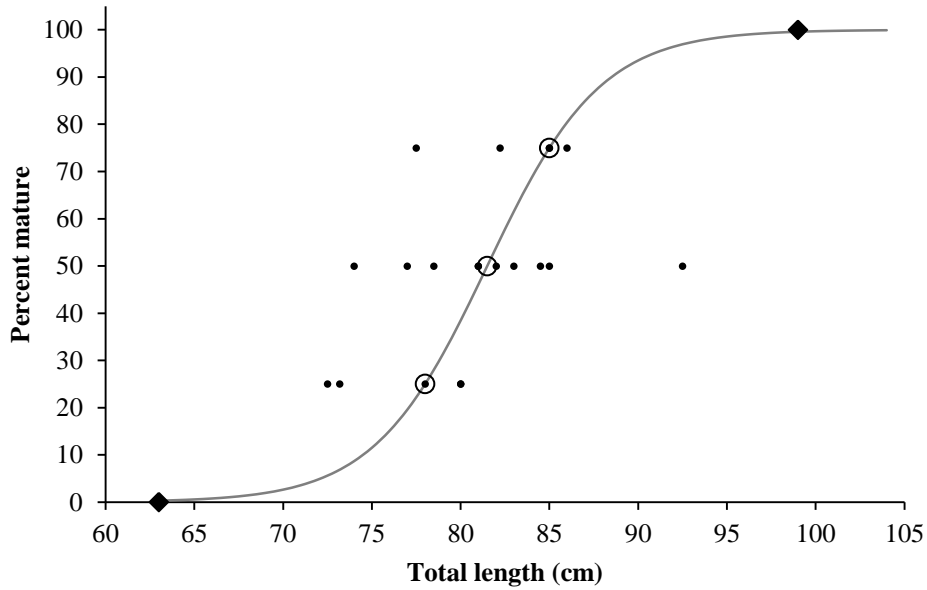
Figure 32: The proportion of mature female spurdog. The curve is described by $p = 1/(1+e^{-(-25.6+0.314*TL)})$, where TL is total length in cm. The open circles represent the median length based on data obtained from different studies for 25%, 50% and 75% maturity (black circles). Note that some data points are masked by others. The median was used instead of the mean, because of large deviation in the corresponding maturity stages across studies. The diamonds represent the length of immature females, obtained from the minimum published length at maturity minus 1 cm, and the maximum published length of all female mature.

The sex ratio at birth is 1:1 (Ford 1921, Gauld 1979, Henderson et al. 2002). Breeding takes place every other year (Holden and Meadows 1962, Sosinski 1978, Fahy 1989), although information of exact gestation period differs among studies and ranges from 18 to 25 months (Ford 1921, Gauld 1979, Jones and Ugland 2001). The embryonic development starts in November (Ford 1921). Pupping occurs from late August or September to December (Ford 1921, Holden and Meadows 1962, Gauld 1979, Jones and Ugland 2001). Copulation is assumed offshore soon after the females give birth (Holden 1965). In accordance, Jones and Ugland (2001) observed fertilization from October to February.

5.2.4 Discussion

Spurdog in the Northeast Atlantic matures earlier than its counterpart in the Eastern Pacific (Ketchen 1972). However, the species are probably distinct from each other (Ebert et al. 2010). The current findings are similar to those from the Western Atlantic, where females reach 50% maturity at a size of about 82 cm (Campana et al. 2009). The reproductive cycle in the Northeast Atlantic was similar to north-eastern Pacific and western Atlantic populations (Ketchen 1972, Campana et al. 2009). Furthermore, average size at birth and litter size are consistent with other areas (Jensen 1965, Ketchen 1972).

Although several studies described the relationship between fecundity and maternal length of spurdog for the Northeast Atlantic empirically (Holden and Meadows 1964, Gauld 1979, Fahy 1989, Jones and Ugland 2001, Ellis and Keable 2008), the findings from Fahy (1989) were used, as a considerable sample of individuals was investigated and the relationship was described by the expected power function (Froese and Luna 2004). The exponent of 2.7 suggests that larger females also have slightly larger pups. The time of birth and mating largely agrees with observations for most spurdog populations worldwide as reviewed by Jensen (1965).

5.3 Age and growth

5.3.1 Introduction

Information about growth of spurdog from the Northeast Atlantic was detailed by several studies and has been summarised to generate one single value for different parameters.

5.3.2 Materials and methods

All studies reviewed, applied the dorsal fin spine method for age determination. The parameters used in this study were obtained by summarising the results across studies via a geometric mean. The study of Holden and Meadows (1962) was recalculated by Fahy (1989), because they first used an eye-fitted regression line. Only the recalculated values of Fahy (1989) were selected. In addition, the von Bertalanffy growth parameters provided by Sosinski (1978) for spurdog in the North Sea were recalculated in this study, because of large differences in male and female growth and the large deviations of parameters compared to all other studies. The asymptotic length was obtained from DATRAS raw data, available at http://datras.ices.dk, consulted on 2012–08–26, and was calculated as the median of maximum length per year over all years, separated by sex. The growth parameters for both sexes combined were estimated via the geometric mean of all male and female studies.

5.3.3 Results

Estimates of the von Bertalanffy growth parameters for the Northeast Atlantic region are presented in Table 22. The maximum size of spurdog is 124 cm (Hammond and Ellis 2005) and the maximum age observed in the Northeast Atlantic is greater than 40 years (Fahy 1989). The age at 50% maturity derived from the von Bertalanffy growth function is 14 years for females and 6 years for males.

Table 22: Von Bertalanffy growth parameters of spurdog from the Northeast Atlantic. In bold are the values used in this study, obtained via geometric means of all studies. The corresponding 95% confidence limits of the asymptotic length L_∞ and the von Bertalanffy growth coefficient k are given in parentheses. The length at birth L_0 was obtained from section 5.2.

sex	L_∞ (cm)	k	L_0	region	source
male	86 (79.7)	0.14 (0.21)		north-west Scottish coast	Holden and Meadows (1962) [1]
	79	0.16		south west Ireland	Fahy (1989)
	79.5	0.15		west coast of Ireland	Henderson et al. (2002)
	85.5 (81.66)	0.146 (0.189)		North Sea	Sosinski (1978) [2]
	82 (79 − 86)	**0.149** (0.142 − 0.156)	**26**	Northeast Atlantic	this study, geometric mean
female	104 (101.4)	0.11 (0.11)		north-west Scottish coast	Holden and Meadows (1962) [1]
	98.8	0.09		south west Ireland	Fahy (1989)
	112	0.07		west coast of Ireland	Henderson et al. (2002)
	107 (137.12)	0.098 (0.054)		North Sea	Sosinski (1978) [2]
	105 (101 − 110)	**0.091** (0.077 − 0.107)	**26**	Northeast Atlantic	this study, geometric mean
combined	**93** (85 − 102)	**0.12** (0.096 − 0.141)	**26**	Northeast Atlantic	this study, geometric mean

[1] recalculated by Fahy (1989), original data given in parentheses.

[2] recalculated in this study, original data given in parentheses.

5.3.4 Discussion

The maximum age reported from the Northeast Atlantic was much lower than estimated for the North-eastern Pacific (Ketchen 1975, McFarlane and Beamish 1987). Similarly, growth from this region was determined to be much lower (Ketchen 1975, Saunders and McFarlane 1993). However, the species are probably distinct from each other (Ebert et al. 2010). All considered values (excluding original data that have been recalculated), were in agreement with each other. Therefore, the results are likely to reflect the growth of the Northeast Atlantic spurdog stock. The estimated age at 50% maturity in this study of 14 year for females is lower than the reported age of 17 years from Norway (Jones and Ugland 2001), yet higher than the estimated age of 9 to 10 years from Scotland, based on aging of mature individuals (Holden and Meadows 1964). However, the findings are in accordance with the 14 to 15 years reported from Ireland (Fahy 1989, Henderson et al. 2002), the 12 to 13 years from Swedish waters (Stenberg 2005) and the findings of Sosinski (1978) which would correspond to an age at 50% maturity of 15 years in females.

5.4 Natural mortality

5.4.1 Introduction

Spurdog is expected to have a low natural mortality rate, as reported from British Columbia waters (Wood et al. 1979).

However, life history traits are different between this area and the Northeast Atlantic and natural mortality is likely to be higher in the latter region. Here, the natural mortality rate of spurdog for the Northeast Atlantic was examined based on empirical equations.

5.4.2 Materials and methods

Natural mortality of spurdog was estimated as described under *Natural mortality* for tope (section 3.4).

5.4.3 Results

The results of the life history approaches to estimate natural mortality are given in Table 23.

Table 23: Natural mortality rates of spurdog estimated from life history. The median value is used for the purpose of this study. The 2.5 and 97.5 percentile of natural mortality are 0.115 and 0.138, respectively.

method	Hoenig (1983)	Pauly (1980)	Jensen (1996) (age)	Jensen (1996) (growth)	median
input	$t_{max} = 40$	$k = 0.091$, $L_\infty = 105$, $T = 7$	$t_m = 14$	$k = 0.091$	
natural mortality	0.104	0.138	0.118	0.137	0.127

5.4.4 Discussion

As expected, the natural mortality of spurdog is higher than the value of 0.094 yr^{-1} reported for British Columbia waters (Wood et al. 1979). This finding is probably due to differences in life history among these regions (Ketchen 1972, Ketchen 1975, Saunders and McFarlane 1993, McFarlane and Beamish 1987, Campana et al. 2009) and the species are probably distinct from each other (Ebert et al. 2010). The derived value of natural mortality in this study is therefore reasonable.

5.5. Habitat and distribution

5.5.1 Introduction

The potential distribution of spurdog was investigated via AquaMaps (Kaschner et al. 2013). Spurdog is highly migratory, usually inhabiting continental and insular shelves, yet can also be found in oceanic waters (Compagno et al. 2005). Therefore spurdog is expected to cover a broad range of the study area.

5.5.2 Materials and methods

Potential distributions were investigated as described under *Habitat and distribution* of tope (section 3.5).

5.5.3 Results

Spurdog can be found to depths of 1446 m (Compagno et al. 2005). The potential distribution obtained from AquaMaps is presented in Figure 33 and the underlying environmental parameters are detailed in Table 24.
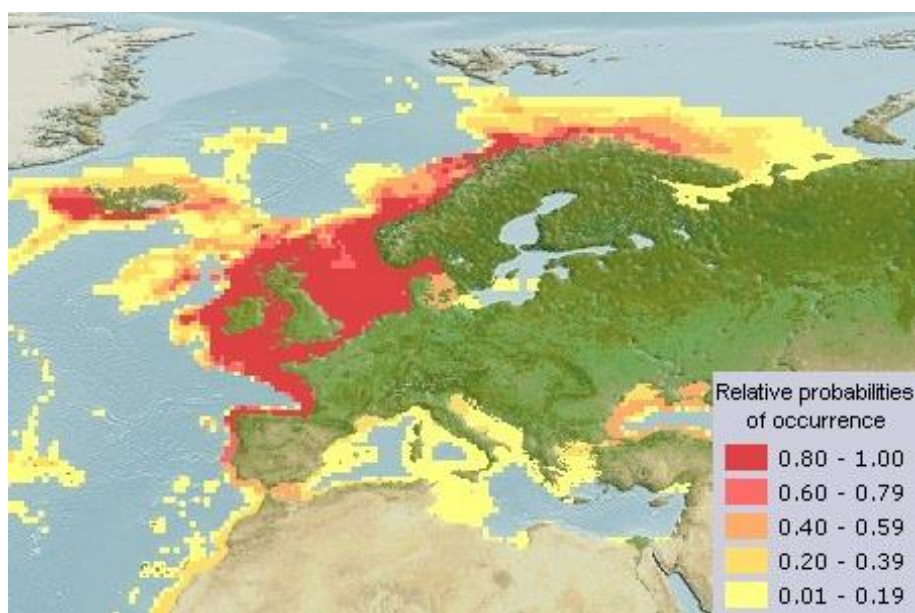
Figure 33: Potential distribution of spurdog in the Northeast Atlantic, obtained from AquaMaps, adjusted by depth.

Table 24: Environmental parameters used to model the potential distribution of spurdog in the Northeast Atlantic.

environmental envelopes	min	preferred min	preferred max	max
depth (m)	0	19	200	1446
bottom water temperature (°C)	1	7	15	24.3
bottom salinity (psu)	7.6	31.3	35.2	39.2
primary production (mgC*m-2*day-1)	300	600	1650	3988

5.5.4 Discussion

The map reflects the extensive distribution of spurdog in the Northeast Atlantic. Pawson and Ellis (2005) suggested that the population is composed of one single stock.

Spurdog is a highly migratory species and both, males and females, have undertaken trans-atlantic migrations (Holden 1967, Templeman 1976). Within the Northeast Atlantic, long distance movements have been reported from the north of Scotland to Iceland, the Bay of Biscay (Holden 1965), the southern North Sea (Aasen 1963, Aasen 1964, Hjertenes 1980), the Skagerrak (Aasen 1964) and the Barents Sea (Aasen 1964). From the coast of Norway spurdog migrated to the Faroe Islands (Aasen 1963, Aasen 1964) and the Bay of Biscay (Aasen 1964). Furthermore, several seasonal migration patterns have been reported (Aasen 1962, Aasen 1963, Holden 1965, Holden 1966, Hjertenes 1980, Gauld and MacDonald 1982, Vince 1991). However, these movement patterns are not consistent for all individuals (Holden 1965) and have changed over time (Hjertenes 1980, Gauld and MacDonald 1982). The shoals formed by spurdog are separated by sex, size (Ford 1921, Hickling 1930, Holden 1965) and depth (Hickling 1930). Shoals of large fishes consist mainly of mature females (Ford 1921, Hickling 1930, Holden 1965), whereas shoals of medium or small size fishes consist of mature males, immature males and females (Holden 1965). Smaller individuals occur in shallower waters, whereas larger individuals inhabit deeper waters (Hickling 1930), except the time of birth, where females move into shallow inshore waters (Hickling 1930, Holden 1965). Higher numbers of females have been reported from the west coast of Scotland and Ireland, whereas males are predominant in the southwest of the British Isles. Furthermore, there may be seasonal variation. Males are dominant in the Irish Sea and North Sea in summer and autumn. Females are most prevalent in the west of Scotland during winter, when males are absent (Vince 1991). Vince (1991) found evidence for the presence of larger females and males in the North Sea, and Holden (1965) found females larger than 80 cm northeast of Scotland in summer. Some information is given about nursery grounds. Large numbers of juvenile spurdog have been reported from the Celtic Sea, the northern Irish Sea and north of Scotland (Ellis et al. 2005a, Ellis et al. 2012). Likewise, Vince (1991) suggested that females might give birth in the eastern Celtic Sea and Holden (1965) reported parturition to occur along the Norwegian coast and north of Scotland. Hickling (1930) reported spawning grounds from the west of Ireland and the Celtic Sea and suggested that the young might leave shallow inshore habitats soon after birth (Hickling 1930). In summary, spurdog cover the broadest range of all investigated species in this study. Critical habitats may be found in the North Sea, around Scotland, the Celtic Sea and the Irish Sea.

5.6 Critical areas

5.6.1 Introduction

Spurdog has been seriously depleted in the Northeast Atlantic (Hammond and Ellis 2005, De Oliveira et al. 2013) and is listed as *Critically Endangered* by the IUCN Red List (Fordham et al. 2006).

Therefore, the identification of critical areas that get protected from fishing pressure is crucial to allow recruitment and recovery. Here, pupping and nursery grounds as well as grounds important for mature specimens in the Northeast Atlantic were investigated based on *CPUE* data.

5.6.2 Materials and methods

The data was based on ICES surveys (section 2.1). Information on the different life history stages was taken from the *Reproductive biology* section. Early juveniles were defined by a length range of 32 cm to 40 cm, which would correspond to an age between 1 and 2 years. The dataset contained 97078 records of spurdog from 1967 to 2012. Specimens were caught in all months. The depth ranged from 17 m to 500 m.

5.6.3 Results

Pupping and nursery grounds seem to be widely distributed in the Northeast Atlantic, although most catches were made off the north-west of Scotland (Figure 34). In total, 4860 pups were recorded within 40 different years, from 1970 to 2012. Pups were caught in all months with a peak of abundance in December. The depth where they occurred varied from 23 m to 260 m. The results are summarised in Table 25. A higher number of early juveniles (n = 14774) was caught regularly over the same time period, mostly in March. The distribution of early juveniles and pups was highest in the west of Scotland (Figure 35).
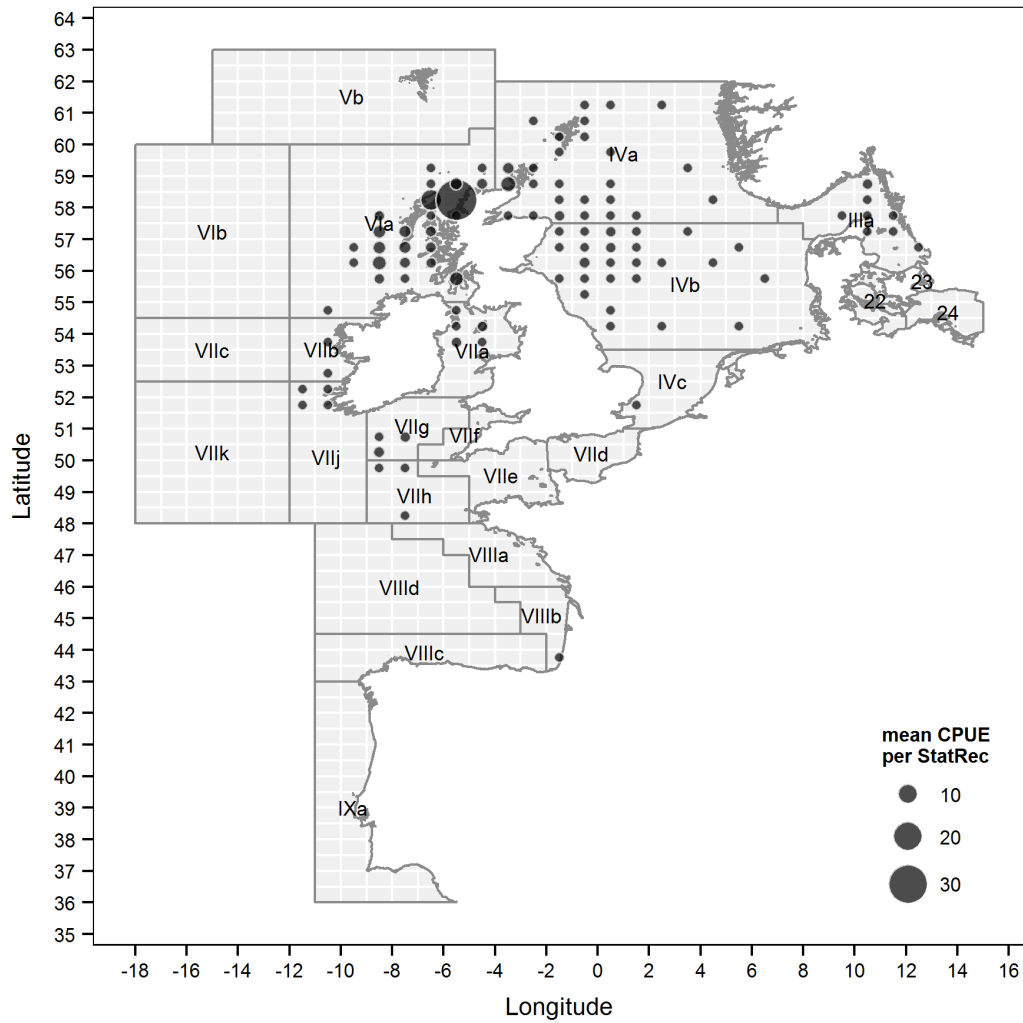
Figure 34: Records of spurdog pups (19 cm − 31 cm) from ICES surveys in the Northeast Atlantic. In total, the sample contained 4860 individuals, reported in 40 different years from 1970 − 2012.
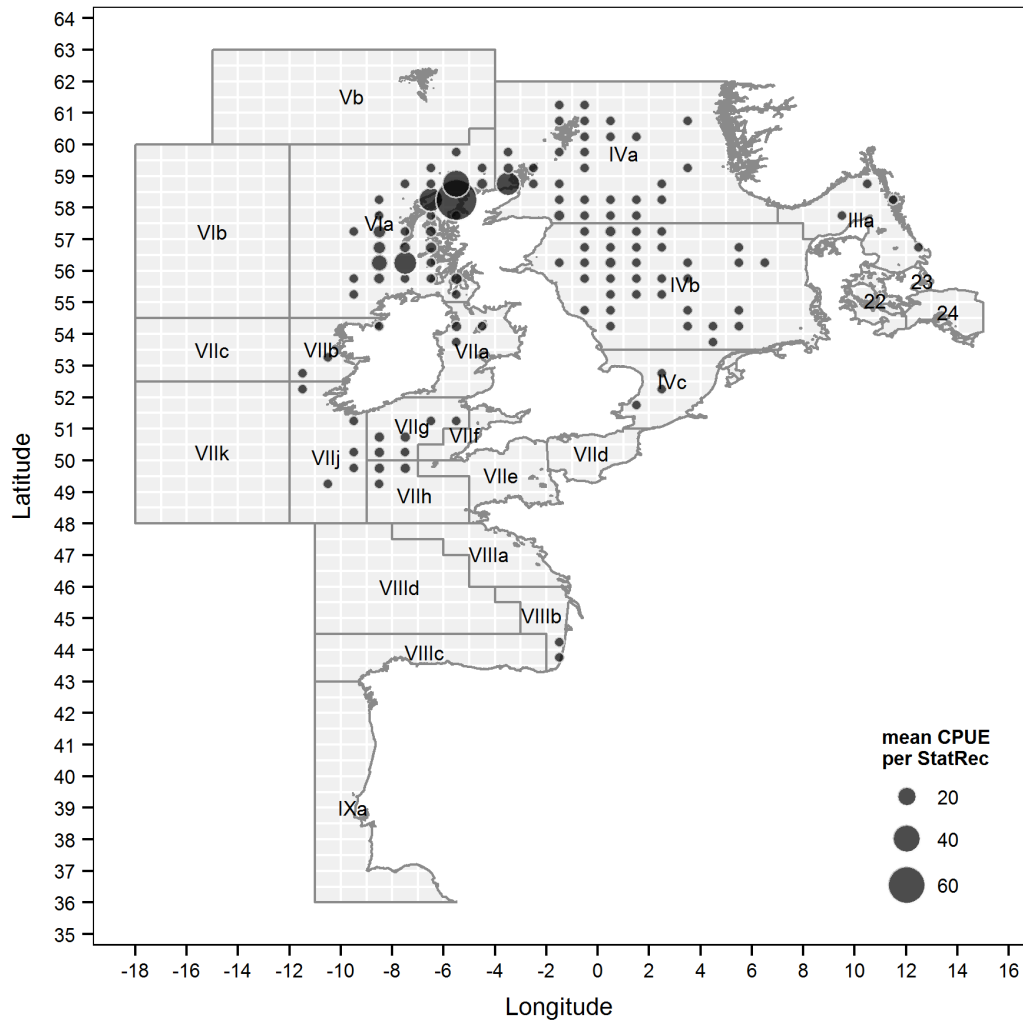
Figure 35: Records of early juvenile spurdog (32 cm − 40 cm), from ICES surveys in the Northeast Atlantic. In total, the sample contained 14774 individuals, reported from 1970 − 2012.

In total, 20190 mature spurdogs were recorded from 1967 to 2012, of which 1880 were females, 14318 males and for the remaining 3992 individuals sex was undetermined. Their depth distributions ranged from 17 m to 500 m. Males were predominantly caught at the Inner Hebrides in November, St. Kilda in January and the Vidal Bank region in February (Figure 36, Table 25). The highest abundance of females and individuals of unknown sex were found off the east coast of England in October. In February, the highest number of females occurred in the central Irish Sea at the Anglesey Reef area. A balanced number of both sexes were caught in the southern Celtic Sea, mostly in October (Figure 37, Table 25).
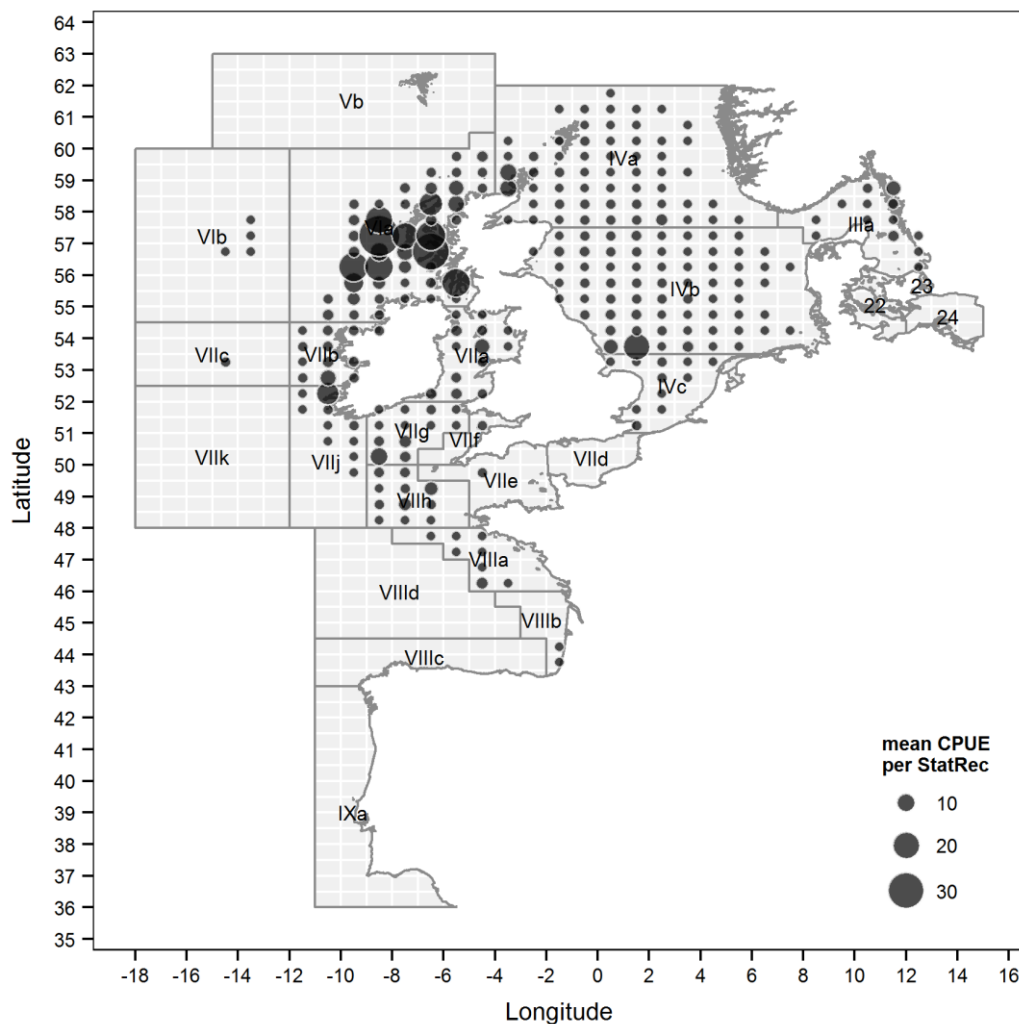
Figure 36: Records of mature spurdog (size of male ≥ 60 cm, size of female and unknown sex ≥ 82 cm) for combined sexes from ICES surveys in the Northeast Atlantic. In total, 20190 mature individuals were recorded from 1967 − 2012.
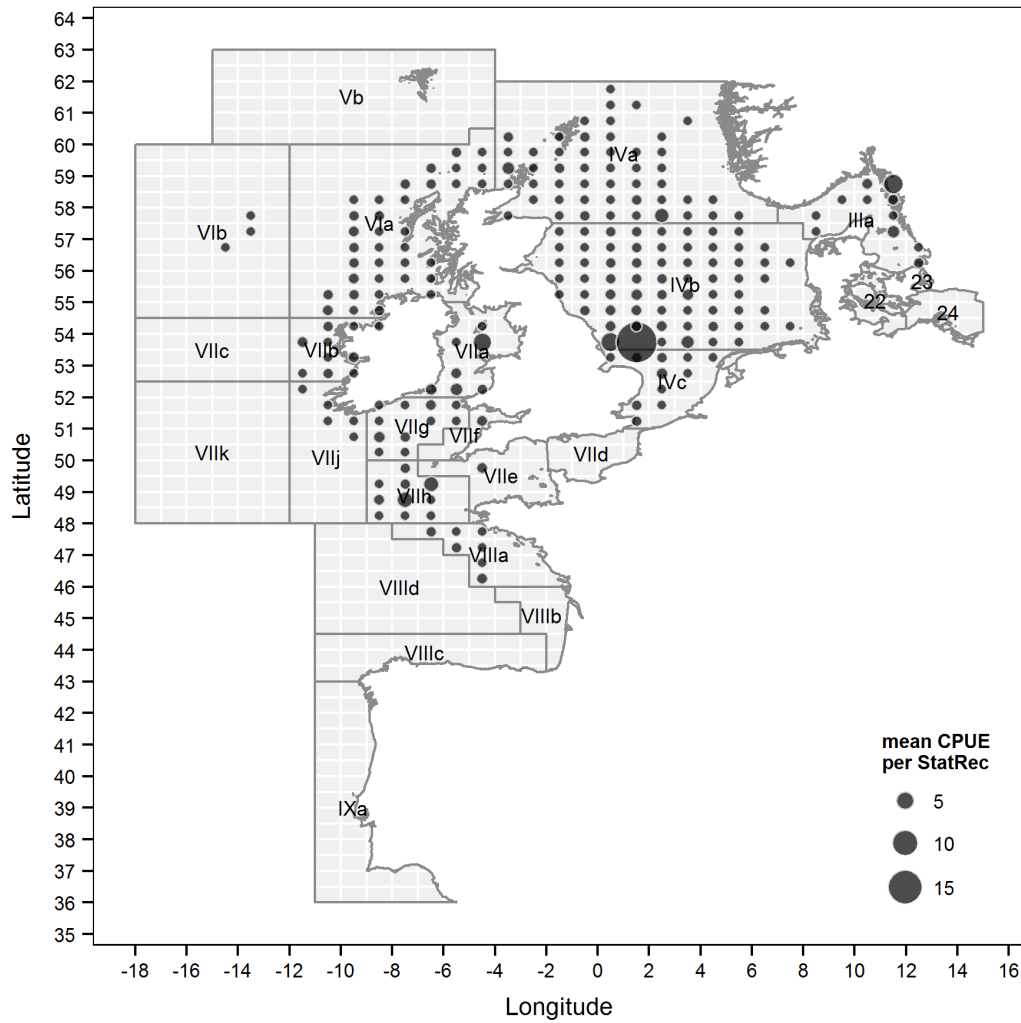
Figure 37: Distribution of mature spurdog (size ≥ 82 cm) with males excluded, i.e. presumably females, from ICES surveys in the Northeast Atlantic. In total, 5872 mature individuals were recorded.

Table 25: Investigated areas of different life stages for spurdog in the Northeast Atlantic. Approximate bounding boxes are given by longitude and latitude. The total number caught is given per sex and the time period when surveys were conducted. The mean *CPUE* refers to the mean catch per unit effort in this area, regardless of the area size. The highest catch per month was obtained by the mean number per month divided by the total effort in this month. In addition, it is indicated if this area is at least partly covered by a protected area (PA). This information was obtained from OSPAR (2013) and JNCC (2013). Areas determined as extremely important for spurdog are shown in bold.

life stage	ICES division	area name	long	lat	depth (m)	years caught	years investigated	period	number females	males	unknown	mean CPUE	highest catch	includes PA
pupping and nursery	IIIa	West Sweden	11, 12	57, 59.5	32-71	5	34	1979-2012	0	2	14	0.52	April	Yes
	IVb	East Scotland	-2, 1	55.5, 57.5	64-110	12	42	1967-2012	112	70	53	4.84	July	Yes
	VIa	North of Scotland	-5, -3	58.5, 59.5	72-160	26	36	1997-2012	221	239	18	6.06	December	Yes
	VIa	**Northwest of Scotland**	**-7, -5**	**57.5, 59.5**	**59-160**	**25**	**27**	**1985-2012**	**1532**	**1380**	**0**	**18.20**	**April**	**Yes**
	VIa	Inner Hebrides	-7, -5	55.5, 57.5	74-172	16	28	1985-2012	71	73	0	5.15	January	Yes
	VIa	Mingulay	-8, -7	56.5, 57.5	135-190	14	28	1985-2012	38	152	0	6.12	February	Yes
	VIa	Skoton Banks	-9, -7	56, 56.5	135-160	9	28	1985-2012	92	114	2	14.97	December	Yes
mature	IIIa	West Sweden	11, 12	57, 59.5	39-132	17	34	1979-2012	60	88	463	5.58	September	Yes
	IVb	East Scotland	-2, 1	55.5, 57.5	56-168	28	42	1967-2012	40	330	135	2.44	October	Yes
	IVa	Ling Bank	2, 4	57.5, 58.5	59-270	17	40	1971-2012	8	36	129	5.14	December	No
	IVc, IVb	**East coast of England**	**0, 3**	**53, 54**	**17-86**	**19**	**38**	**1967-2012**	**77**	**15**	**1864**	**19.04**	**October**	**Yes**
	VIa	North of Scotland	-5, -3	58.5, 59.5	60-160	28	36	1997-2012	25	847	99	8.26	August	Yes
	VIa	Northwest of Scotland	-7, -5	57.5, 59.5	59-180	25	27	1985-2012	71	2255	7	7.57	January	Yes
	VIa	**Inner Hebrides**	**-7, -5**	**55.5, 57.5**	**55-180**	**20**	**28**	**1985-2012**	**11**	**1792**	**0**	**27.78**	**November**	**Yes**
	VIa	Skoton Banks	-9, -7	56, 56.5	86-174	27	28	1985-2012	5	1136	1	12.54	January	Yes
	VIa	**St. Kilda**	**-9, -8**	**57, 58**	**122-166**	**25**	**28**	**1985-2012**	**26**	**1939**	**3**	**38.5**	**January**	**Yes**
	VIa	Mingulay	-8, -7	56.5, 57.5	128-194	17	28	1985-2012	3	878	0	16.83	December	Yes
	VIa	North coast of Ireland	-9, -7 / -10, -9	54, 56 / 54.5, 55.5	28-260	25	28	1985-2012	81	596	0	3.88	January	Yes
	VIa	**Vidal Bank**	**-10, -9**	**55.5, 57**	**112-500**	**26**	**28**	**1985-2012**	**56**	**1112**	**1**	**16.19**	**February**	**No**
	VIIb, VIIj	Tralee Bay	-11, -9	52, 53	58-141	10	12	1991-2008	10	269	2	14.06	November	Yes
	VIIa	Southern Irish Sea	-8, -4	52, 53	33-96	4	7	1997-2008	25	11	0	3.68	November	Yes
	VIIa	**North-west Anglesey Reef**	**-5, -4** / -9, -7	**53, 54** / 50, 50.5	**40-107**	**8**	**11**	**1996-2006**	**140**	**52**	**0**	**8.33**	**February**	**No**
	VIIg	Northern Celtic Sea	-9, -6 / -9, -5	50.5, 51 / 51, 52	51-138	17	17	1991-2012	115	545	2	3.87	December	Yes
	VIIh	**Southern Celtic Sea**	**-9, -7** / **-9, -5** / **1, -5**	**49.5, 50** / **48, 49.5** / **46, 47**	**109-179**	**17**	**18**	**1990-2012**	**161**	**174**	**0**	**3.33**	**October**	**Yes**
	VIIIa	Northern Bay of Biscay	-2, -6 / -3, -8	47, 47.5 / 47.5, 48	110-358	10	16	1997-2012	123	131	2	2.95	October	Yes

5.6.4 Discussion

The fact that pups were caught in all months may be an artefact of net abortion or of length variability at birth. However, the month with highest abundance corresponds to the time of birth (Ford 1921, Holden and Meadows 1962, Gauld 1979, Jones and Ugland 2001). The distribution of pups and early juveniles was overlapping and thus indicated that the pupping grounds serve also as nursery grounds. The most important pupping and nursery grounds exist north and north-west of Scotland, an area already proposed by others (Holden 1965, Ellis et al. 2012). Though protected areas exist in this region, most are small and none are established at the northern Outer Hebrides (OSPAR 2013, JNCC 2013). Spurdog is known to give birth in coastal waters (Hickling 1930, Holden 1965). Based on the findings here, the existing protected areas along the north-west coast of Scotland should be expanded, and a new protected area may be established at the northern Outer Hebrides. Moreover, fishing should be banned at the coastline in these regions to allow recovery of the depleted spurdog. Furthermore, the western Scottish sea seems to be important for mature males at the end of autumn and winter. Adult spurdog segregate by sex (Ford 1921, Hickling 1930, Holden 1965). In accordance, areas where both sexes occur might provide evidence of mating grounds. Copulation is assumed to occur offshore after birth (Holden 1965) and fertilisation was observed from October to February (Jones and Ugland 2001). Both sexes were found in the Anglesey Reef area (central Irish Sea) in February and November, in the southern Celtic Sea in November and off the east coast of England in October. Note that especially in the latter there was a high degree of uncertainty in the occurrence of both sexes due to the lack of sex determination. Furthermore, not all months are sampled in all areas and therefore other areas may have been overlooked. However, possible mating sites include the Anglesey Reef in the central Irish Sea, the southern Celtic Sea and the east coast of England. Likewise, the Celtic Sea was suggested by Hickling (1930) as a spawning ground. In the southern part of the Celtic Sea, only a small protected area exists, which covers the tip of France (OSPAR 2013, JNCC 2013). The majority of spurdog fisheries occur in the North Sea (IV), West of Scotland (VIa) and the Celtic Seas (VII) (ICES 2012), all of which include critical habitats for spurdog. Thus, the development and establishment of new protected areas in these regions, including no fishing zones, will be crucial for the future development of spurdog populations.

5.7 Biological reference points for fishing mortality

5.7.1 Introduction

Spurdog is a species with very low productivity (Smith et al. 1998). Therefore its capacity to withstand fishing or recover from depletion is low. Here, the fishing mortality which produces maximum sustainable yield was investigated.

5.7.2 Materials and methods

The methods applied to obtain proxies of maximum sustainable fishing mortality were covered in section 2.3. Maximum age was assumed at 40 years, age at maturity at 14 years (section 5.3) and natural mortality at 0.127 yr^{-1} (section 5.4).

5.7.3 Results

The results of the life table approach are given in Table 26. The intrinsic rate of population increase was estimated as 0.038 yr^{-1}. The sustainable fishing mortality rate based on the intrinsic rate of population increase was estimated at 0.019 yr^{-1}. The sustainable fishing mortality rate based on natural mortality was estimated at 0.064 yr^{-1}.

5.7.4 Discussion

The result is in agreement with the estimated intrinsic rate of population of 0.034 yr^{-1} reported from the Northwest Atlantic (Smith et al. 1998). This indicates low resilience (Musick 1999) and confirms the low capacity of spurdog to withstand fishing. Spurdog experienced a dramatic decline in the Northeast Atlantic and as such were categorised as *Critically Endangered* on the IUCN Red List (Fordham et al. 2006). It is the most important commercial shark species in European waters and has been fished over decades (Bonfil 1994, Fowler et al. 2004). To follow a precautionary approach, a value of 0.019 yr^{-1} should be utilised as reference point for the fishing mortality rate which produces maximum sustainable yield F_{msy}.

Table 26: Life table for spurdog from the Northeast Atlantic. The results are shown from age at maturity to maximum age. To account for sex ratio, resting stages and the complete reproductive cycle, the product of the proportion mature and litter size was multiplied with 0.25 to obtain the age specific fecundity (female pups per female) m_x. The annual reproductive rate per generation is the product of survival to age l_x and m_x. The intrinsic rate of population increase r was estimated at 0.038 yr^{-1}.

length (cm)	age	% mature	litter size	m_x	l_x	$l_x m_x$
83	14	0.61	5.62	0.86	0.17	0.145
85	15	0.74	5.98	1.11	0.15	0.165
87	16	0.83	6.33	1.32	0.13	0.173
88	17	0.89	6.65	1.48	0.12	0.171
90	18	0.93	6.96	1.61	0.10	0.164
91	19	0.95	7.24	1.72	0.09	0.154
92	20	0.97	7.51	1.81	0.08	0.143
93	21	0.98	7.76	1.89	0.07	0.132
94	22	0.98	7.99	1.96	0.06	0.120
95	23	0.99	8.21	2.02	0.05	0.109
96	24	0.99	8.41	2.08	0.05	0.099
97	25	0.99	8.59	2.13	0.04	0.089
98	26	0.99	8.76	2.18	0.04	0.080
98	27	0.99	8.92	2.22	0.03	0.072
99	28	1.00	9.07	2.26	0.03	0.064
99	29	1.00	9.20	2.29	0.03	0.058
100	30	1.00	9.33	2.32	0.02	0.051
100	31	1.00	9.44	2.35	0.02	0.046
101	32	1.00	9.55	2.38	0.02	0.041
101	33	1.00	9.64	2.41	0.02	0.036
101	34	1.00	9.73	2.43	0.01	0.032
102	35	1.00	9.81	2.45	0.01	0.029
102	36	1.00	9.89	2.47	0.01	0.026
102	37	1.00	9.96	2.49	0.01	0.023
103	38	1.00	10.02	2.50	0.01	0.020
103	39	1.00	10.08	2.52	0.01	0.018
103	40	1.00	10.13	2.53	0.01	0.016

5.8 Annual fishing mortality

5.8.1 Introduction

Aasen (1964) first described the exploitation of spurdog as very high and in the same year, Holden and Meadows (1964) raised concern that the stock is not replacing itself. Soon after, Holden (1968) postulated that fishing restrictions are necessary to prevent a drastic decline of the stock. Thereafter, Norwegian fisheries collapsed in the late 1970's (Hjertenes 1980). In 1988 the first total allowable catch (TAC) was established for the North Sea (Fowler et al. 2004), but a zero TAC was not adapted for the Northeast Atlantic before 2010 (ICES 2012). Today, spurdog is listed as *Critically Endangered* by the IUCN Red List (Fordham et al. 2006) and catches are mainly due to bycatch in other fisheries (ICES 2012). Here, the current and historical development of annual fishing mortality rates was examined to investigate the recent exploitation levels. Fishing mortality was obtained from total mortality based on pooled catch at age ratio.

5.8.2 Materials and methods

The method of estimating mortality via pooled catch at age ratios, i.e. the decrease in total numbers from age at recruitment to maximum age to the decrease in total numbers one age older, was described in detail in section 2.4. Catches were extracted from the survey data. Only valid hauls were considered, as specified in DATRAS data. The time period from 1985 to 2012 was selected, because surveys were representative of all age classes (Supplementary Information, Figure 4). The log-normal length frequency distribution of the whole survey area allowed the analysis of all available data (Figure 38). On this basis, age classes were obtained from length by applying the von Bertalanffy growth function. If sex was not given, the von Bertalanffy growth function of both sexes combined was used (section 5.3). In most years a peak was visible at age 10 with decreasing numbers till age 21. Therefore, age recruitment was set to 10 and maximum age to 21. Fishing mortality was obtained from total mortality by assuming a constant natural mortality at 0.127 yr^{-1} (section 5.4).

5.8.3 Results

Annual fishing mortality rates decreased from 0.54 yr^{-1} in 1990 to 0.152 yr^{-1} in 2012 (Figure 39). The decrease was most pronounced at the end of the 1990's and is consistent since 2004. The exploitation since 1985 never achieved sustainable levels and is still above a fishing mortality that would produce maximum sustainable yield (section 5.7).
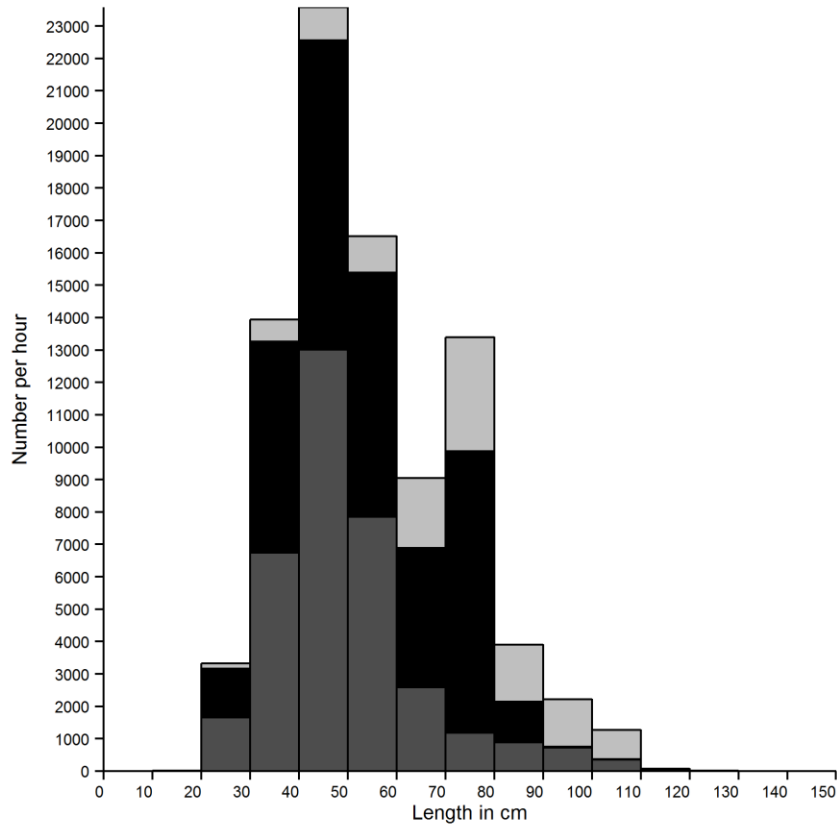
Figure 38: Length frequency distribution of spurdog in the Northeast Atlantic, with data pooled over the years 1985 − 2012. The dark-grey bars represent the number of females, the black bars the number of males and sex was not determined for the light-grey bars.
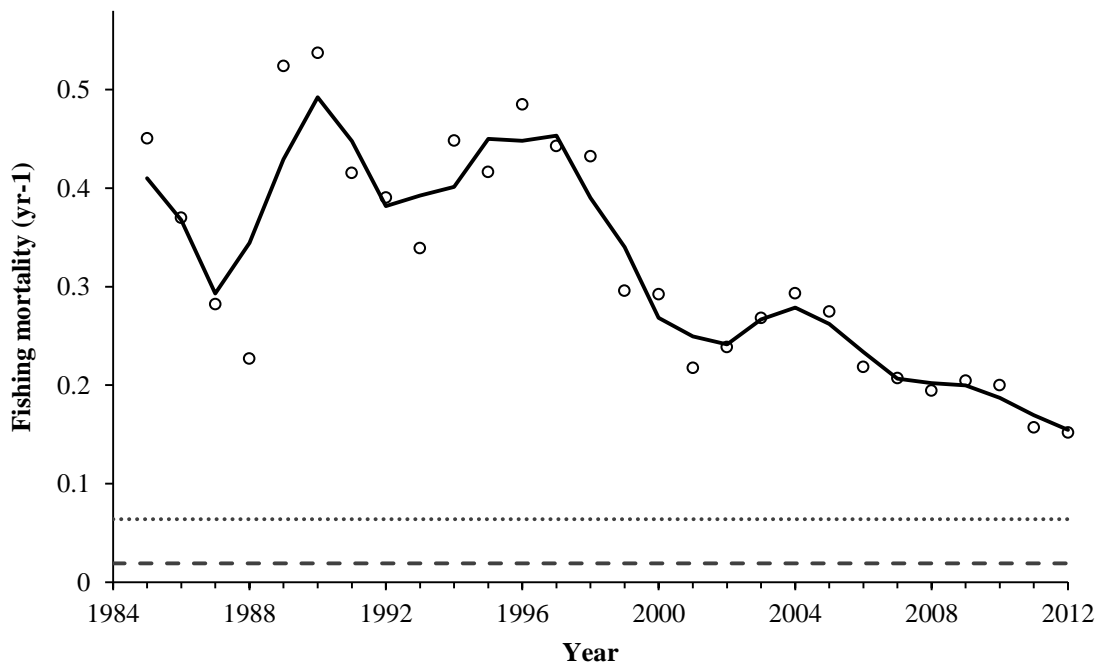
Figure 39: Annual fishing mortality rates of spurdog in the Northeast Atlantic (open circles). The bold line represents the three years moving average. Note that the first and last year only consist of two values, because of border effects. The grey dashed line shows the fishing mortality that would produces maximum sustainable yield F_{msy} estimated from the intrinsic rate of population increase ($F_{msy0.5r} = 0.019$ yr^{-1}), the grey dotted line shows F_{msy} estimated from natural mortality ($F_{msy0.5M} = 0.064$ yr^{-1}).

5.8.4 Discussion

The results agree with Fahy (1989), who estimated the total mortality of fully recruited females in south west Ireland at 0.24 yr^{-1} and at 0.3 yr^{-1} for males in the late 1980's, although the estimate here was slightly higher at 0.35 yr^{-1}. In contrast to the findings provided by ICES, which state that exploitation levels are sustainable in recent years (ICES 2012), the current results show fishing mortality rates far above that producing the maximum sustainable yield. However, a consistent decrease has occurred since 2004. The ICES advice for a zero quota was adopted by the EU in 2010, but bycatch was allowed to 10% of the 2009 quotas in this year. Although bycatch regulations and minimum landing sizes have been introduced, they differ among countries and still allow for some fishing, resulting in increasing discard rates (ICES 2009, ICES 2012, STECF 2012). The unsustainable mortality rates can be explained, even though total allowable catch is zero, as bycatch driven. De Oliveira et al. (2013) suggested that the population would double within 30 years by an annual allowable catch (TAC) of 1422 mt (which was the TAC of 2009). However, the current findings raise concern regarding the future development of the population and therefore management decisions should be carefully considered to account for this.

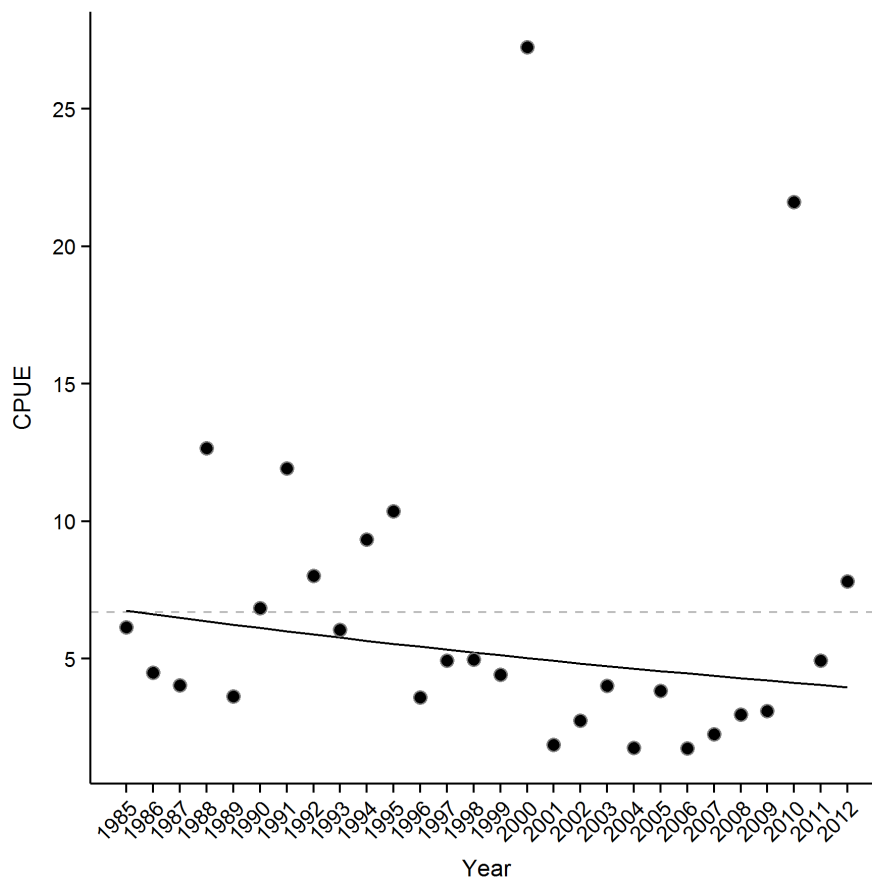**5.9 Abundance**

5.9.1 Introduction

Spurdog was the most important commercial species caught in European shark fisheries for over 70 years. It is specifically targeted for its meat (Fowler et al. 2004) and has a high European market demand (Fowler et al. 2004, Fordham et al. 2006). As a result, spurdog is seriously depleted in the Northeast Atlantic (Hammond and Ellis 2005, De Oliveira et al. 2013), although recent assessments suggest this trend stopped (De Oliveira et al. 2013). Here, the abundance trend of spurdog from 1985 to 2012 in the Northeast Atlantic was examined on the basis of mean *CPUE* values.

5.9.2 Materials and methods

The method applied to investigate the abundance trends was described in detail in section 2.6. The catches were extracted from the survey data. Only valid hauls were considered, as specified in DATRAS data. The time period from 1985 to 2012 was selected, because surveys were representative of all age classes (Supplementary Information, Figure 4).

5.9.3 Results

The abundance of spurdog increased slightly since 2004 with the last estimate in 2012 above the mean *CPUE*. However, there was a negative tendency across the entire period (Figure 40). A decrease in abundance was observed in the Irish and ROCKALL survey from the mid-2000, whereas the France and Scottish surveys exhibited an increase in abundance at this time. The abundance in North Sea survey decreased since the early 1990's (Figure 41). The most recent estimates were all above the mean *CPUE*, except for the Irish and North Sea surveys. Note, that none of the trends was explained significantly by an exponential model (*p* > 0.05), even if the change in abundance of all surveys combined (Figure 40) was examined independently for the periods 1985 to 2004 and 2005 to 2012.

Figure 40: Abundance trends of spurdog in the Northeast Atlantic from 1985 to 2012. There was a tendency of a decreasing abundance trend (black line) across the entire time period, but this could not be explained by an exponential model (*p* > 0.05). The dashed line indicates the mean catch per unit effort (*CPUE*) of 6.67 from 1985 to 2012.
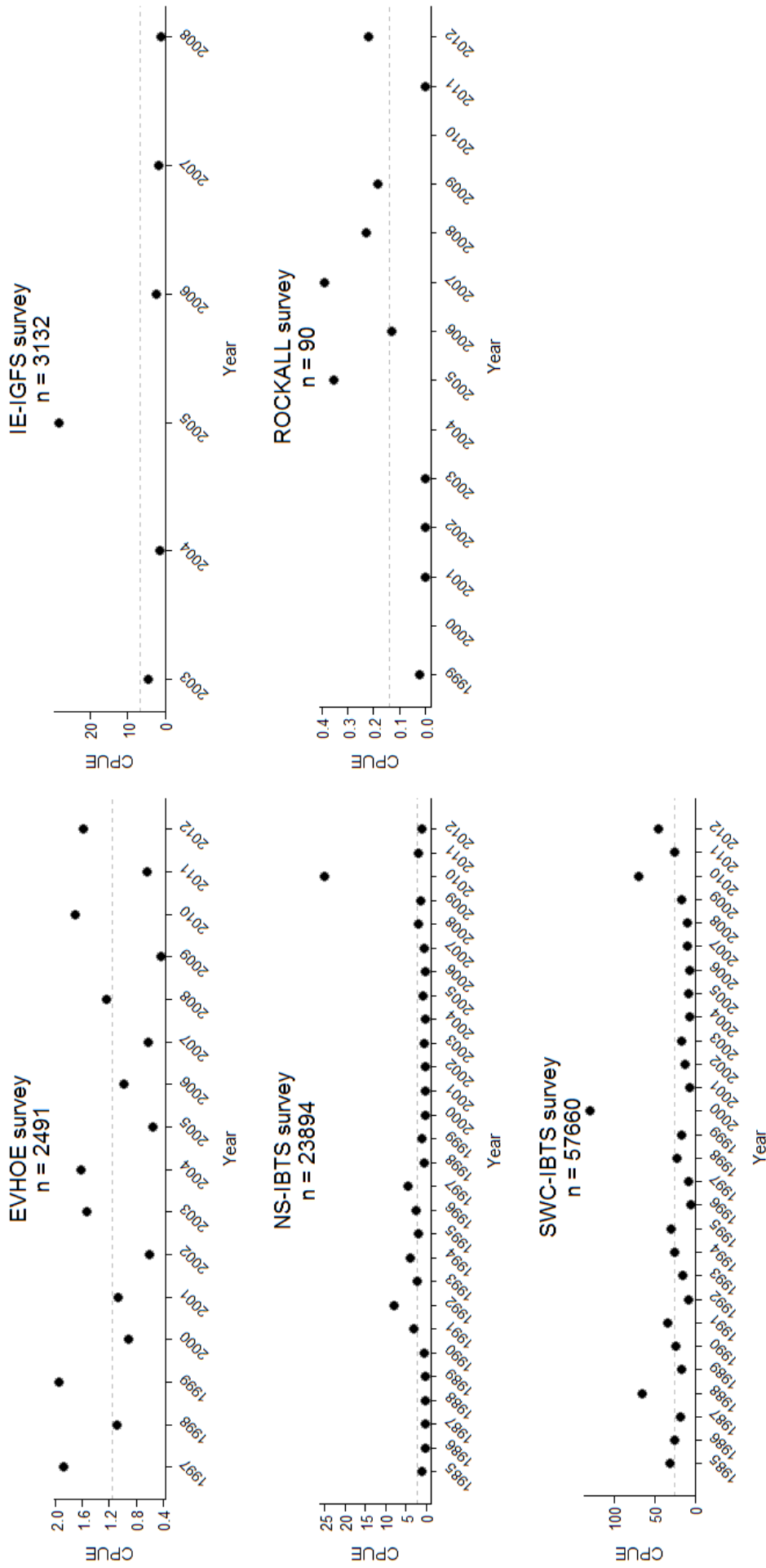
Figure 41: Abundance trends of spurdog across the single surveys. The grey dashed line indicates the mean *CPUE* over the time period. The abbreviation *n* gives the total number of individuals caught in this survey and time period.

5.9.4 Discussion

The analysis of the entire survey area showed evidence that the population increased, post 2004. The observations are in agreement to the results obtained in section 5.8, where a consistent decrease in fishing mortality was observed from the year 2004 with the lowest rate in 2012. Furthermore, the findings agree with those from De Oliveira et al. (2013), who suggested that the decline stopped in the mid of 2000. However, in previous assessments biomass in the year 2000 was estimated to be 5% from virgin biomass (Hammond and Ellis 2005), whereas more recent assessments calculated biomass in 2010 to be 19% relative to 1905 (De Oliveira et al. 2013). Both studies clearly demonstrated that, although there is a tentative sign of an increasing abundance trend, this is far from a recovery. In accordance, only the most recent estimate was marginally above the mean *CPUE*. Combined with the results of section 5.8, the future trend of spurdog remains questionable, with real potential to reverse suddenly. The results presented here are somewhat contradictory to the findings that the fishing mortality is far above F_{msy} (section 5.8), although the increase in abundance overlaps with a decrease in fishing mortality. This suggests that the recovery would not result in a biomass which produces the maximum sustainable yield. However, the mortality estimates did not include all age classes (< age 10 and > age 21), whereas the abundance analysis did. Therefore, the increase may be caused by early juveniles, which are not represented in the fishing mortality rates. In addition, this study utilised proxies of F_{msy} and thus, cannot completely replace a full analytical assessment. In conclusion, the conservation measures of spurdog should be expanded to prevent a reversal of the current trend. In addition, the trends have to be monitored carefully and consistently over time and the fishing mortality rate of juveniles should be examined in future studies.

6. General Discussion

This study revealed that tope, starry smoothhound and spurdog have followed a different trend in the Northeast Atlantic, yet the status for each of the species is far from what could be termed in 'good or stable condition'. The abundance of tope has declined by more than 70% since 1992, whereas spurdog and starry smoothhound showed some evidence of recent increasing trends. This may be explained by a reduction of fishing pressure in important habitats. However, spurdog is still extremely depleted compared to its virgin biomass (Hammond and Ellis 2005, De Oliveira et al. 2013) and thus remains highly vulnerable to exploitation. On the other hand, the virgin biomass of starry smoothhound is unknown and therefore the results should be interpreted with caution. In addition, none of the three species investigated experienced sustainable exploitation, raising concerns about the future development of such populations. A sudden collapse of populations is a well-documented phenomenon in sharks (Camhi et al. 1998) and recovery, if possible, can promptly be reversed by already light exploitation (Ward-Paige et al. 2012). Moreover, there are several examples of shark species which did not recover after historical depletion (e.g. Walker 1998, Baum et al. 2003, Hammond and Ellis 2005, Ward-Paige et al. 2012). Therefore, management plans for tope and starry smoothhound should be developed promptly and remain rigorously tight for spurdog. Due to the presumably high proportion of fishing mortality caused by bycatch, a strict commercial fishing ban on tope is proposed, to prevent scenarios that this species has experienced in other regions (Ripley 1946, Stevens et al. 2000). Likewise, the results raise questions regarding the possibility of sustainable exploitation in spurdog, where total allowable catch is now zero as of recent years. However, some bycatch remains legal (ICES 2012) and could counteract a recovery, although live discard and survival may be possible. Even though this study found evidence that tope, starry smoothhound and spurdog experience unsustainable exploitation levels, this has to be considered carefully. The fishing mortality rates of starry smoothhound and spurdog did not cover all age classes and the exploitation levels of early juveniles remain unclear. On the other hand, the uncertainty of the estimated fishing mortality rate which would produce the maximum sustainable yield F_{msy} was reduced by approximating this value via two different methods. In classical surplus production modelling, the intrinsic rate of population increase r is calculated at very low biomass, giving the maximum growth rate of a population. From this it follows that sustainable fishing is achieved at half the intrinsic rate of population increase (Ricker 1975). It is reasonable to assume that in overexploited populations, age structure or reproductive rate has changed.

General Discussion

In contrast to the classical model, the demographic method applied in this study to estimate r, does assume a stable age structure (Pianka 2000). Therefore, the estimates of r reflect the highest possible growth based on the best available assumptions of natural mortality, fecundity at age, longevity and age at maturity. This static behaviour of life tables may result in an underestimation of the intrinsic rate of population increase (Simpfendorfer 2005). The second method applied in this study was based on a relationship between F_{msy} and natural mortality M (e.g. Gulland 1971, Shepherd 1981, Clark et al. 1985, Beverton 1990, Patterson 1992, MacCall 2009, Pikitch et al. 2012). A relationship of $F_{msy} = M$ has long been suggested (Gulland 1971). However, $F_{msy} \gg 0.5M$ should be carefully justified (Walters and Martell 2002) and a relationship of $F_{msy} = 0.4M$ is more likely for chondrichthyans (Zhou et al. 2012). In contrast to teleosts, several shark species are characterised by a biennial reproductive cycle (Fowler et al. 2005). Moreover, the methods of estimating natural mortality utilised in this study derived their empirical relationship almost exclusively from data referring to teleosts (Pauly 1980, Hoenig 1983, Jensen 1996). From this it follows that the approximated values for F_{msy} may be too high. Hence, the two estimates of F_{msy} obtained in this study bracket the range of possible F_{msy} values. However, to follow a precautionary approach, the lower proxy should be considered in management of tope, starry smoothhound and spurdog. In addition, future assessments of starry smoothhound and spurdog should address the fishing mortality of early juveniles, to examine if this life stage is exploited at levels that would explain the observed increase in abundance. Besides considering the exploitation status, this study revealed that the inclusion of length at first capture is essential for the success of shark conservation. Like for teleosts (Froese et al. 2008, Colloca et al. 2013), the optimum size increases the cohort biomass of slow growing, late maturing and long lived shark species. However, sustainability may not be achieved if these animals are caught at young ages, even under apparent sustainable exploitation levels. This supports that low productive shark species are vulnerable to even light exploitation (Myers and Worm 2005, Ward-Paige et al. 2012). Therefore, the development and enlargement of protected areas seems to be critically important as additional conservation tool for these species. Many shark species are migratory (Camhi et al. 1998) and the implementation of a marine protected area (MPA) network as planned by the EU (OSPAR 2013) is essential to their protection beyond national borders. However, current marine protected areas guided by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) do not coordinate purposes or measures related to fisheries management (OSPAR 1992, Annex V, Article 4).

However, no take zones are required to allow appropriate conservation success and their establishment should be included in protected areas management. Although this study did not cover all parts of the Northeast Atlantic, and important areas such as the English Channel (Martin et al. 2010, Martin et al. 2012) are missing, recommendations regarding important areas for shark conservation can be given. Even though it has been addressed that the protection of adult habitats may be most beneficial for conservation purposes (Kinney and Simpfendorfer 2009), the recommendations here utilise the combined results from nursery grounds and critical habitats of mature specimens. Existing protected areas (Figure 42) should be extended with the inclusion of no fishing zones off the east coast of England, the Outer Thames Estuary and the Frisian Islands. Worryingly, the latter region has suffered severely from degradation and exploitation (Lotze et al. 2005) and serves not only as nursery for tope but also for other elasmobranches (Ellis et al. 2005a). Minor parts of the northern coast of Ireland, north-west of Scotland and the southern Celtic Sea are protected (OSPAR 2013, JNCC 2013). Here, the establishment of new protected areas or the enlargement of existing ones will contribute towards the conservation of the populations by protecting important life stages of the species. Areas northwest of Scotland, serve as important nursery grounds, particularly for spurdog. These are also a nursery ground for other elasmobranch species such as the common skate (*Dipturus batis*) (Ellis et al. 2012) and the blackmouth catshark (*Galeus melastomus*) (Henry et al. 2013). The north-eastern part of the Celtic Sea was found to be important for elasmobranchs by others (Shephard et al. 2012). Here it has been shown, that the southern Celtic Sea could be of similar importance, possibly serving as a migration pathway and mating ground. Therefore, this area may exhibit the highest conservation value especially as it became highly exploited in recent years which resulted in a decrease in the mean trophic level (Pinnegar et al. 2002) and fish size (Blanchard et al. 2005). The south-eastern Irish Sea has some established MPAs along the coastline, e.g. in Cardigan Bay (OSPAR 2013, JNCC 2013), however in offshore areas and in the central Irish Sea such protection is lacking. Here, the addition of an MPA covering the Anglesey Reef (central Irish Sea) is recommended, and is currently under investigation (JNCC 2013). The designation of new MPAs may also focus on the Vidal Bank region in the western Scottish sea, which to date lacks protection, yet has considerable abundances of all three species. These recommendations are summarised in Figure 42. Note that important parameters such as habitat quality and food availability (Heithaus 2007) were not investigated.

General Discussion

In addition, the identified critical areas may serve as refuge for the species due to limited fishing effort, as has been shown for the north-eastern Celtic Sea (Shephard et al. 2012), but if the aggregation pattern of sharks in the above mentioned regions is due to depletion or displacement from other areas still remains unclear. It is likely that certain habitats in an area serve as aggregation points, but the resolution used in this study made this impossible to detect. Therefore, these questions should be addressed in future studies.
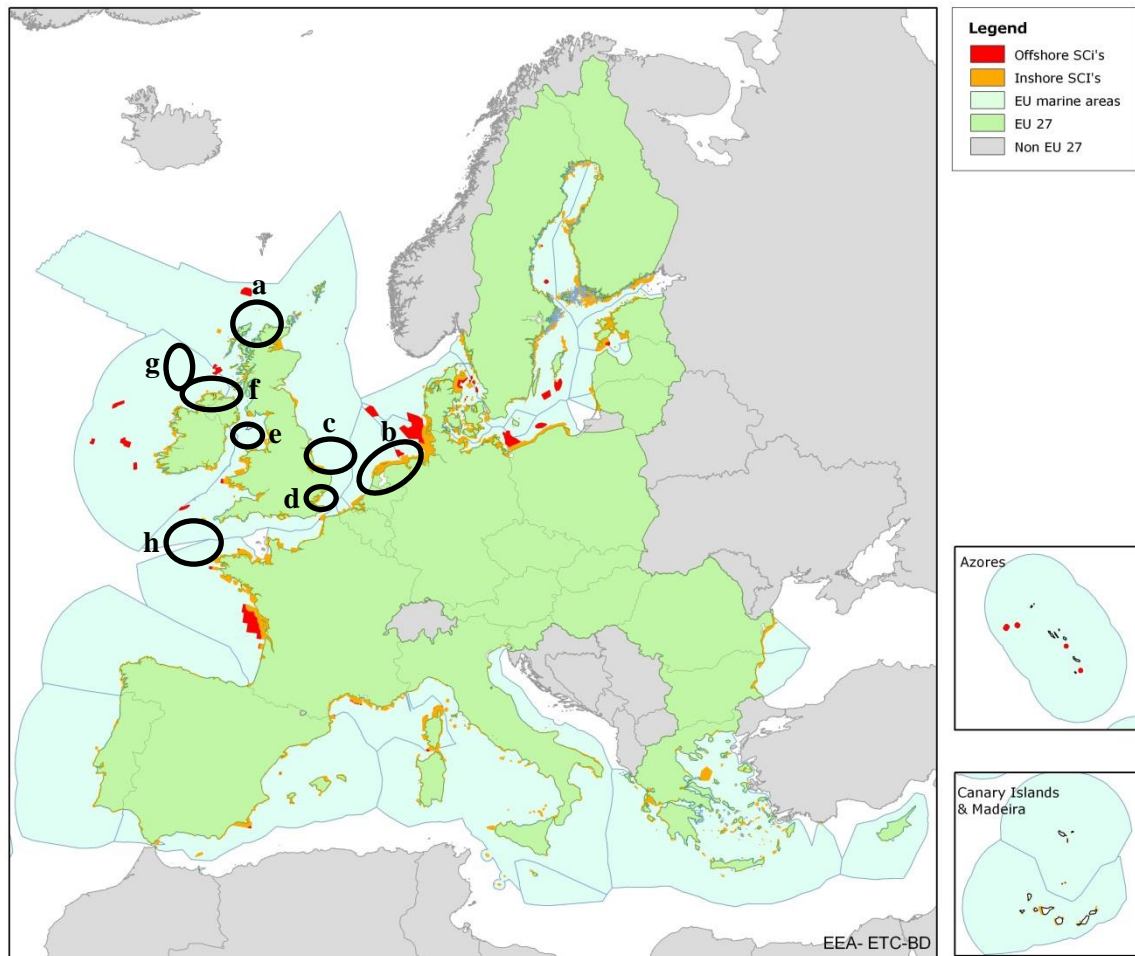
Figure 42: The map shows the existing marine protected areas (MPA) in the Northeast Atlantic, taken from http://biodiversity.europa.eu and modified. The black circles indicate boundaries of areas where sharks would benefit from the designation of new protected areas or the extension of already existing ones, as found in this study. The areas are: a) north-west of Scotland, b) Frisian Islands, c) east coast of England, d) Outer Thames Estuary, e) Anglesey Reef (central Irish Sea), f) north coast of Ireland, g) Vidal Bank, h) southern Celtic Sea.

To conclude, this study has shown that low productive sharks suffer significantly from exploitation, yet sustainability even lacks in more reproductive species. Therefore the European Union is far away from achieving their declared aims in shark conservation, with an additional species, tope, that may qualify to become another species of shark shifted from *Data Deficient* to a threatened category on the IUCN Red List.

The global exploitation of shark species has increased over recent decades (Bonfil 1994) and current estimates suggest no significant decline (Worm et al. 2013). Serious depletion in abundances has been reported for a variety of elasmobranch species in the Northeast Atlantic (Stevens et al. 2000). However, current catch regulations of some species (ICES 2012) may reverse such trends, but increasing protective effort is encouraged to prevent species from depletion and to rebuild the population of others for the fulfilment of legally binding legislation. All surveys showed a skewed pattern towards males, in particular for tope. Future studies should address this observation, as evidence was found that female topes are overexploited. Therefore, the investigation, if such a pattern is triggered by exploitation, behaviour or sampling, is crucial for evaluating the species status. The fact that the data lacked some sex determination, the general rarity of sharks in the ICES surveys or their tendency to aggregate (ICES 2012) and possible errors within the ICES database (Daan 2001), warrants some caution while interpreting the results of this study, however, it is hoped that the findings help to develop appropriate management protocols for sharks in the Northeast Atlantic by the inclusion of this information in conservation strategies and management decisions.

7. References

Aasen O. 1962. Norwegian Dogfish Tagging. Annales biologiques, Copenhagen, 17: 106-107.

Aasen O. 1963. The Norwegian Taggings of Spiny Dogfish (*Squalus acanthias*). Annales biologiques, Copenhagen 18: 85–95.

Aasen O. 1964. The exploitation of the spiny dogfish (*Squalus acanthias* L.) in European waters. Fiskeridirektoratets Skriftek Serie Havundersokelser 13(7): 5–16.

Agri-Food & Biosciences Institute. 2009. Position statement on sharks, skates and rays in Northern Ireland waters. Northern Ireland Environment Agency Research and Development Series No. 09/03.

Baum J, Worm B. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78: 699–714.

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299: 389–392.

Beerkircher L, Shivji M, Cortes E. 2003. A Monte Carlo demographic analysis of the silky shark (Carcharhinus falciformis): implications of gear selectivity. Fishery Bulletin 101: 168–174.

Beverton RJH. 1990. Small marine pelagic fish and the threat of fishing; are they endangered? Journal of Fish Biology 37 (Suppl. A): 5–16.

Beverton RJH. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. Journal of Fish Biology 41: 137–160.

Blanchard JL, Dulvy NK, Jennings S, Ellis JR, Pinnegar JK, Tidd A, Kell LT. 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? ICES Journal of Marine Science 62: 405–411.

Bonfil R. 1994. Overview of world elasmobranch fisheries. FAO Fisheries Technical Paper No. 341. Rome: 119pp.

References

Cadrin SX, Boutillier JA, Idoine JS. 2004. A hierarchical approach to determining reference points for Pandalid shrimp. Canadian Journal of Fisheries and Aquatic Sciences 61: 1373−1391.

Cailliet GM, Smith WD, Mollet HF, Goldman KJ. 2006. Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. Environmental Biology of Fishes 77 (3–4): 211–228.

Cailliet GM. 1992. Demography of the central Californian population of the leopard shark (Triakis semifasciata). Australian Journal of Marine and Freshwater Research 43: 183–193.

Camhi M, Fowler SL, Musick JA, Bräutigam A, Fordham SV. 1998. Sharks and their Relatives − Ecology and Conservation. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. iv + 39pp.

Campana SE, Joyce W, Kulka DW. 2009. Growth and reproduction of spiny dogfish off the eastern coast of Canada, including inferences on stock structure. pp: 195-208. In: Gallucci VF, McFarlane GA, Bargmann GG. (eds.) 2009. Biology and management of dogfish sharks. American Fisheries Society, Bethesda Maryland: 435pp.

Campana SE. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59: 197-242.

Capapé C, Ben Souissi J, Méhri H, Guelorget O, Hemida F. 2005. The reproductive biology of the school shark, *Galeorhinus galeus* Linnaeus 1758 (Chondrichthyes: Triakidae), from the Maghreb shore (southern Mediterranean). Acta Adriatica 46 (2): 109–124.

Capapé C, Mellinger J. 1988. Nouvelles données sur la biologie de la reproduction du milandre, *Galeorhinus galeus* (Linné, 1778), (Pisces, Triakidae) des côtes tunisiennes. Cahiers Biologie Marine 29:135–146.

Capapé C. 1983. Nouvelles donnes sur la biologie de la reproduction de *Mustelus asterias* Cloquet, 1821 (Pisces, Pleurotremata, Triakidae) des cotes Tunisiennes. Vie et Milieu-Life and Environment 33: 143–152.

Christensen V, Guénette S, Heymans JJ, Walters CJ, Watson R, Zeller D, Pauly D. 2003. Hundred-year decline of North Atlantic predatory fishes. Fish and Fisheries 4: 1–24.

Clark CW, Charles AT, Beddington JR, Mangel M. 1985. Optimal capacity decisions in a developing fishery. Marine Resource Economics 2: 25–54.

References

Clarke S. 2004. Understanding pressures on fishery resources through trade statistics: a pilot study of four products in the Chinese dried seafood market. Fish and Fisheries 5: 53–74.

Colloca F, Cardinale M, Maynou F, Giannoulaki M, Scarcella G, Jenko K, Bellido JM, Fiorentino F. 2013. Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. Fish and Fisheries 14: 89–109.

Compagno LJV, Dando M, Fowler S. 2005. Sharks of the World. Princeton University Press, Princeton: 368pp.

Compagno LJV. 1984a. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis 125 (4): 1–249.

Compagno LJV. 1984b. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO Fisheries Synopsis 125 (4): 251–655.

Compagno LJV. 2005. Global Checklist of Living Chondrichthyan Fishes. pp: 401–423. In: Fowler SL, Cavanagh RD, Camhi M, Burgess GH, Cailliet GM, Fordham SV, Simpfendorfer CA, Musick JA. (eds.) 2005. Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes. IUCN SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Correia JPS, Smith MFL. 2003. Elasmobranch landings for the Portuguese commercial fishery from 1986-2001. Marine Fisheries Review 65: 32–40.

Coull KA, Jermyn AS, Newton AW, Henderson GI, Hall WB. 1989. Length/weight relationships for 88 species of fish encountered in the north east Atlantic. Scottish Fisheries Research Report 43: 1–81.

Couto AS. 2013. Aspects of the reproduction and distribution of the main elasmobranch species in Azores, Madeira and Cape Verde. Master of Science in Marine Biodiversity and Conservation. University of the Azores.

Daan N. 2001. The IBTS database: a plea for quality control. ICES CM 2001/T: 03: 19pp.

De Oliveira JAA, Ellis JR, Dobby H. 2013. Incorporating density dependence in pup production in a stock assessment of NE Atlantic spurdog *Squalus acanthias*. ICES Journal of Marine Science 70 (7): 1341–1353.

References

Ebert DA, Stehmann MFW. 2013. Sharks, batoids, and chimaeras of the North Atlantic FAO Species Catalogue for Fishery Purposes. No. 7. Rome: FAO: 523pp.

Ebert DA, White WT, Goldman KJ, Compagno LJV, Daly-Engel TS, Ward RD. 2010. Resurrection and redescription of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae). Zootaxa 2612: 22–40.

EC. 2009. On a European Community Action Plan for the Conservation and Management of Sharks. COM (40) final: 15pp.

EFSA. 2013. European Federation of Sea Anglers Acceptable Species & European Records. The tope (GALEORHINUS GALEUS), available at http://www.efsa.co.uk/record/tope.htm, consulted on 09–21–2013.

Ellis JR, Cruz-Martinez A, Rackham BD, Rogers SI. 2005a. The distribution of chondrichthyan fishes around the British Isles and implications for conservation. Journal of Northwest Atlantic Fishery Science 35: 195–213.

Ellis JR, Dulvy NK, Jennings S, Parker-Humphreys M, Rogers SI. 2005b. Assessing the status of demersal elasmobranchs in UK waters: a review. Journal of the Marine Biological Association of the United Kingdom 85: 1025–1047.

Ellis JR, Keable J. 2008. Fecundity of Northeast Atlantic spurdog (*Squalus acanthias*). ICES Journal of Marine Science: 65: 979–981.

Ellis JR, Milligan SP, Readdy L, Taylor N, Brown MJ. 2012. Spawning and nursery grounds of selected fish species in UK waters. Sci. Ser. Tech. Rep., Cefas Lowestoft, 147: 56pp.

EU. 2008. DIRECTIVE 2008/56/EC OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL. Official Journal of the European Union L 164/19.

Fabens AJ. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29: 265–289.

Fahy E. 1989. The spurdog *Squalus acanthias* (L.) fishery in south-west Ireland. Irish Fisheries Investigations Series B (Marine) 32: 22p.

References

Farrell ED, Clarke MW, Mariani S. 2009. A simple genetic identification method for Northeast Atlantic smoothhound sharks (*Mustelus* spp.). ICES Journal of Marine Science 66: 561–565.

Farrell ED, Mariani S, Clarke MW. 2010a. Age and growth estimates for the starry smoothhound (*Mustelus asterias*) in the Northeast Atlantic Ocean. ICES Journal of Marine Science 67: 931–939.

Farrell ED, Mariani S, Clarke MW. 2010b. Reproductive biology of the starry smooth-hound shark *Mustelus asterias*: Geographic variation and implications for sustainable exploitation. Journal of Fish Biology 77: 1505–1525.

Farrell ED. 2010. The life history and population biology of the starry smoothhound, *Mustelus asterias*, in the Northeast Atlantic Ocean. PhD thesis. University College Dublin, Dublin, Ireland.

Ferreira BP, Vooren CM. 1991. Age, growth and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil. Fishery Bulletin 89: 19–31.

Ferretti F, Myers RA, Sartor P, Serena F. 2005. Long term dynamics of the chondrichthyan fish community in the upper Tyrrhenian Sea. ICES CM 2005/N:25: 34pp.

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK. 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecology Letters 13: 1055–1071.

Fitzmaurice P. 1979. Tope, *Galeorhinus galeus* (L), migrations from Irish coastal waters and notes on Irish specimens. pp: 26–33. In: Annual Report of Irish Specimen Fish Committee for the year 1979.

Ford E. 1921. A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. Journal of the Marine Biological Association of the UK 12: 468–505.

Fordham S, Fowler SL, Coelho R, Goldman KJ, Francis M. 2006. *Squalus acanthias* (Northeast Atlantic subpopulation). In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. www.iucnredlist.org, consulted on 01–01–2012.

Fowler S, Caroline Raymakers C, Grimm U. 2004. Trade in and Conservation of two Shark Species,. Porbeagle (*Lamna nasus*) and. Spiny Dogfish (*Squalus acanthias*). BfN - Skripten 118: 58pp.

References

Fowler SL, Cavanagh RD, Camhi M, Burgess GH, Cailliet GM, Fordham SV, Simpfendorfer CA, Musick JA. 2005. Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes. Status Survey. IUCN/ SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. x + 461pp.

Francis MP, Francis R. 1992. Growth rate estimates for New Zealand rig (*Mustelus lenticulatus*). Australian Journal of Marine and Freshwater Research 43: 1157–1176.

Francis MP, Maolagáin CÓ. 2000. Age, growth and maturity of a New Zealand endemic shark (*Mustelus lenticulatus*) estimated from vertebral bands. Marine and Freshwater Research 51: 35–42.

Francis MP, Mulligan KP. 1998. Age and growth of New Zealand school shark, *Galeorhinus galeus*. New Zealand Journal of Marine and Freshwater Research 32: 427–440.

Francis MP. 1981. Von Bertalanffy growth-rates in species of *Mustelus* (Elasmobranchii, Triakidae). Copeia: 189–192.

Francis RICC. 1988. Maximum likelihood estimation of growth and growth variability from tagging data. New Zealand Journal of Marine and Freshwater Research 22: 43–51.

Frisk MG, Miller TJ, Fogarty MJ. 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. Canadian Journal of Fisheries and Aquatic Sciences 58: 969–981.

Froese R, Binohlan C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. Journal of Fish Biology 56: 758-773.

Froese R, Kesner-Reyes K. 2002. Impact of fishing on the abundance of marine species. ICES CM 2002/L:12, 15pp.

Froese R, Luna S. 2004. No Relationship between Fecundity and Annual Reproductive Rate in Bony Fish. Acta Ichthyologica et Piscatoria 34 (1): 11–20.

Froese R, Stern-Pirlot A, Winker H, Gascuel D. 2008. Size Matters: How Single-Species Management Can Contribute To Ecosystem-based Fisheries Management. Fisheries Research 92: 231–241.

References

Froese R, Zeller D, Kleisner K, Pauly D. 2012. What catch data can tell us about the status of global fisheries. Marine Biology 159: 1283–1292.

Froese R. 2004. Keep it simple: three indicators to deal with overfishing. Fish and Fisheries 5: 86–91.

Froese R. 2006. Cube law, condition factor, and weight-length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology 22 (4): 241–253.

Gauld J. 1979. Reproduction and fecundity of the Scottish-Norwegian stock of spurdog, *Squalus acanthias* (L.). International Council for the Exploration of the Sea CM 1979/H:54: 9pp.

Gauld JA, MacDonald WS. 1982. The results of tagging experiments on spurdogs *Squalus acanthias* L. around Scotland. International Council for the Exploration of the Sea CM Doc, 1982/No. H:51: 7pp.

Gibson C, Valenti SV, Fordham SV, Fowler SL. 2008. The Conservation of Northeast Atlantic Chondrichthyans: Report of the IUCN Shark Specialist Group Northeast Atlantic Red List Workshop: viii + 76pp.

Grant CJ, Sandland RL, Olsen AM. 1979. Estimation of growth, mortality and yield per recruit of the Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. Australian Journal of Marine and Freshwater Research. 30: 625-637.

Greenstreet S, Fraser H, Piet G, Robinson L, Callaway R, Reiss H, Ehrich S, Kröncke I, Craeymeersch J, Lancaster J, Jorgensen L, Goffin A. 2007. Species composition, diversity, biomass and production of the demersal fish community of the North Sea. Fisheries Research Services, Col. Report No 07/07: 95pp.

Gulland JA, Holt SJ. 1959. Estimation of growth parameters for data at unequal time intervals. Journal du Conseil International pour l' Exploration de la Mer 25: 47–49.

Gulland JA. 1971. Preface. The fisheries resources of the ocean. London: Fishing News.

Hammond TR, Ellis JR. 2005. Bayesian assessment of Northeast Atlantic spurdog using a stock production model, with prior for intrinsic population growth rate set by demographic methods. Journal of Northwest Atlantic Fishery Science 35: 299–308.

References

Hampel F. 2001. Robust statistics: a brief introduction and overview. Seminar für Statistik, Eidgenössische Technische Hochschule (ETH), Zürich, Switzerland. Research Report No. 94: 5pp.

Hareide NR, Carlson J, Clarke M, Clarke S, Ellis J, Fordham S, Fowler S, Pinho M, Raymakers C, Serena F, Seret B, Polti F. 2007. European Shark Fisheries: a preliminary investigation into fisheries, conversion factors, trade products, markets and management measures. European Elasmobranch Association: 61pp.

Heithaus MR. 2007. Nursery areas as essential shark habitats: a theoretical perspective. American Fisheries Society Symposium 50: 3–13.

Henderson AC, Flannery K, Dunne J. 2002. Growth and reproduction in spiny dogfish *Squalus acanthias* L. (Elasmobranchii: Squalidae), from the west coast of Ireland. Sarsia 87: 350–361.

Henderson AC, Flannery K, Dunne J. 2003. Biological observations on shark species taken in commercial fisheries to the west of Ireland. Biology and Environment: Proceedings of the Royal Irish Academy 103B: 1–7.

Henry LA, Navas JM, Hennige SJ, Wicks LC, Vad J, Roberts MR. 2013. Cold-water coral reef habitats benefit recreationally valuable sharks. Biological Conservation 161: 67–70.

Heupel MR, Carlson JK, Simpfendorfer CA. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337: 287–297.

Hickling CF. 1930. A contribution towards the life-history of the spurdog. Journal of the Marine Biological Association of the U.K 16: 529–576.

Hjertenes PO. 1980. The spurdog (*Squalus acanthias*) in the North Sea area: the Norwegian fishery and observations on changes in migration pattern. International Council for the Exploration of the Sea Document CM 1980/H: 60: 13pp + 7 figures.

Hoenig JM. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 82: 898–903.

Holden MJ, Horrod RG. 1979. The migrations of the tope, *Galeorhinus galeus* (L), in the eastern North Atlantic as determined by tagging. Journal du Conseil International pour l' Exploration de la Mer 38 (3): 314–317.

References

Holden MJ, Meadows PS. 1962. The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination. Journal of the Marine Biological Association of the U.K 42: 179–197.

Holden MJ, Meadows PS. 1964. The fecundity of the spurdog (*Squalus acanthias* L). Journal du Conseil - Conseil International pour l'Exploration de la Mer 28 (1): 418–424.

Holden MJ. 1965. The stocks of spurdogs (*Squalus acanthias* L.) in British waters, and their migrations. Fisheries Investigations Series II Marine Fisheries Great Britain Ministry of Agriculture, Fisheries and Food 24 (4): 1–20.

Holden MJ. 1966. English Taggings of Picked Dogfish (Spurdog). Annales biologiques, Copenhagen, 21: 172–174.

Holden MJ. 1967. Transatlantic Movement of a Tagged Spurdogfish. Nature 214: 1140–1141.

Holden MJ. 1968. The rational exploitation of the Scottish-Norwegian stocks of spurdogs (*Squalus acanthias* L.). Fisheries Investigations Series II. Vol. XXV, Number 8. Ministry of Agriculture, Fisheries and Food, London: 1–28.

ICES. 2006. Report of the Workshop on Implementation in DATRAS of Confidence Limits Estimation of, 10-12 May 2006. International Council for the Exploration of the Sea Headquaters, Copenhagen: 39pp.

ICES. 2009. Report of the Joint Meeting between ICES Working Group on Elasmobranch Fishes (WGEF) and ICCAT Shark Subgroup, 22–29 June 2009, Copenhagen, Denmark. International Council for the Exploration of the Sea CM 2009/ACOM 16: 90pp.

ICES. 2012. Report of the Working Group on Elasmobranch Fishes (WGEF), 19–26 June 2012, Lisbon, Portugal. International Council for the Exploration of the Sea CM 2012/ACOM 19: 547pp.

ICES. 2013. Official Catch Statistics 1992-2011 dataset 2013, International Council for the Exploration of the Sea, Copenhagen. Version 07−03−2013, available at www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx.

IUCN. 2013. The IUCN (International Union for the Conservation of Nature) Red List of Threatened Species. Version 2013.1, available at http://www.iucnredlist.org/, consulted on 25–05–2013.

References

Jennings S, Reynolds JD, Mills SC. 1998. Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London 265 (B): 333–339.

Jensen AC. 1965. Life history of the spiny dogfish. Fisheries Bulletin 65 (3): 527–554.

Jensen AL. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53: 820-822.

JNCC. 2013. Marine Protected Areas. Interactive map, available at http://jncc.defra.gov.uk/page-5201, consulted on 10–15–2013.

Jones TS, Ugland KI. 2001. Reproduction of female spiny dogfish, *Squalus acanthias*, in the Oslofjord. Fishery Bulletin 99: 685–690.

Kaschner K, Rius-Barile J, Kesner-Reyes K, Garilao C, Kullander SO, Rees T, Froese R. 2013. AquaMaps: Predicted range maps for aquatic species. World wide web electronic publication, www.aquamaps.org, Version 08/2013.

Ketchen KS. 1972. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias* L.) in British Columbia waters. Journal of the Fisheries Research Board Canada 29: 1717–1723.

Ketchen KS. 1975. Age and growth of dogfish *Squalus acanthias* in British Columbia waters. Journal of the Fisheries Research Board Canada 32: 43–59.

Kinney MJ, Simpfendorfer CA. 2009. Reassessing the value of nursery areas to shark conservation and management. Conservation Letters 2: 53–60.

Knip DM, Heupel MR, Simpfendorfer CA. 2012. Mortality rates for two shark species occupying a shared coastal environment. Fisheries Research 125–126: 184–189.

Little W. 1995. Common skate and tope: first results of Glasgow museum's tagging study. Glasgow Naturalist 22: 455–466.

Little W. 1998. Tope and skate tagging off west Scotland. Glaucus 9: 36–38.

Lotze HK, Reise K, Worm B, van Beusekom J, Busch M, Ehlers A, Heinrich D, Hoffmann RC, Holm P, Jensen C, Knottnerus OS, Langhanki N, Prummel W, Vollmer M, Wolff WJ. 2005. Human transformations of the Wadden Sea ecosystem through time: a synthesis. Helgoland Marine Research 59: 84–95.

References

Lotze HK. 2005. Radical changes in the Wadden Sea fauna and flora over the last 2000 years, Helgoland marine research 59: 71–83.

Lucifora LO, Menni RC, Escalante AH. 2004. Reproductive biology of the school shark, *Galeorhinus galeus*, off Argentina: support for a single south western Atlantic population with synchronized migratory movements. Environmental Biology of Fishes 71: 199–209.

MacCall AD. 2009. Depletion-corrected average catch: a simple formula for estimating sustainable yields in data-poor situations. ICES Journal of Marine Science 66: 2267–2271.

Martin CS, Vaz S, Ellis JR, Lauria V, Coppin F, Carpentier A. 2012. Modeled distributions of ten demersal elasmobranchs of the eastern English Channel in relation to the environment. Journal of Experimental Marine Biology and Ecology 418–419: 91–93.

Martin CS, Vaz S, Ellis JR, Coopin F, Le Roy D, Carpentier A. 2010. Spatio-temporal patterns in demersal elasmobranchs from trawl surveys in the eastern English Channel (1988–2008). Marine Ecology Progress Series 417: 211–228.

McCord ME. 2005. Aspects of the ecology and management of the soupfin shark (*Galeorhinus galeus*) in South Africa. Master of Science in Fisheries Science. Rhodes University, Grahamston, South Africa.

McFarlane GA, Beamish RJ. 1987. Validation of the dorsal spine method of age determination for spiny dogfish. pp: 287–300. In: Summerfelt RC, Hall GE. (eds.) 1987. Growth of Fish. Iowa State, University Press, Ames Iowa: 544pp.

Moulton PL, Saddlier SR, Knuckey IA. 1989. New time-at-liberty record set by tagged school shark *Galeorhinus galeus* caught off southern Australia. North American Journal of Fisheries Management 9: 254–5.

Moulton PM, Walker TI, Saddlier SR. 1992. Age and growth studies of gummy shark, *Mustelus antarcticus* (Günther) and school shark, *Galeorhinus galeus* (Linneaus), from southern-Australian waters. Australian Journal of Marine and Freshwater Research 43: 1241-1267.

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S. 2000. Management of sharks and their relatives (Elasmobranchii). Fisheries 25: 9–13.

Musick JA. 1999. Criteria to define extinction risk in marine fishes. Fisheries 24: 6–14.

References

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315: 1846–1850.

Myers RA, Worm B. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423: 280–283.

Myers RA, Worm B. 2005. Extinction, survival, or recovery of large predatory fishes. Proceedings of the Royal Society B 360: 13–20.

Natanson LJ, Kohler NE, Ardizzone D, Cailliet GM, Wintner SP, Mollet HF. 2006. Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. Environmental Biology of Fishes 77: 367–383.

NEFSC. 2002. Application of index methods: catch and fishery independent abundance surveys. pp: 199–257. In The 35th Northeast Regional Stock Assessment Workshop. NEFSC (Northeast Fisheries Science Center) Reference Document 02-14: 259pp.

Nevell L. 1998. Tope: Biological Notes. Glaucus 9: 38.

Olsen AM. 1954. The biology, migration, and growth rate of the school shark, *Galeorhinus australis* (Macleay) (Carcharhinidae) in south-eastern Australian waters. Australian Journal of Marine and Freshwater Research 5: 353–410.

Olsen AM. 1959. The status of the school shark fishery in south-eastern Australian waters. Australian Journal of Marine and Freshwater Research 10: 150–176.

Olsen AM. 1984. Species synopsis of school shark, *Galeorhinus australis* (Macleay, 1881). Food and Agriculture Organisation of the United Nations: Rome. FAO Fisheries Synopsis No. 139: 42pp.

OSPAR. 1992. Convention for the protection of the marine environment of the north-east Atlantic, annex V. The Protection and Conservation of the Ecosystems and Biological Diversity of the Maritime Areas.

OSPAR. 2013. OSPAR (Convention for the Protection of the Marine Environment of the North-East Atlantic) Commission 2012 Status Report on the OSPAR Network of Marine Protected Areas. Publication Number: 618/2013.

Patterson K. 1992. Fisheries for small pelagic species: an empirical approach to management targets Reviews in Fish Biology and Fisheries 2 (4): 321–338.

References

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. 1998. Fishing down marine food webs. Science 279: 860–863.

Pauly D, Moreau J, Gayanilo Jr FC. 1996. A new method for comparing the growth performance of fishes, applied to wild and farmed tilapias. pp: 433-441. In: Pullin RSV, Lazard J, Legendre M, Amon Kothias JM, Pauly D. (eds.) 1996. The Third International Symposium on Tilapia in Aquaculture. ICLARM Conf. Proc. 41. Biometry. Third edition. W.H. Freeman and Company, San Francisco: 887pp.

Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l' Exploration de la Mer 39: 175–192.

Pawson MG, Ellis JR. 2005. Stock Identity of Elasmobranchs in the Northeast Atlantic in Relation to Assessment and Management. Journal of Northwest Atlantic Fishery Science 35: 173–193.

Peres MB, Vooren CM. 1991. Sexual development, reproductive cycle, and fecundity of the school shark *Galeorhinus galeus* off southern Brazil. Fishery Bulletin 89: 655–667.

Pianka ER. 2000. Evolutionary Ecology. Sixth Edition. Benjamin-Cummings, Addison-Wesley-Longman. San Francisco: 528pp.

Pikitch E, Boersma PD, Boyd IL, Conover DO, Cury P, Essington T, Heppell SS, Houde ED, Mangel M, Pauly D, Plagányi É, Sainsbury K, Steneck RS. 2012. Little fish, big impact: managing a crucial link in ocean food webs. Lenfest Ocean Program. Washington, DC: 108pp.

Pinnegar JK, Jennings S, O'Brien CM, Polunin NVC. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. Journal of Applied Ecology 39: 377–390.

Punt AE, Pribac F, Taylor BL, Walker TI. 2005. Harvest Strategy Evaluation for School and Gummy Shark . Journal of Northwest Atlantic Fishery Science 35: 387–406.

Punt AE, Walker TI. 1998. Stock assessment and risk analysis for the school shark (*Galeorhinus galeus*) off southern Australia. Marine and Freshwater Research 49: 719–731.

Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin Fisheries Research Board of Canada 191: 1–382.

References

Ripley WE. 1946. The soupfin shark and the fishery. California Division of Fish and Game Fish Bulletin 64 (64): 7–37.

Saunders MW, McFarlane GA. 1993. Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia, Canada. Environmental Biology of Fishes 38: 49–57.

Serena F, Mancusi C, Ellis J. 2009. *Mustelus asterias*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. www.iucnredlist.org, consulted on 09–07–2013.

Serena F. 2005. Field identification guide to the sharks and rays of the Mediterranean and Black Sea. FAO Species Identification Guide for Fishery Purposes. Rome, FAO: 97pp.

Sheperd JG. 1981. Cautious management of marine resources. Mathematical Bioscience 55: 179–181.

Shephard S, Gerritsen H, Kaiser MJ, Reid DG. 2012. Spatial Heterogeneity in Fishing Creates de facto Refugia for Endangered Celtic Sea Elasmobranchs. PLoS ONE 7 (11) e49307: 1–8.

Simpfendorfer CA. 2000. Growth rates of juvenile dusky sharks, Carcarhinus obscurus (Lesueur, 1818), from southwestern Australia estimated from tag-recapture data. Fishery Bulletin 98: 811–822.

Simpfendorfer CA. 2005. Demographic models: life tables, matrix models and rebound potential. pp: 143–153. In: Musick JA, Bonfil R. (eds.) 2005. Management Techniques for Elasmobranch Fisheries. FAO Fisheries Technical Paper No. 474. Food and Agriculture Organisation of the United Nations, Rome, Italy: 261pp.

Smith SE, Au DW, Show C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Marine and Freshwater Research 49: 663–678.

Sosinski J. 1978. Characteristics of the North Sea Spurdog (*Squalus acanthias* L.) Stock. Fish Biology 8: 9–22.

SSTP. 2010. Scottish Shark Tagging Programme Progress Report December 2010.

SSTP. 2011. Scottish Shark Tagging Programme Christmas Newsletter 2011.

STECF. 2012. Scientific, Technical and Economic Committee for Fisheries (STECF) Review of Scientific Advice for 2013 – Part 2. (STECF-12-08): 328pp.

References

Stenberg C. 2005. Life History of the Piked Dogfish (*Squalus acanthias* L.) in Swedish Waters. Journal of Northwest Atlantic Fishery Science 35: 155-164.

Stevens J, Fowler SL, Soldo A, McCord M, Baum J, Acuña E, Domingo A. 2006. *Lamna nasus* (Northeast Atlantic subpopulation). In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. www.iucnredlist.org, consulted on 01–01–2013.

Stevens JD, Bonfil R, Dulvy NK, Walker PA. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystem. ICES J. Mar. Sci. 57: 476–494.

Stevens JD, Bonfil R, Dulvy NK, Walker PA. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystem. ICES Journal of Marine Science 57: 476–494.

Stevens JD. 1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. Journal of the Marine Biological Association of the UK 70: 707–720.

Sutcliffe R. 1994. Twenty years of tagging common skate and tope off the west coast of Scotland. pp: 14–16. In: Earll RC, Fowler SL. (eds.) 1994. Tag and release schemes and shark and ray management plans. Proceedings of the second European Shark and Ray Workshop, Natural History Museum, London, 15-16 February 1994.

Taylor CC. 1958. Cod growth and temperature. ICES Journal of Marine Science 23: 366–370.

Templeman W. 1976. Transatlantic migrations of spiny dogfish (*Squalus acanthias*). Journal of the Fisheries Research Board of Canada 33: 2605–2609.

The Tope (Prohibition of Fishing) Order. 2008. The Tope (Prohibition of Fishing) Order. 2008. Sea Fisheries, England 2008 No. 691.

UNCLOS. 1982. United Nations Convention on the Law of the Sea. 1833 UNTS 3. Available at: http://www.un.org/Depts/los/convention_agreements/texts/unclos/unclos_e.pdf, consulted on 01–01–2013.

Vince MR. 1991. Stock identity in spurdog (*Squalus acanthias* L.) around the British Isles. Fisheries Research 12: 341–354.

References

von Bertalanffy L. 1938. A quantitative theory of organic growth. Human Biology 10: 181–213.

Walker TI, Cavanagh RD, Stevens JD, Carlisle AB, Chiaramonte GE, Domingo A, Ebert DA, Mancusi CM, Massa A, McCord M, Morey G, Paul LJ, Serena F, Vooren CM. 2006. *Galeorhinus galeus*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. www.iucnredlist.org, consulted on 10–7–2013.

Walker TI. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. Marine and Freshwater Research 49: 553–572.

Walker TI. 1999. *Galeorhinus galeus* fisheries of the world. In Case studies of management of elasmobranch fisheries. FAO Fisheries Technical Paper 378/2. 24: 728–773.

Walters C, Martell SJD. 2002. Stock assessment needs for sustainable fisheries management. Bulletin of Marine Science 70: 629–638.

Ward-Paige CA, Keith D, Worm B, Lotze HK. 2012. Recovery potential and conservation options for elasmobranchs. Journal of Fish Biology 80: 1844–1869.

Wheeler A. 1969. The fishes of the British Isles and North West Europe. Macmillian and Co. Ltd.

Winter HV, van Overzee HMJ. 2013. Langlopend merkprogramma voor haaien en roggen in de Zeeuwse kustwateren: de resultaten van 2011-2012. IMARES - Institute for Marine Resources & Ecosystem Studies, Wageningen, Netherlands. Rapport C085/13: 26pp.

Wood CC, Ketchen KS, Beamish RJ. 1979. Population dynamics of spiny dogfish (*Squalus acanthias*) in British Columbia waters. Journal of the Fisheries Research Board of Canada 36: 647–655.

Worm B, Davis B, Kettermer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber SH. 2013. Global catches, exploitation rates, and rebuilding options for sharks. Marine Policy 40: 194–204.

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA, Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PA, McClanahan TR, Minto C, Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R, Zeller D. 2009. Rebuilding global fisheries. Science 325: 578–585.

References

Zhou SJ, Yin SW, Thorson JT, Smith ADM, Fuller M. 2012. Linking fishing mortality reference points to life history traits: an empirical study. Canadian Journal of Fisheries and Aquatic Sciences 69: 1292–1301.

8. Declaration of authorship

Herewith I certify that the present thesis, apart from the consultation of my supervisors, was independently prepared by me. No other than the indicated resources and references were used. This thesis was presented to no other place within the scope of an examination procedure. The written thesis is identical with the electronic one.

_____

(Manuel Dureuil)   Kiel, 11–02–2013

9. Declaration of consent

I agree on including this thesis in the library of the Helmholtz Centre for Ocean Research (GEOMAR) as well as in the library of the Christian-Albrechts-Universität zu Kiel.

_____

(Manuel Dureuil)   Kiel, 11–02–2013

10. Supplementary Information

Table 1: Life history information of *Galeorhinus galeus* from other regions.

| parameter	sex	value	region	source
maximum age	female	53	Australia	Olsen (1984)
	female	41	Southern Brazil	Ferreira and Vooren (1991)
	male	45	Australia	Moulton et al. (1989)
	unknown	33	South Africa	McCord (2005)
maximum *TL*	female	174	Australia	Olsen (1984)
	female	155	Southern Brazil	Ferreira and Vooren (1991)
	female	195	Northeast Pacific	Ripley (1946)
	male	163	Australia	Olsen (1984)
	male	148	Southern Brazil	Peres and Vooren (1991)
	male	185	Northeast Pacific	Ripley (1946)
age at maturity	female	10	Australia	Olsen (1954)
	female	15.7	Southern Brazil	Peres and Vooren (1991)
	female	$13-15$	New Zealand	Francis and Mulligan (1998)
	male	8	Australia	Olsen (1954)
	male	11.4	Southern Brazil	Peres and Vooren (1991)
	male	$12-17$	New Zealand	Francis and Mulligan (1998)
	male	6	South Africa	McCord (2005)
TL 1st maturity	female	135	Australia	Olsen (1954)
	female	118	Southern Brazil	Peres and Vooren (1991)
	female	150	Northeast Pacific	Ripley (1946)
	male	120	Australia	Olsen (1954)
	male	107	Southern Brazil	Peres and Vooren (1991)
	male	135	Northeast Pacific	Ripley (1946)
TL 50% maturity	female	123	Southern Brazil	Peres and Vooren (1991)
	female	158	Northeast Pacific	Ripley (1946)
	male	111	Southern Brazil	Peres and Vooren (1991)
	male	101.1	South Africa	McCord (2005)
TL 100% maturity	female	128	Southern Brazil	Peres and Vooren (1991)
	female	190	Northeast Pacific	Ripley (1946)
	male	117	Southern Brazil	Peres and Vooren (1991)
$L\infty$	female	163	Southern Brazil	Ferreira and Vooren (1991)
	female	179.2	New Zealand	Francis and Mulligan (1998)
	male	152	Southern Brazil	Ferreira and Vooren (1991)
	male	142.9	New Zealand	Francis and Mulligan (1998)
	combined	215.8	Bass Strait (Australia)	Moulton et al. (1992)
	combined	173.7	Southern Australia	Moulton et al. (1992)
	combined	182.9	Australia	Moulton et al. (1992)
	combined	162.6	Bass Strait (Australia)	Moulton et al. (1992)
	male	158.33	south-eastern Australia	Grant et al. (1979)
	female	161.83	south-eastern Australia	Grant et al. (1979)
	combined	160.4	south-eastern Australia	Grant et al. (1979)
	male	154.27	South Africa	McCord (2005)
	combined	156.03	South Africa	McCord (2005)
k	female	0.075	Southern Brazil	Ferreira and Vooren (1991)
	female	0.086	New Zealand	Francis and Mulligan (1998)
	male	0.092	Southern Brazil	Ferreira and Vooren (1991)
	male	0.154	New Zealand	Francis and Mulligan (1998)
	combined	0.084	Bass Strait (Australia)	Moulton et al. (1992)
	combined	0.144	Southern Australia	Moulton et al. (1992)
	combined	0.124	Australia	Moulton et al. (1992)
	combined	0.168	Bass Strait (Australia)	Moulton et al. (1992)
	male	0.168	south-eastern Australia	Grant et al. (1979)
	female	0.160	south-eastern Australia	Grant et al. (1979)
	combined	0.164	south-eastern Australia	Grant et al. (1979)
	male	0.210	South Africa	McCord (2005)
	combined	0.190	South Africa	McCord (2005)
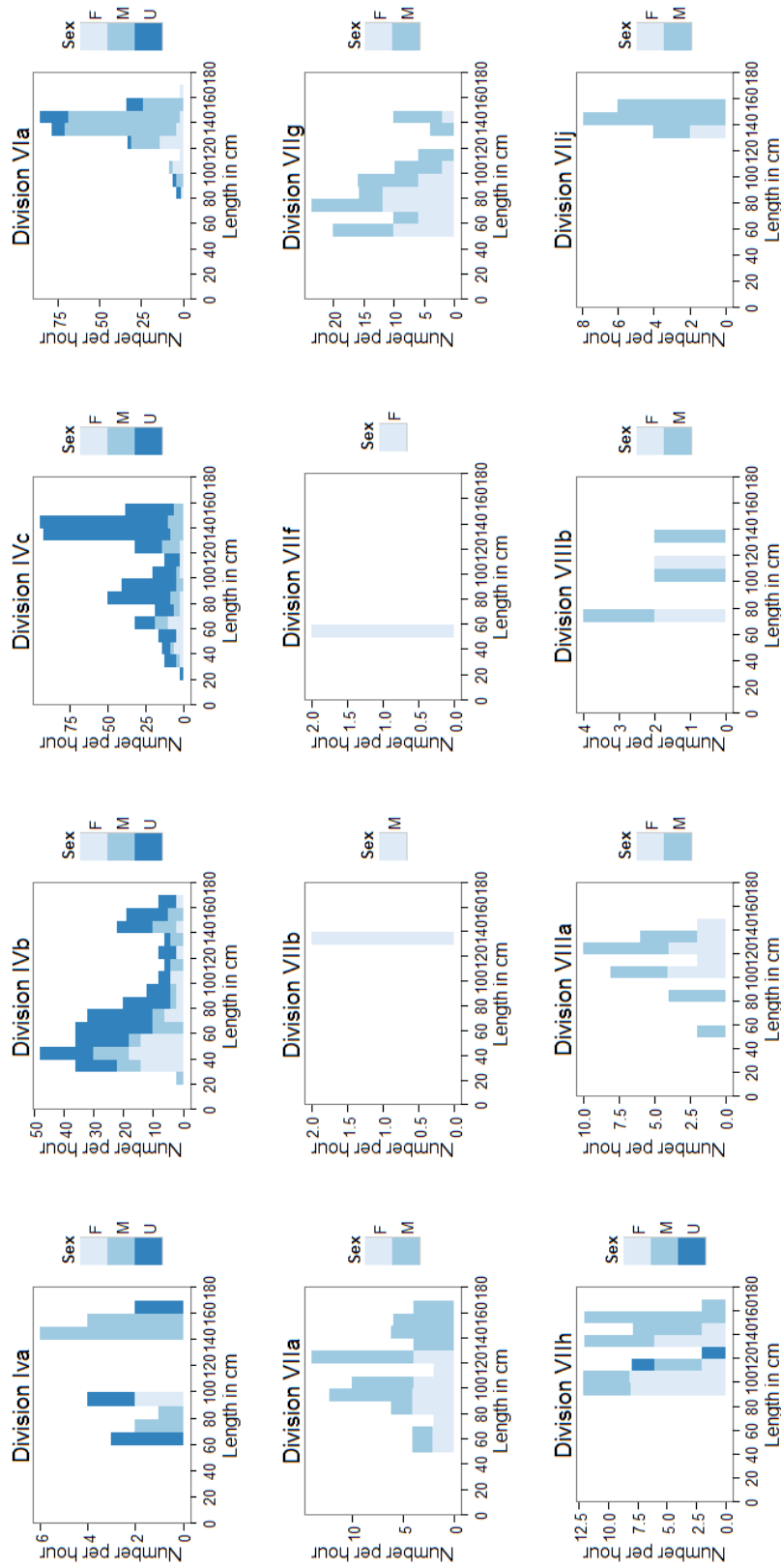
Figure 1: Length frequency distributions of tope in the different ICES divisions.
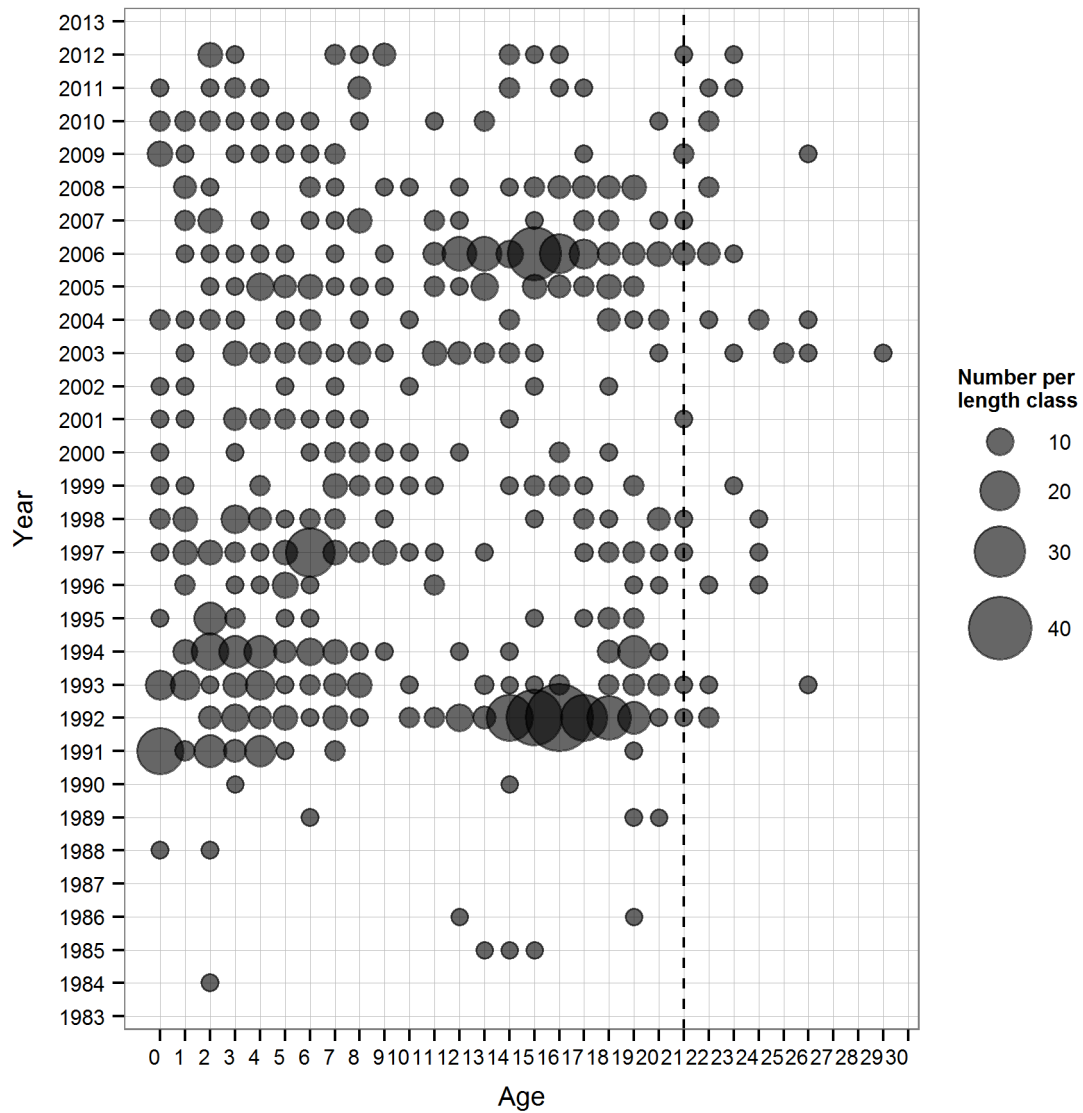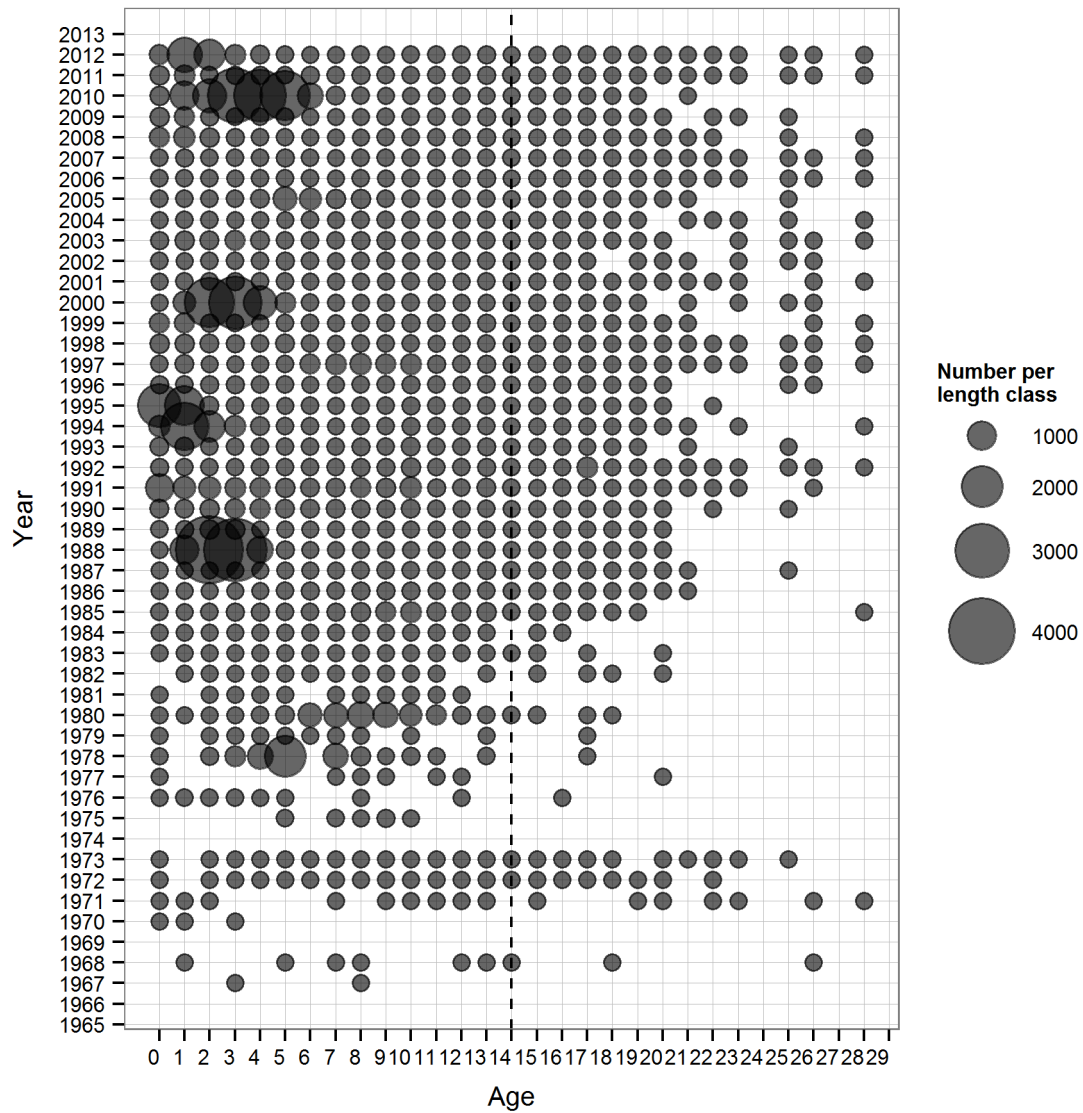
Figure 2: Tope time versus age graph used to identify a time period where all ages have been caught representatively (1992 − 2012). The dashed vertical line gives the female age at 50% maturity. Number per length class was standardised to one hour of hauling.
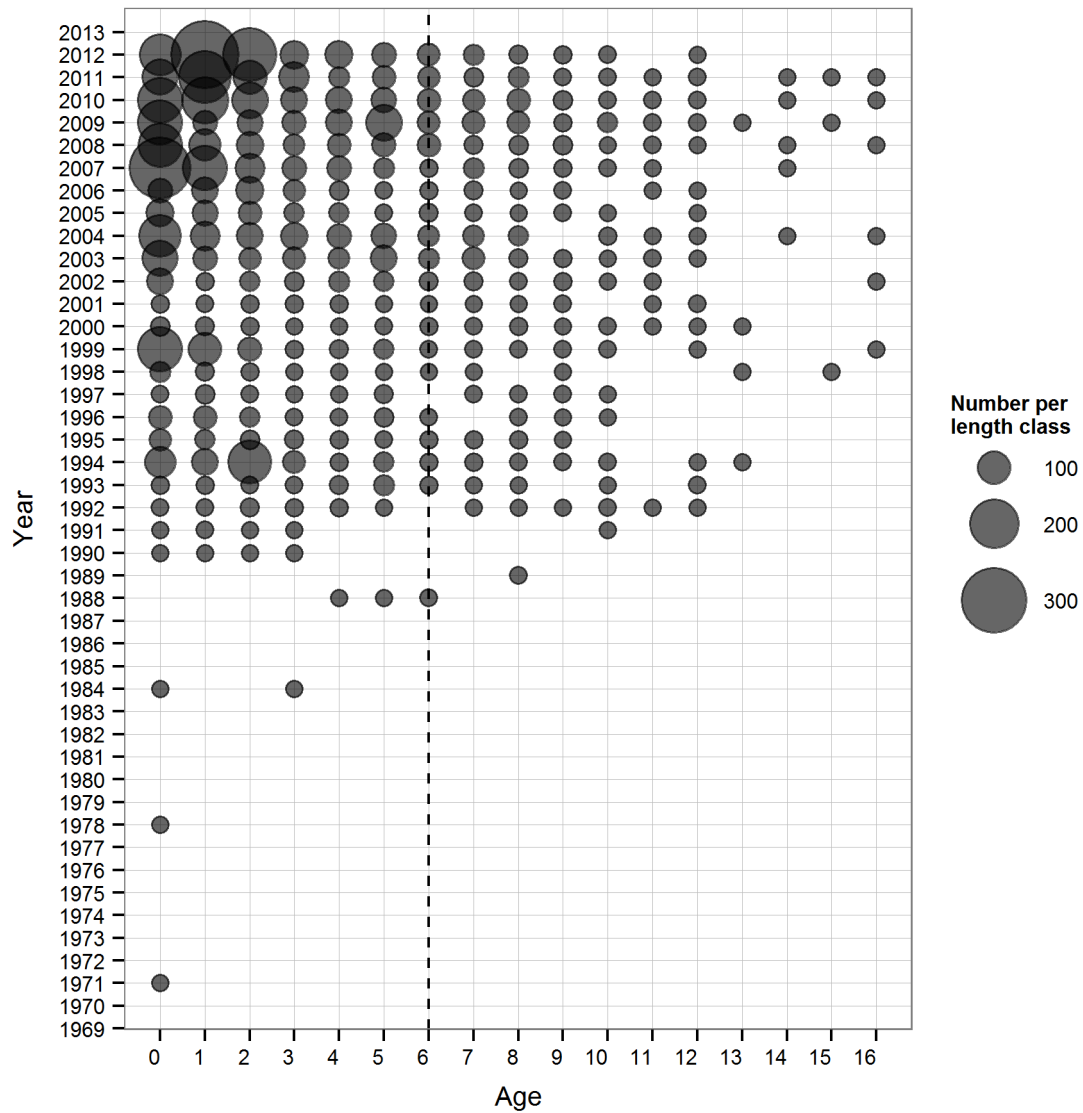
Figure 3: Starry smoothhound time versus age graph used to identify a time period where all ages have been caught representatively (1992 − 2012). The dashed vertical line gives the female age at 50% maturity. Number per length class was standardised to one hour of hauling.

Figure 4: Spurdog time versus age graph used to identify a time period where all ages have been caught representatively (1985 − 2012). The dashed vertical line gives the female age at 50% maturity. Number per length class was standardised to one hour of hauling.

Table 2: Summary table of life history traits of tope for the Northeast Atlantic. Total length *TL* is referred to in cm and age in years. The sources and methods are detailed in the corresponding section of this thesis.

trait	male	female
length-weight relationship	$0.0042*TL^{3.01}$	$0.0029*TL^{3.1}$
asymptotic size (cm)	174	198
von Bertalanffy *k*	0.087	0.066
size at birth (cm)	28	28
size at maturity (cm)	121	155
age at maturity	12	21
longevity		55
litter size		$0.0001*TL^{2.36}$
proportion of females mature		$1/(1+e^{-(-40.8+0.263*TL)})$
reproductive cycle		biennial
natural mortality		$0.094 \ \text{yr}^{-1}$
intrinsic rate of population increase		$0.062 \ \text{yr}^{-1}$

Table 3: Summary table of life history traits of starry smoothhound for the Northeast Atlantic. Total length *TL* is referred to in cm and age in years. The sources and methods are detailed in the corresponding section of this thesis. Note that a considerable amount of data was obtained from Farrell et al. (2010a) and Farrell et al. (2010b).

trait	male	female
length-weight relationship	$0.003*TL^{3.05}$	$0.001*TL^{3.27}$
asymptotic size (cm)	103.7	123.5
von Bertalanffy *k*	0.195	0.146
size at birth (cm)	38.1	34.9
size at maturity (cm)	78	87
age at maturity	5	6
longevity	13	18
litter size		$0.0004*TL^{2.64}$
proportion of females mature		$1/(1+e^{-(-48.596+0.561*TL)})$
reproductive cycle		biennial
natural mortality		$0.219 \ \text{yr}^{-1}$
intrinsic rate of population increase		$0.079 \ \text{yr}^{-1}$

Supplementary Information

Table 4: Summary table of life history traits of spurdog for the Northeast Atlantic. Total length *TL* is referred to in cm and age in years. The sources and methods are detailed in the corresponding section of this thesis.

trait	male	female
length-weight relationship	$0.0043*TL^{2.96}$	$0.002*TL^{3.15}$
asymptotic size (cm)	82	105
von Bertalanffy *k*	0.149	0.091
size at birth (cm)	26	26
size at maturity (cm)	60	82
age at maturity	6	14
longevity		40
litter size		$0.000034*TL^{2.72}$
proportion of females mature		$1/(1+e^{-(-25.6+0.314*TL)})$
reproductive cycle		biennial
natural mortality		0.127 yr^{-1}
intrinsic rate of population increase		0.038 yr^{-1}